

AMPHIBIANS FROM THE MIDDLE JURASSIC BALABANSAI SVITA IN THE FERGANA DEPRESSION, KYRGYZSTAN (CENTRAL ASIA)

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Abstract: Larval and metamorphosed *Ferganobatrachus riabinini* (Temnospondyli, Brachyopoidea), metamorphosed *Kokartus honorarius* (Caudata, Karauridae), an indeterminate karaurid (Karauridae indet.) and, presumably, anurans (?Anura indet.) are represented by isolated cranial and post-cranial skeletal elements in the Middle Jurassic (Bathonian–Callovian) Balabansai Svita of the Fergana Depression, Kyrgyzstan. The Balabansai vertebrate assemblage is one of

the few faunas in which non-lissamphibian temnospondyls, stem caudates and anurans occur together. The presence of a supraglenoid foramen and a complex strap-like glenoid on the scapulocoracoid in *Kokartus* supports its basal phylogenetic position within the Caudata.

Key words: Balabansai Svita, Caudata, *Ferganobatrachus*, Fergana Depression, Karauridae, *Kokartus*, Temnospondyli.

THE Middle Jurassic Balabansai Svita in the Fergana Depression, Kyrgyzstan, has yielded an important and diverse brackish-water to terrestrial tetrapod fauna (see Averianov 2000; Alifanov and Averianov 2003; Martin and Averianov 2004, 2006; Averianov *et al.* 2005, 2006 for an updated faunal list). One significant aspect of this fauna is that it contains remains of both late and relict non-lissamphibian temnospondyls and some of the earliest lissamphibians. The only other Jurassic locality with such a combined record is the Middle Jurassic Peski Quarry near Moscow, Russia (Shishkin 2000a; Alekseev *et al.* 2001; Gambaryan and Averianov 2001).

The Balabansai Svita spans the late Bathonian–Callovian time interval and is approximately contemporaneous with the Forest Marble Formation in Great Britain. The latter unit has produced remains of some of the geologically oldest known salamanders, such as *Marmorerpeton* Evans, Milner and Mussett, 1988 (two species) and two other unnamed taxa: a large stem ‘salamander A’ and a crown ‘salamander B’ (Evans *et al.* 1988; Milner 2000). Vertebrate faunas from both the Balabansai and Forest Marble formations are generally similar, and recently discovered docodontans, klameliid triconodontans and choristoderes in the former stratigraphic unit increase this

similarity (Kermack *et al.* 1987; Sigogneau-Russell 2003; Martin and Averianov 2004, 2006; Averianov *et al.* 2006).

Only two amphibian taxa from the Balabansai Svita have been described and figured (Nesov 1988, 1990; Nesov *et al.* 1996). The first is the non-lissamphibian temnospondyl *Ferganobatrachus*, a genus with unclear affinities within the Temnospondyli. The second taxon, *Kokartus*, is one of the oldest and most primitive stem caudates that is potentially useful for documenting the primitive caudate condition and patterns of character state transformations within Caudata.

The aim of this paper is to describe and analyse new amphibian remains from the Balabansai Svita, collected during 2000–2003 in a joint project between the Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, of the Freie Universität in Berlin (Germany), the Zoological Institute of the Russian Academy of Sciences in St Petersburg (Russia), and the Institute of Geology of the National Academy of Sciences in Bishkek (Kyrgyzstan). Consequently, in the ‘Systematic Palaeontology’ section under ‘Material’ we list only newly collected, previously unpublished specimens.

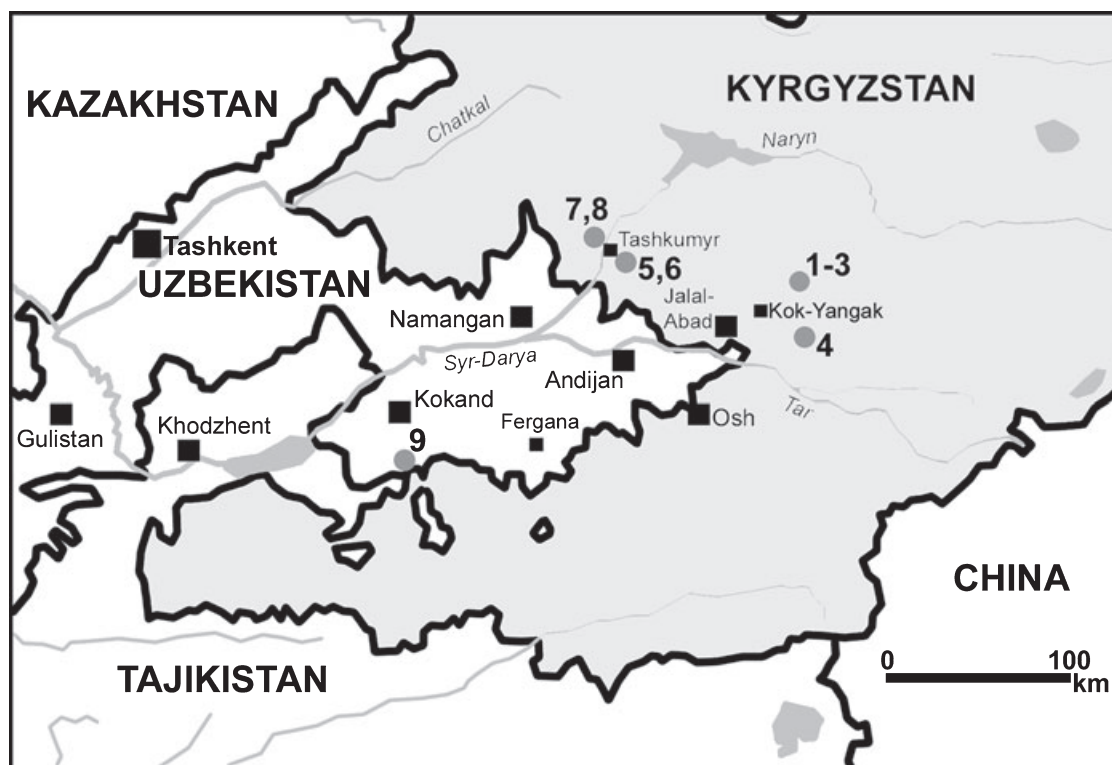
Institutional abbreviations. CCMGE, Chernyshev Central Museum of Geological Exploration, St Petersburg, Russia; PIN,

Paleontological Institute, Russian Academy of Sciences, Moscow; ZIN PH, Paleoherpetological Collection, Zoological Institute, Russian Academy of Sciences, St Petersburg.

LOCALITIES

There are nine Middle Jurassic localities in the Fergana Depression where amphibian remains have been found (Text-fig. 1); eight of these are in Jalal-Abad Province, Kyrgyzstan (1–8 below) and one is in Fergana Province, Uzbekistan (9 below). Their geological setting is described in detail by Kaznyshkin (1988, 1990), Nesov and Fedorov (1989), Nesov *et al.* (1994, 1996), and Averianov *et al.* (2005).

1. Nichke 1, at the outfall of Nichke stream, a tributary of the Kyzylsu River, in the vicinity of Kalmakerchin settlement, western Fergana. Dark grey clays of the upper part of Irgysai Svita; Bathonian. Nesov and Fedorov (1989) reported a phalanx of a supposed salamander from this locality. The Irgysai Svita underlies the Balabansai Svita in eastern Fergana and spans the Bajocian–Bathonian (Nesov and Fedorov 1989).
2. Kyzylsu 1, right bank of the Kyzylsu River in the lower stream, close to the mouth of the Nichke stream, in the vicinity of Kalmakerchin settlement, eastern Fergana. Dark green schistose clays of the lower part of the Balabansai Svita; late Bathonian. Type locality for *Kokartus honorarius* Nesov, 1988, represented there by isolated cranial and postcranial bones (Nesov 1988, fig. 2.1–3, 5; Nesov and Fedorov 1989; Nesov *et al.* 1996).
3. Kugart 1 (site KUG-3), right bank of the Kugart River, 2 km upstream of the Kalmakerchin settlement, eastern Fergana. Red clays of the lower part of the Balabansai Svita; late Bathonian. Abundant isolated remains of *Kokartus honorarius* (Nesov 1988, fig. 2.4; Nesov and Fedorov 1989). Nesov (1988) reported one possible non-lissamphibian temnospondyl bone from this or the previous locality. We found numerous remains of *Kokartus* and fragments of non-lissamphibian temnospondyl teeth here in 2000. Nesov *et al.* (1994) reported an anuran humerus from a nearby locality on the Kugart River. We were unable to locate this specimen in any collection.
4. Changet, left bank of the Changet River at the mouth of Atchisai stream, eastern Fergana. Balabansai Svita; late Bathonian. One stereospondylous hypocentrum was found by P. V. Fedorov in 1987 (Nesov and Fedorov 1989). According to Shishkin (2000a, p. 299), this hypocentrum is 'indistinguishable from those of *Gobiops*' and it was designated as 'cf. *Gobiops* sp.' on Nesov's label.
5. Sarykamyshtsai 1 (sites FTA-30 and FTA-31), 3–4 km east of Tashkumyr city, northern Fergana. Lower, grey to greenish coloured part of the Balabansai Svita, Callovian. Isolated



TEXT-FIG. 1. Map of the Fergana Depression and adjacent territories showing the Middle Jurassic localities that have yielded amphibians: 1, Nichke 1; 2, Kyzylsu 1; 3, Kugart 1; 4, Changet; 5, Sarykamyshtsai 1; 6, Tashkumyr 1; 7, Uurusay; 8, Dzhidasai; 9, Kamysht-Bashi.

cranial bones and postcranial bones of *Ferganobatrachus riabinini* Nesov, 1990 (Nesov 1988, pl. 13, figs 1–10; 1990, fig. 1a–s). At the site FTA-30 non-lissamphibian temnospondyl remains make up 0.14 per cent of a sample of 15,235 vertebrate remains (Kaznyshkin *et al.* 1990). Additional non-lissamphibian temnospondyl remains were collected by us in 2000–2003.

6. Tashkumyr 1 (site FTA-131), left bank of the Naryn River close to Tashkumyr city, northern Fergana. Bonebed within a calcareous sandstone of the lower part of the Balabansai Svita; Callovian. We found several stereospondylous hypocentra in 2001 and 2003.
7. Uurusay (site FBX-7), 1 km west of Tashkumyr city, northern Fergana. Variegated sandstones and siltstones of the lower part of the Balabansai Svita; Callovian. A non-lissamphibian temnospondyl phalanx was reported by Nesov (1988, pl. 13, fig. 11; 1990, fig. 1t).
8. Dzhiddasai (site FBX-23), 5 km west of Tashkumyr city, northern Fergana. Upper, red-coloured part of the Balabansai Svita; Callovian. An amphicoelous salamander vertebra was reported from this locality by Nesov (1988, 1990). This is apparently ZIN PH 2/47 from a possibly neotenus *Karauridae* indet. found in 1984 (see description below). We found one non-lissamphibian temnospondyl hypocentrum in 2003.
9. Kamysh-Bashi, 30 km south of Kokand city, southern Fergana. Brown clays of the upper part of Balabansai Svita; Callovian. One stereospondylous hypocentrum was figured by Kaznyshkin (1990, pl. 10, fig. 23).

hypocentrum fragment, FTA-31, 2001; ZIN PH 15/47, hypocentrum fragment, FTA-31, 2001; ZIN PH 16/47, hypocentrum, FTA-131, 2001; ZIN PH 17/47, hypocentrum, FTA-30, 2001; ZIN PH 18/47, hypocentrum, FBX-23, 2003; ZIN PH 59/47, hypocentrum, FTA-131, 2003; ZIN PH 60/47, hypocentrum, FTA-131, 2003; ZIN PH 8/47, left clavicle fragment, FTA-30, 2001.

Comment. Unfortunately Nesov (1990; see also Shishkin 2000a) published the type and additional material of *Ferganobatrachus riabinini* under an incorrect CCMGE collection number (12217). This material actually belongs to CCMGE collection number 11998. The CCMGE collection 12217 includes material of lungfish and turtles from the Balabansai Svita described by Nesov and Kaznyshkin (1985).

Description. The dorsal hypocentra vary in size from 8.9 to 32.6 mm in width and are interpreted as an ontogenetic series. The smaller hypocentra are 9–15 mm wide and have a large, dorsally wide-open notochordal canal, whereas in ZIN PH 60/47 (width 13.3 mm) and the larger hypocentra (over 17 mm) the notochordal canal is small and dorsally closed. ZIN PH 16/47 (width 17.0 mm) has a distinct suprachordal cleft (Text-fig. 2F–I), whereas in the larger ZIN PH 9/47 (width 27.5 mm) and 59/47 (width 32.6 mm) this cleft is indiscernible (Text-fig. 2C–E, T–W). The parapophysis is well developed even in smaller hypocentra and adjacent to the posterior articulation surface.

The clavicle (Text-fig. 2R–S; Nesov 1988, pl. 13, fig. 8; 1990, fig. 1k–l) has a wide clavicular plate, with an angle of 60–65 degrees between the anterolateral and posterolateral edges. The ventral ornament of the plate is honeycombed at the base of the dorsal process and has a ridge-like radiating pattern over the remaining part.

Discussion. *Ferganobatrachus* is one of the geologically youngest records for non-lissamphibian Temnospondyli. Other Jurassic, Asiatic records of non-lissamphibian temnospondyls include *Sinobrachyops placenticephalus* Dong, 1985 from the Bathonian Lower Shaximiao Formation in Sichuan Province, China (Dong 1985), ‘*Superstogyrinus ultimus*’ (*nomen nudum*) from the Bathonian Wucaiwan Formation in Xinjiang Uygur Autonomous Region of China (Dong 1985, 1992), *Gobiops desertus* Shishkin, 1991 from the Toutunhe Formation (Bathonian–Callovian) and ?*Brachyopoidea* gen. et sp. indet. from the Qigu Formation (Oxfordian), Xinjiang Uygur Autonomous Region of China (Maisch *et al.* 2001, 2003; Maisch and Matzke 2005), temnospondyl hypocentra from the Middle Jurassic Kradung Formation in Thailand (Buffetaut *et al.* 1994a, b), and *Gobiops desertus* from the Upper Jurassic Shar Teg beds in southern Mongolia (Shishkin 1991, 2000a). A *Gobiops*-like hypocentrum has also been reported from the Middle Jurassic Peski locality near Moscow, Russia (Shishkin 2000a; Alekseev *et al.* 2001).

SYSTEMATIC PALAEOLOGY

AMPHIBIA Linnaeus, 1758

TEMNOSPONDYLI Zittel, 1887–90

BRACHYOPOIDEA Lydekker, 1885

FERGANOBATRACHUS Nesov, 1990

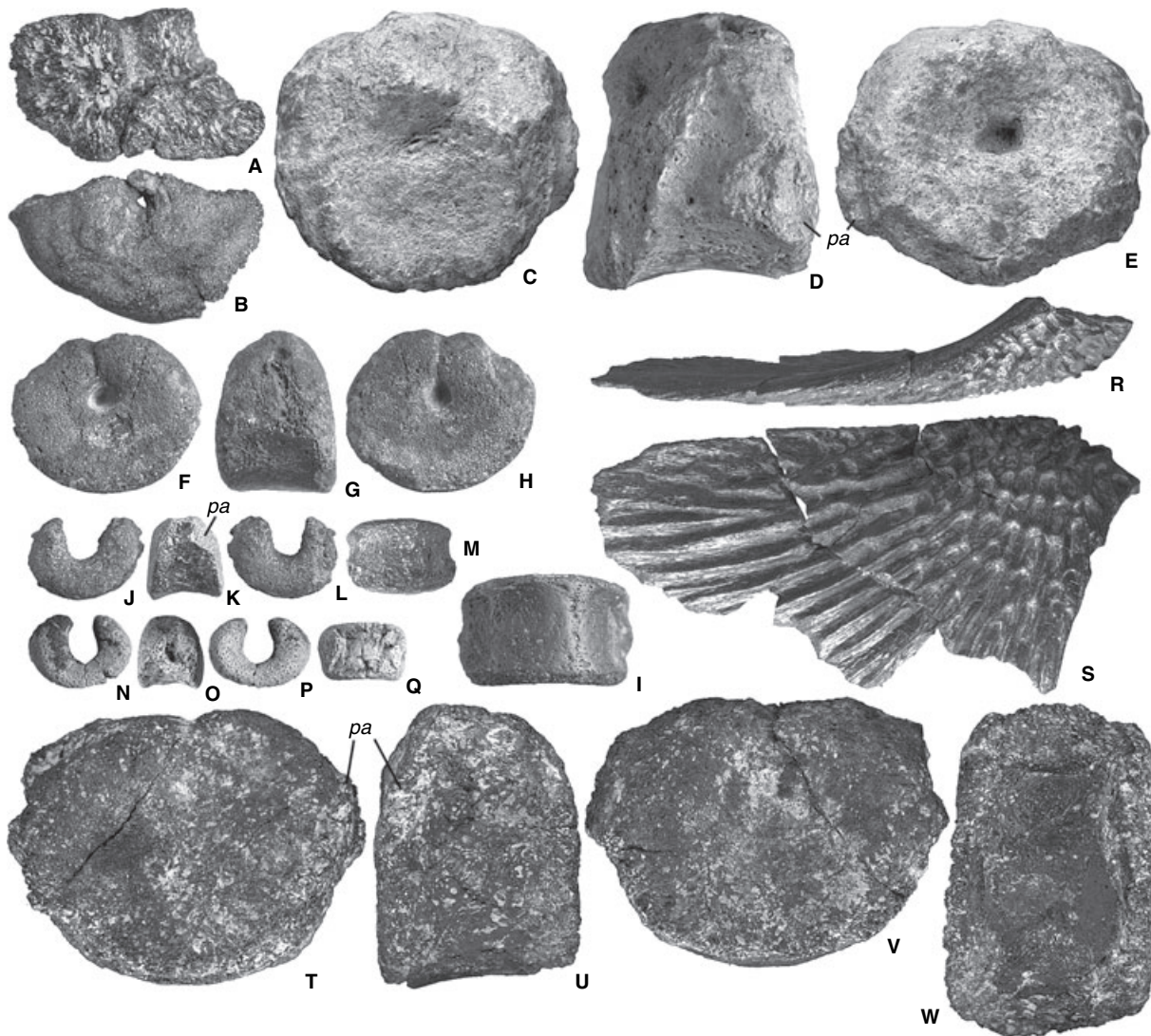
Type species. *Ferganobatrachus riabinini* Nesov, 1990 from the Callovian of Kyrgyzstan.

Ferganobatrachus riabinini Nesov, 1990

Text-figure 2

- 1988 ‘labyrinthodont, probably belonging to the Capitosauroida branch’ Nesov, p. 477, pl. 13, figs 1–11.
- 1990 *Ferganobatrachus riabinini* Nesov, p. 89, fig. 1a–s.
- 1993 *Ferganobatrachus riabinini* Nesov; Milner, p. 669.
- 2000a *Ferganobatrachus riabinini* Nesov; Shishkin, p. 299.
- 2000 *Ferganobatrachus riabinini* Nesov; Warren and Marsicano, p. 473.

Material. ZIN PH 9/47, hypocentrum, Changet, 1987; ZIN PH 13/47, hypocentrum fragment, FTA-31, 2001; ZIN PH 14/47,



TEXT-FIG. 2. Isolated postcranial bones of *Ferganobatrachus riabinini* from the Middle Jurassic (Bathonian–Callovian) Balabansai Svita, Fergana Depression, Kyrgyzstan. A–B, CCMGE 9/11998, axis hypocentrum, FTA-30 site: A, dorsal and B, anterior views. C–E, ZIN PH 9/47, hypocentrum, Changet site: C, anterior, D, lateral, and E, posterior views. F–I, ZIN PH 16/47, hypocentrum, FTA-131 site: F, posterior, G, lateral, H, anterior, and I, ventral views. J–M, ZIN PH 17/47, hypocentrum, FTA-30 site: J, anterior, K, lateral, L, posterior, and M, ventral views. N–Q, ZIN PH 18/47, hypocentrum, FBX-23 site: N, anterior, O, lateral, P, posterior, and Q, ventral views. R–S, ZIN PH 8/47, left clavicle, FTA-30 site: R, lateral and S, ventral views. T–W, ZIN PH 59/47, hypocentrum, FTA-131 site: T, posterior, U, lateral, V, anterior, and W, ventral views. Abbreviation: pa, parapophysis. All $\times 1.6$.

Ferganobatrachus was described by Nesov (1990) based on a left clavicle (holotype) and several attributed specimens, including a postorbital, presumed supratemporal, parts of other dermal bones, teeth and hypocentra (all specimens from the type locality). Nesov's original diagnosis of the genus includes the following characters: ornament of the dermal skull bones mostly with a ridge-like radiating pattern (even in old individuals) and rarely with a pitted pattern; ventral surface of clavicle with a moderately elongate outline (ratio of length to width, 2:3);

clavicle with a long and nearly straight medial side (reconstructed after the impression on the matrix) and a nearly straight posterior edge; dorsal process of clavicle thin and small, considerably inclined posteriorly and oval in cross-section; postorbital wide and short, with only a small portion of the anterior edge entering the orbit; hypocentra of young individuals with a deep suprachordal cleft; a very narrow canal situated near the middle of the height of the bone after almost complete closure of the notochordal canal. New material reported here is referred

to *Ferganobatrachus* based on the similar structure of the clavicle and hypocentra, and provides the opportunity to revise the taxonomic position of *Ferganobatrachus* within the Temnospondyli.

The taxonomic position of *Ferganobatrachus* is difficult to assess because it is known only from incomplete material. Nesov (1990) attributed it to the Capitosauridae based on the shape and strong ossification of the hypocentra, both of which resemble the condition in the Mastodonsauridae and Cyclotosauridae, and the structure of the dorsal clavicular process, which he considered to be different from that in the Brachyopidae. According to Shishkin (2000a) material then available showed no capitosauroid characters. Shishkin (2000a, p. 299) stated that 'the strong dorsoventral compression of the axis hypocentrum figured by Nesov strongly suggests an assignment to Brachyopidae' and formally assigned *Ferganobatrachus* to that family. This assignment is based on the interpretation of the incomplete stereospondylous hypocentrum CCMGE 9/11998 (published previously under the incorrect number 4/12217; Text-fig. 2A–B; Nesov 1988, pl. 13, fig. 4; 1990, fig. 1z). Shishkin (1991) considered this specimen to be an axis hypocentrum, because of the convexity of its anterior surface. However, as was correctly noted by Shishkin (1991), this hypocentrum is dorsally incomplete. There are no parapophyses on the fragment preserved. The complete hypocentrum may have been as high as the axis hypocentrum in *Gobiops* (Shishkin 1991, fig. 4g–e) and the characteristic 'strong dorsoventral compression' is not applicable to it. Nevertheless, the familial assignment of *Ferganobatrachus* to the Brachyopidae, first suggested by Shishkin (1991), was later accepted by Milner (1993, 1994).

In the opinion of Warren and Marsicano (2000, p. 473) the available material of *Ferganobatrachus* 'is not determinable within the Stereospondyli'. They referred this taxon to Brachyopoidea *incertae sedis* merely because 'all known post-Triassic stereospondyls are brachyopoid'.

According to Shishkin (2000a, p. 299) *Ferganobatrachus* 'may be close to, or congeneric with, *Gobiops*'. Earlier Shishkin (1991) cited two characters differentiating the two genera: (1) dorsally closed dorsal hypocentra even in the smallest specimens [of *Gobiops*] and (2) peculiarities of the clavicle dorsal process. Some of the latter peculiarities are artefacts following misinterpretation of the *Gobiops* clavicle fragment PIN 4174/101 (Shishkin 1991, fig. 5a–v, pl. 7, fig. 4), which is from the left side, not the right. However, the clavicle of *Gobiops* differs from that of *Ferganobatrachus* in having a coarser honeycomb sculptural pattern and a more gently sloping dorsal process, although these differences might be ontogenetic. Maisch and Matzke (2005) regarded the short dorsal process on the clavicle as a potential autapomorphy for *Gobiops*.

According to these authors, *Ferganobatrachus* with a similarly short dorsal clavicular process is possibly congeneric with *Gobiops*, although they avoided formal synonymization because of the incompleteness of the available *Ferganobatrachus* material. Should the two genera be synonymized, the latter name has priority. Maisch and Matzke (2005) also questioned the difference between *Gobiops* and *Ferganobatrachus* in the degree of closure of the notochordal canal in the hypocentra. However, according to our observations, this difference is real: in *Ferganobatrachus*, hypocentra that are 9–15 mm wide have a wide-open notochordal canal, whereas in hypocentra of *Gobiops* that are 8–12 mm wide the notochordal canal is already closed dorsally (Shishkin 1991, p. 88). This difference may indicate that *Ferganobatrachus* was more paedomorphic than *Gobiops* or reached a larger adult size so that the larger vertebrae are ontogenetically younger.

In conclusion it can be said that *Ferganobatrachus* is closely related to *Gobiops*; as the latter is attributed to Brachyopoidea (Warren and Marsicano 2000), *Ferganobatrachus* may also be referred to that group.

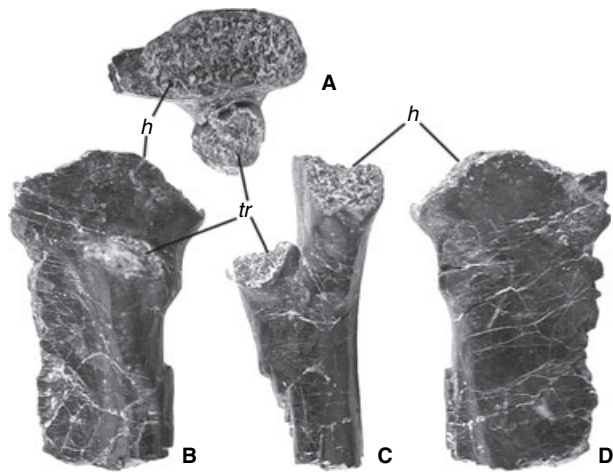
?*Ferganobatrachus riabinini* Nesov, 1990

Text-figure 3

Material. ZIN PH 7/47, left femur proximal end, FTA-30, 2001; ZIN PH 10/47, left femur proximal end, FTA-30, 2001; ZIN PH 12/47, right femur proximal end, FTA-30, 2001.

Description. There are three small proximal femoral fragments in which the maximum width of the head is 3.4–6.3 mm. The femur is relatively wide mediolaterally, very flat, plank-shaped dorsoventrally, and only slightly constricted below the head. The head is mediolaterally expanded, oval in proximal view and clearly divided into two articular surfaces orientated at an angle of c. 120 degrees. The lateral bone edge is about twice as thin as the sharp medial edge. The trochanter is large and massive, with a subcircular capitulum and a distinct, but low, trochanteric crest. There are several parallel subvertical ridges between the continuous trochanter + trochanteric crests and the medial margin.

Remarks. The small proximal femoral fragments from FTA-30 are very distinctive in being mediolaterally wide and dorsoventrally flat, with a sharp medial margin. This morphology is not characteristic for Caudata, in which the proximal part of the femur is subcircular to subrectangular in cross-section, but it is similar to the condition in non-lissamphibian temnospondyls (Warren and Snell 1991). Taking the small size of these fragments in account, it is assumed that they belong to larvae of non-lissamphibian temnospondyls, possibly of *Ferganobatrachus riabinini*.



TEXT-FIG. 3. Proximal end of a possible larval left femur of *Ferganobatrachus riabinini* from the Middle Jurassic (Callovian) Balabansai Svita, Fergana Depression, Kyrgyzstan; FTA-30 site. ZIN PH 7/47, in A, proximal, B, ventral, C, medial, and D, dorsal views. Abbreviations: h, head; tr, trochanter. All $\times 3.9$.

CAUDATA Scopoli, 1777
 KARAUROIDEA Ivakhnenko, 1978
 KARAUROIDEA Ivakhnenko, 1978

KOKARTUS Nesov, 1988

Type species. *Kokartus honorarius* Nesov, 1988 from the Bathonian of Kyrgyzstan.

Kokartus honorarius Nesov, 1988
 Text-figures 4–7

- 1988 *Kokartus honorarius* Nesov, pp. 434–435, fig. 2.
 1993 *Kokartus honorarius* Nesov; Milner, p. 675.
 1996 *Kokartus honorarius* Nesov; Nesov *et al.*, p. 3, fig. 1.
 2000a *Kokartus honorarius* Nesov; Shishkin, p. 305.

Material. All specimen numbers prefixed by ZIN PH. 50/47, right squamosal; 33, 36 and 38/47, right exoccipital fragments; 53 and 54/47, left exoccipital fragments; 46/47, right dentary symphysis; 30/47, right dentary fragment; 45/47, maxillary or premaxillary fragment; 47/47, unidentified jaw fragment; 3/47, atlas with a partially preserved neural arch; 4–6/47, 11/47 and 26/47, atlantal centra; 55/47, 57/47 and 61–63/47, trunk vertebrae; 56/47, trunk vertebra neural spine; 64/47, sacral vertebra; 27 and 52/47, right scapulocoracoid fragments; 24, 28, 29, 35/47 and 58/47, left scapulocoracoid fragments; 22, 23 and 25/47, right humerus proximal fragments; 21/47, left humerus proximal fragment; 40/47, right humerus distal fragment; 49 and 51/47, right ilium fragments; 31, 32, 34, 37 and 48/47, left ilium fragments; 41/47, right femur proximal fragment; 42–44/47, left femur proximal fragments; 39/47, right femur distal

fragment; and numerous less complete uncatalogued specimens. All specimens come from KUG-3 and were collected in 2000.

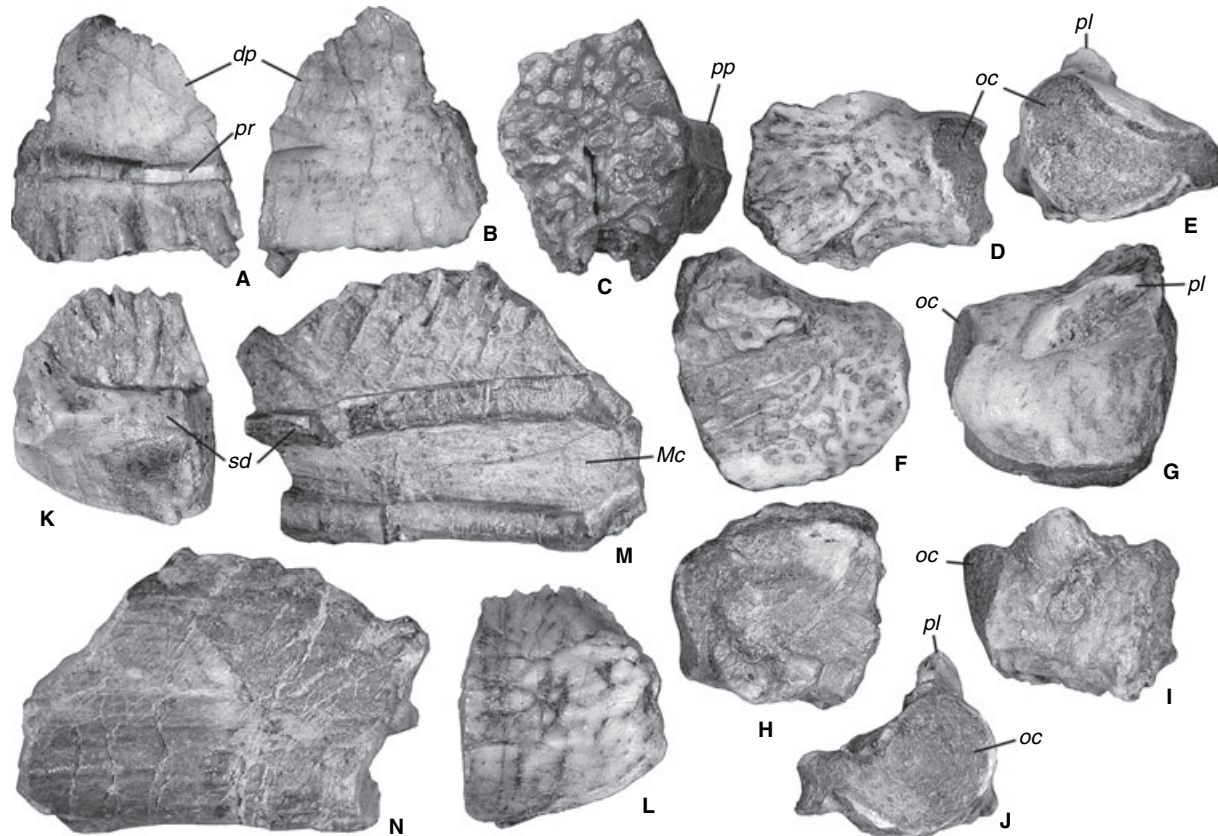
Description. There are numerous, mostly unidentifiable, skull bone fragments with characteristic sculpture. In thinner and possibly juvenile bones the sculpture is formed by isolated tubercles. In thicker bones from larger and, presumably, older individuals the tubercles are bigger and usually united in short ridges, sometimes anastomosing with other ridges. The unsculptured surfaces of the cranial bones and all surfaces of the postcranial bones are covered by numerous nutrient foramina. On the surfaces of limb bones there are short, parallel, longitudinal grooves connected with perforations for blood vessels. Only four elements of the skull (squamosal, exoccipital, dentary, and maxillary or premaxillary) and seven postcranial elements (atlas, dorsal and sacral vertebrae, scapulocoracoid, humerus, ilium and femur) can be confidently identified in the material.

The squamosal (Text-fig. 4C) is represented by a dorsal plate with a sculptured dorsal surface and the base of the unsculptured posteroventrally directed posterior process. A groove runs along the ventral side of the posterior process.

Five exoccipital fragments have been identified, which vary in size but closely correspond morphologically (Text-fig. 4D–J). The exoccipital is anteroposteriorly short and not fused with the opisthotic: two specimens (ZIN PH 33/47 and 53/47; Text-fig. 4D, F–G) preserve the complete articulation suture for the opisthotic. The occipital condyle is large and kidney-shaped, corresponding to the shape of the anterior cotyle of the atlas. A thin processus lamellosus is present along the dorsolateral edge of the bone. Only its most ventral portion is preserved in all specimens, none of which preserves the vagus foramen. Medial to this process the dorsal surface of the exoccipital is concave and smooth. The ventral and lateral bone surfaces are sculptured. Along the ventrolateral edge of the bone, opposite the processus lamellosus, is a prominent rugosity.

The dentary is represented by a few fragments. ZIN PH 46/47 preserves the mandibular symphysis, which is deep and not rounded in cross-section (Text-fig. 4K–L). The subdental shelf is massive and placed at the mid-height of the bone. Ventral to the subdental shelf the medial bone surface is slightly concave. The anterior portion of Meckel's canal is preserved, forming a pocket under the seventh and eighth teeth that is covered medially by a thin bone lamina. At the mesial end three to four teeth were anteriorly inclined, judging by the preserved lower parts of the crowns and the pedicels. The remaining teeth are broken off and their crown structure cannot be determined. The preserved parts of the crowns and pedicels are vertically orientated and all teeth are crowded. The lateral surface of the dentary is strongly convex and sculptured. ZIN PH 30/47 is a fragment from further back along the dentary (Text-fig. 4M–N). It is dorsoventrally deep, with a wide Meckel's canal that narrows anteriorly and is bordered dorsally by a shallow subdental shelf and ventrally by a thickened bony margin. The teeth are closely spaced and posteriorly inclined. The lateral surface is not sculptured. It bears a wide horizontal groove at the level of the subdental shelf.

A single maxillary or premaxillary fragment (Text-fig. 4A–B) is broken anteriorly and posteriorly, but its dorsal process is intact on one side. The dorsal process of the fragment is flat and



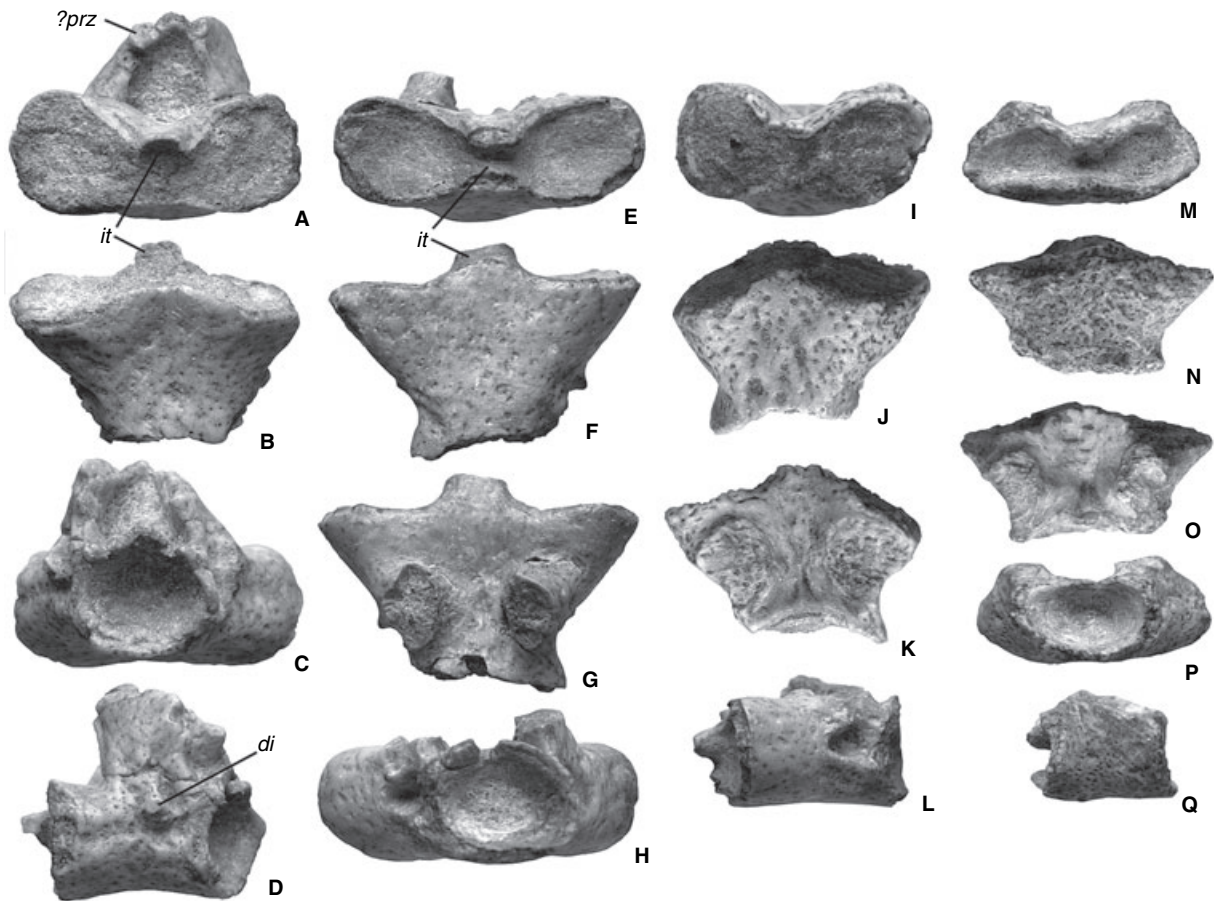
TEXT-FIG. 4. Isolated skull and mandible fragments of *Kokartus honorarius* from the Middle Jurassic (Bathonian) Balabansai Svita, Fergana Depression, Kyrgyzstan. All bones are from site KUG-3. A–B, ZIN PH 45/47, maxillary or premaxillary fragment: A, medial and B, lateral views. C, ZIN PH 50/47, right squamosal fragment in dorsal view. D–G, ZIN PH 53/47, left exoccipital fragment: D, lateral, E, posterior, F, ventral, and G, dorsal views. H–J, ZIN PH 54/47, right exoccipital fragment: H, dorsal, I, lateral, and J, posterior views. K–L, ZIN PH 46/47, right dentary symphysis: K, medial and L, lateral views. M–N, ZIN PH 30/47, right dentary fragment: M, medial and N, lateral views. Abbreviations: dp, dorsal process; Mc, Meckel's canal; oc, occipital condyle; pl, processus lamellosus; pp, posterior process; pr, palatine ridge; sd, subdental shelf. All $\times 5.5$.

very thin, triangular and straight. There are no facets preserved on the dorsal process and the lateral surface is not sculptured. There is a foramen on the medial side of the dorsal process and immediately dorsal to the palatine ridge. The palatine ridge is mediolaterally narrow and dorsomedially shallow, forming a supradental shelf. Seven tooth positions are preserved, four occupied by incomplete inclined teeth with broken tips, leaving the structure of the crown unknown.

The atlas (Text-fig. 5) has a relatively short and anteriorly broad centrum (anterior centrum width, 7.1–9.9 mm, $M = 8.3 \pm 0.44$; centrum length, excluding the intercotylar tubercle, 4.3–6.5, $M = 5.4 \pm 0.29$, $n = 6$; Table 1). The centrum is triangular in both dorsal and ventral views, with the ventral surface slightly concave or flat, without a keel or fossa. The anterior cotyles vary in shape but are mostly mediolaterally wide and dorsoventrally depressed. The width to height ratio of the anterior cotyle varies from 1.13 to 1.38 ($M = 1.25 \pm 0.04$, $n = 6$; Table 1). The articular surfaces of the cotyles are slightly concave, extend to the medial side, and are joined medially by a narrow strip. The intercotylar tubercle is developed in larger atlantes with an anterior centrum width above 8.7 mm, and is absent in smaller

atlantes with an anterior centrum length of 7.1–7.6 mm. When developed, the intercotylar tubercle is not fully ossified and is represented by dorsal and ventral lips that are capped by a narrow strip of the articular surface between the anterior cotyles; sometimes only the dorsal lip is present and the presence or absence of the ventral lip may represent intraspecific variation in *Kokartus honorarius*.

The presence of the transverse process is also size correlated. It is well developed and bipartite in the two largest atlantes (ZIN PH 11 and 3/47). In ZIN PH 3/47 the transverse process is bipartite on the right side, whereas the parapophysis is greatly reduced on the left side (Text-fig. 5D). In these atlantes the base of the transverse process is bracketed anteriorly and posteriorly by two slit-like depressions in the centrum wall. In smaller atlantes (ZIN PH 5–6 and 26/47; Text-fig. 5L, Q) there are no transverse processes and the slit-like depressions are variably developed. In ZIN PH 4/47, which is of intermediate size, the parapophysis is absent and the diapophysis is a small, spine-like tubercle located dorsal to a large, deep depression. Basapophyses are absent. The posterior cotyle is oval in outline, slightly dorsoventrally compressed, deeply amphicoelous and without a



TEXT-FIG. 5. Atlantes of *Kokartus honorarius* from the Middle Jurassic (Bathonian) Balabansai Svita, Fergana Depression, Kyrgyzstan. All bones are from site KUG-3. A–D, ZIN PH 3/47: A, anterior, B, ventral, C, posterior, and D, right lateral views. E–H, ZIN PH 4/47: E, anterior, F, ventral, G, dorsal, and H, posterior views. I–L, ZIN PH 5/47: I, anterior, J, ventral, K, dorsal, and L, right lateral views. M–Q, ZIN PH 9/47: M, anterior, N, ventral, O, dorsal, P, posterior, and Q, right lateral views. Abbreviations: di, diapophysis; it, intercotylar tubercle; ?prz, ?prezygapophysis. All $\times 4.3$.

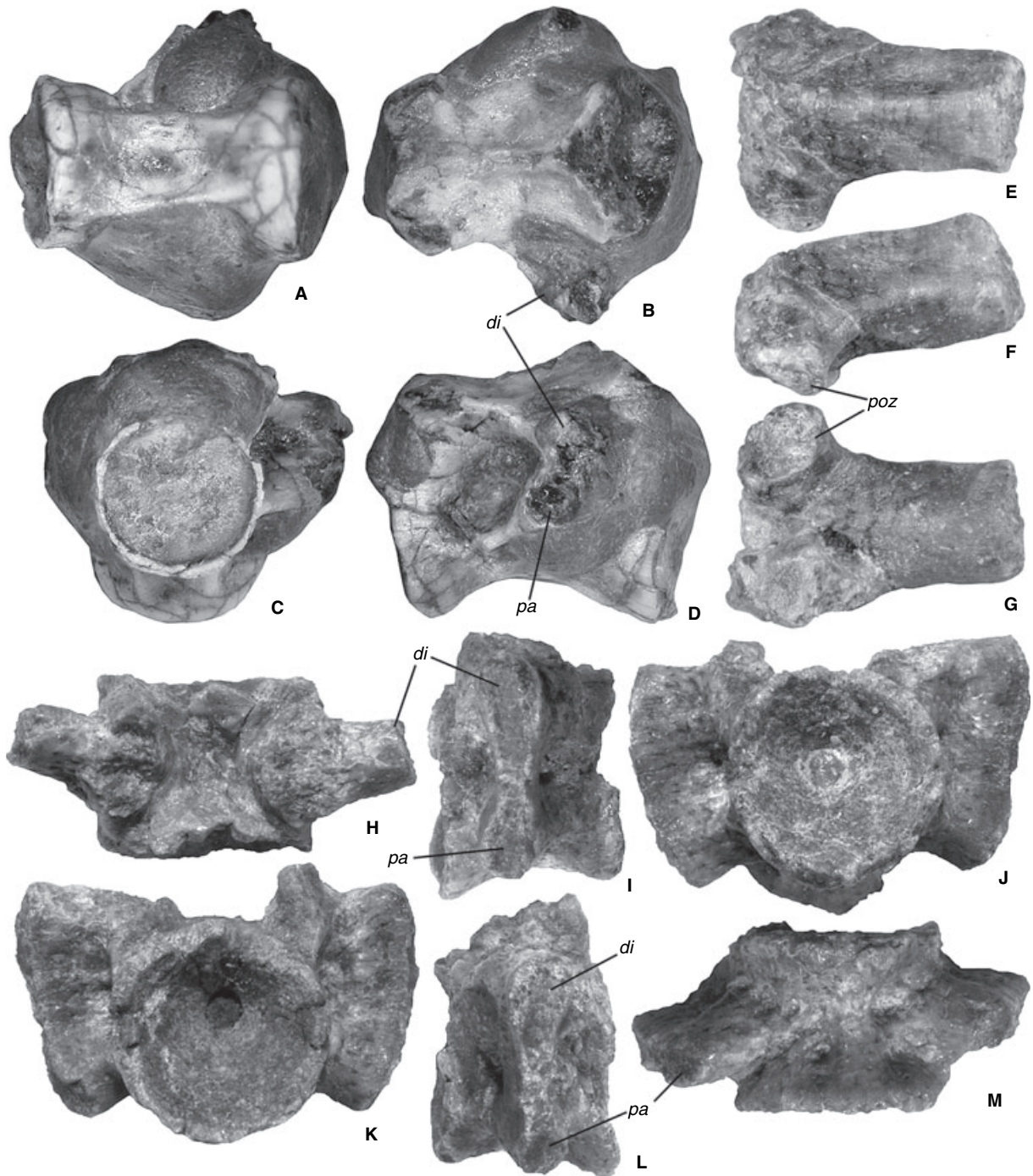
TABLE 1. Atlas measurements (in mm) of *Kokartus honorarius* from the Middle Jurassic (Bathonian) Balabansai Svita, Fergana Depression, Kyrgyzstan (KUG-3 site).

Specimen	Centrum length	Anterior centrum width	Posterior centrum width	Anterior cotyle width	Anterior cotyle height	Ratio of anterior cotyle width to height
ZIN PH 6/47	4.3	7.1	4.2	3.4	3.0	1.13
ZIN PH 26/47	5.3	7.5	4.3	3.9	3.4	1.15
ZIN PH 5/47	5.7	7.6	4.2	4.5	3.7	1.22
ZIN PH 4/47	5.2	8.7	4.1	4.6	3.4	1.35
ZIN PH 3/47	5.5	9.0	4.1	5.1	3.7	1.38
ZIN PH 11/47	6.5	9.9	4.8	5.1	4.1	1.24

notochordal perforation. The size of the neural arch pedicels varies from relatively large in smaller atlantes to relatively small in larger atlantes. Between the pedicels on the floor of the neural canal, there is a variably developed short longitudinal groove. There is no spinal nerve foramen or notch in the leading edge of the neural arch wall that might be homologous with a spinal foramen. The neural arch is preserved only in ZIN PH 3/47,

where it is incomplete posteriorly and dorsally. The anterior edge is nearly complete and bears distinct structures that presumably represent prezygapophyses with articulation facets for the proatlans; this structure is better developed on the right side (Text-fig. 5A).

There are a number of amphicoelous trunk vertebrae with a closed notochordal canal and additional fragments of these



TEXT-FIG. 6. Vertebrae of *Kokartus honorarius* from the Middle Jurassic (Bathonian) Balabansai Svita, Fergana Depression, Kyrgyzstan. All bones are from site KUG-3. A–D, ZIN PH 55/47, trunk vertebra: A, ventral, B, dorsal, C, anterior, and D, left lateral views; $\times 4.2$. E–G, ZIN PH 56/47, dorsal neural spine: E, dorsal, F, left lateral, and G, ventral views; $\times 9.0$. H–M, ZIN PH 64/47, sacral vertebra: H, dorsal, I, right lateral, J, posterior, K, anterior, L, left lateral, and M, ventral views; $\times 8.0$. Abbreviations: di, diapophysis; pa, parapophysis; poz, postzygapophysis.

bones. The most complete trunk vertebra is partially covered by a limonite crust that holds it together (ZIN PH 55/47; Text-fig. 6A–D). Its ventral centrum length is 7.6 mm. The anterior and posterior cotyles are circular in shape. The preserved proxi-

mal part of the transverse process is bipartite, large and posteriorly deflected. Anterior to its base there is a large, deep depression, which is bound dorsally and ventrally by prominent diapophyseal and parapophyseal ridges.

The ventral surface of the centrum is anteroposteriorly and mediolaterally concave, and flanked on either side by a sharp lateral ridge. There is a foramen or deep pit in the middle of the ventral centrum surface, but it is difficult to determine how deep the opening extends into the bone because this structure is filled with limonite matrix. The wall of the neural arch is tall and the anterior part of the roof is flat. The neural spine is broken and its preserved base is thick. There is a very low neural crest extending from the anterior margin of the neural arch to the neural spine. The prezygapophyses are broken. Spinal nerve foramina and basapophyses are absent.

An isolated dorsal neural spine (ZIN PH 56/47; Text-fig. 6E–G) is relatively long and robust, with a rhomboid cross-section. There is a distinct dorsal neural crest and a weaker crest along the ventral side. The neural spine tip was not ossified. The postzygapophyses are relatively small and closely located, with oval articular surfaces. The ceiling of the neural canal is bordered posteriorly by a thick transverse ridge. Dorsal to this ridge and medial to the postzygapophysis there is a foramen, which is better developed on the right side.

The sacral vertebra (ZIN PH 64/47; Text-fig. 6H–M) is relatively short (centrum length 3.5) and has a dorsoventrally broad transverse process. On the transverse process the diapophyseal part is larger than the parapophyseal part. Just anterior to the transverse process there is a distinct, pit-like depression in the wall of the centrum at the level between the parapophysis and diapophysis. There are two large and several small, irregularly shaped foramina on the ventral centrum surface.

The scapulocoracoid is represented by six fragments, the most complete of which is ZIN PH 27/47, preserving part of the scapular blade and the complete glenoid facet (Text-fig. 7A). ZIN PH 28/47 has an unfused coracoscapular suture (Text-fig. 7B–C) and is presumably from a younger individual. The glenoid facet is a complex strap-like structure with two distinct articulation areas: a larger kidney-shaped portion dorsally for contact with the humeral head and a smaller sigmoid portion ventrally for contact with the ventral crest of the humerus (Text-fig. 7A). There is a deep, well-delimited depression adjacent anteriorly to the glenoid facet (Text-fig. 7A–B, D, F). The supraglenoid foramen is small and not perforate (Text-fig. 7D), except in ZIN PH 52/47 in which it is considerably larger, but even in that specimen the foramen does not perforate the entire bone (Text-fig. 7F). The scapular blade is a narrow process that curves posteriorly. The acromion is an anteriorly directed, blade-like protrusion separated from the scapular blade by an incision (Text-fig. 7A).

The humerus is represented by one distal and three proximal fragments (Text-fig. 7G–K). It is markedly expanded dorsoventrally at the proximal end and anteroposteriorly at the distal end. There is no dorsal crest and the ventral crest is confluent with the humerus head, forming a common unossified articulation surface. In proximal view the head is oval and the ventral crest is sigmoid. The proximal end of the humerus is convex on the anterior side and concave on the posterior side. On the distal end of the humerus the radial condyle is dorsoventrally wider and protrudes more distally than the ulnar condyle. On the ventral surface of the radial condyle there is an incisura for the ball-like cartilaginous articulation of the radial condyle. The ventral surface of the distal end of the humerus is gently concave and

there is a longitudinal groove on the dorsal surface separating the radial and ulnar condyles.

There are seven ilial fragments with the acetabulum and base of the iliac blade preserved (Text-fig. 7L–O). The acetabulum is kidney-shaped and bordered anteriorly and posteriorly by slit-like depressions. The distal end of the ilium is convex with an anteriorly widened articular surface for the pubic cartilage.

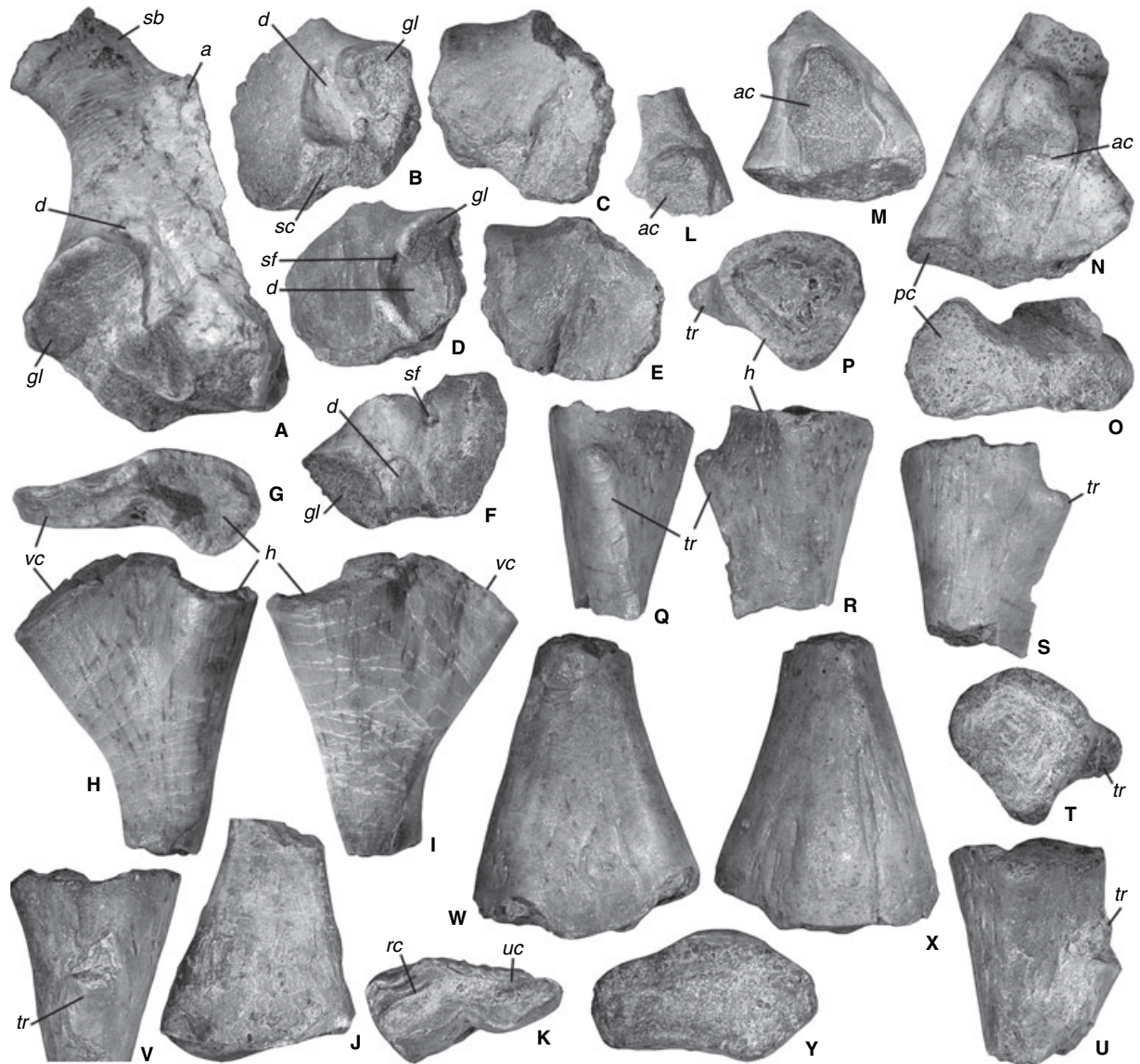
The proximal femoral head is thickened and rhomboid in proximal view, with a convex rounded medial side and a pointed lateral side (Text-fig. 7P, T). There is a high, massive trochanteric crest extending distolaterally from a blunt trochanter (Text-fig. 7P–V). The distal femoral head is mediolaterally broad and dorsoventrally compressed. The dorsal surface is strongly convex and the ventral surface is mainly concave (Text-fig. 7W–Y).

Discussion. Nesov *et al.* (1996, fig. 1) presented a skull reconstruction for *Kokartus* based on isolated skull bones and articulated parts of the skull roof from the Kyzylsu 1 and Kugart 1 localities, provided a revised diagnosis for this taxon, and discussed the homology of some cranial bones in the Caudata. Nesov's emended diagnosis of *Kokartus* (1996) included the following characters (–, primitive; +, derived; ?, uncertain polarity; *, Nesov's interpretation of the bone homology): (1) dorsal processes of premaxilla rather elongated (+); (2) maxilla relatively small (+); (3) isolated postrostral* could be present during an extended period of ontogenesis (–); (4) elements of the frontoparietal complex* (= frontal and parietal in most other literature on caudates) of each side could be fused into one bone (+) and (5) its posterolateral sides develop a sculptured outer surface only at a relatively late stage of ontogeny (?); (6) frontoparietal bone* (= parietal in most other literature on caudates) relatively elongate (?); (7) quadratojugal small (+); (8) quadrate present (–); (9) anterior end of parasphenoid has a relatively wide incisure (?); (10) pterygoid/parasphenoid contact weak (+); (11) pterygoid with a long, arc-like ridge (+), (12) a sharp, long anterior process (–), and (13) a shallow lateral incisure (–); (14) atlas with a high, strong subvertical neural spine, which has an almost horizontal surface on top (?); (15) bones of the proximal parts of the limbs relatively long, with thin mid-shafts (?).

The newly collected caudate material comes from the type horizon of *K. honorarius* and occurs in only one recognizable form; it is referred by us to this taxon based on morphological and size resemblance.

Our skull material referred to *Kokartus* is too fragmentary to allow a discussion of the homology of some cranial bones in Caudata or the phylogenetic position of this taxon. The structure of the scapulocoracoid supports the conclusion of Nesov *et al.* (1996) that *Kokartus* is one of the most primitive members of the Caudata.

Most notably, the supraglenoid foramen described here for *Kokartus* is present only in basal caudates, such



TEXT-FIG. 7. Postcranial skeletal elements of *Kokartus honorarius* from the Middle Jurassic (Bathonian) Balabansai Svita, Fergana Depression, Kyrgyzstan. All bones are from site KUG-3. A, ZIN PH 27/47, right scapulocoracoid in lateral view. B–C, ZIN PH 28/47, left scapulocoracoid fragment: B, lateral and C, medial views. D–E, ZIN PH 29/47, left scapulocoracoid fragment: D, lateral and E, medial views. F, ZIN PH 52/47, right scapulocoracoid fragment in lateral view. G–I, ZIN PH 21/47, proximal end of left humerus: G, proximal, H, posterior, and I, anterior views. J–K, ZIN PH 40/47, distal end of right humerus: J, ventral and K, distal views. L, ZIN PH 49/47, right ilium in lateral view. M, ZIN PH 51/47, right ilium in lateral view. N–O, ZIN PH 48/47, left ilium: N, lateral and O, ventral views. P–S, ZIN PH 42/47, proximal end of left femur: P, proximal, Q, ventral, R, anterior, and S, posterior views. T–V, ZIN PH 41/47, proximal end of right femur: T, proximal, U, anterior, and V, ventral views. W–Y, ZIN PH 39/47, distal end of right femur: W, ventral, X, dorsal, and Y, distal views. Abbreviations: a, acromion; ac, acetabulum; d, depression; gl, glenoid; h, head; pc, articular surface for pubic cartilage; rc, radial condyle; sb, scapular blade; sc, scapular suture; sf, supraglenoid foramen; tr, trochanter; uc, ulnar condyle; vc, ventral crest. All $\times 4.5$.

as *Marmorerpeton* and Kirtlington ‘salamander A’, and is lost in living urodeles (Borsuk-Białynicka and Evans 2002). Similarly, the complex strap-like glenoid, closely similar to that of archaic tetrapods, is known among caudates only in *Kokartus* and *Marmorerpeton*. This suggests that the glenoid must have evolved in parallel in

the Salientia and Caudata (Borsuk-Białynicka and Evans 2002, p. 86).

The variation in the samples of atlantes from the Kugart 1 locality is interpreted as intraspecific rather than interspecific. The width and height of the anterior cotyle are correlated ($r = 0.88$, $P < 0.05$), and both parameters

correlate with the length of the centrum ($r = 0.82$ and 0.98 , $P < 0.05$ respectively). This does not support the presence of more than one species in the sample. The shape of the anterior cotyles and development of the intercotylar tubercle and transverse process are ontogenetically correlated. In the Recent hynobiid *Salamandrella keyserlingii* Dybowski, 1870 the intercotylar tubercle appears only after metamorphosis and is not fully ossified until individuals are 2–3 years old (Antipenkova 1994, p. 153). Based on the pattern in *S. keyserlingii*, smaller specimens of *Kokartus honorarius* without an intercotylar tubercle and transverse process can be referred tentatively to unmetamorphosed individuals. The anterior cotyles become less dorsoventrally compressed with increasing age and are almost circular in a large atlas from the Kugart River figured by Nesov (1988, figs 2, 4; anterior centrum width *c.* 11.5 mm).

Some larger and, presumably, older specimens of *Kokartus* have transverse processes on the atlas. However, atlantal ribs were lacking, as is evident from the absence of articular surfaces on these processes. Among crown-group caudates, atlantal transverse processes are known in neotenous forms, such as fossil and Recent sirenids and proteids (Mivart 1870; Gardner 2003). The absence of atlantal transverse processes is considered to be one of the 'initial apomorphies' of Temnospondyli (Shishkin 2000*b*, pp. 543–544). Accordingly, the presence of this character in *Kokartus* and neotenous urodeles must be interpreted as a phylogenetic reversal.

Kokartus is very similar to the contemporaneous *Marmorperpeton* from the Middle Jurassic (Bathonian) Forest Marble Formation in England and Kilmaluaug Formation in Scotland, which is now also regarded as a karaurid (Evans *et al.* 1988; Evans and Waldman 1996; Borsuk-Bialynicka and Evans 2002; Evans *et al.* 2005). Differences between the two taxa are quite subtle and include, with the exclusion of paedomorphic characters, the proportions of the atlas centrum, which is somewhat longer in *Marmorperpeton*, and a deeper, not rounded, mandibular symphysis with crowded teeth in *Kokartus*.

A robust trochanteric crest for the caudifemoralis muscle attachment on the femur of *Kokartus* suggests well-developed terrestrial locomotion in this taxon. The femur of *K. honorarius* is similar to the femur and only known specimen of *Comonecturoides marshi* Hecht and Estes, 1960 from the Late Jurassic Morrison Formation in the USA (Hecht and Estes 1960), which, in our opinion, might be a karaurid. Further remains of a large salamander from the Morrison Formation were described by Evans and Milner (1993). More definitive karaurid remains, including several atlantes, were reported by Nesov (1992) from the Brushy Basin Member of the Morrison Formation at Dinosaur National Monument, Utah.

Karauridae indet.

Text-figure 8

Material. ZIN PH 2/47, caudal vertebra, FBX-23a, 1984.

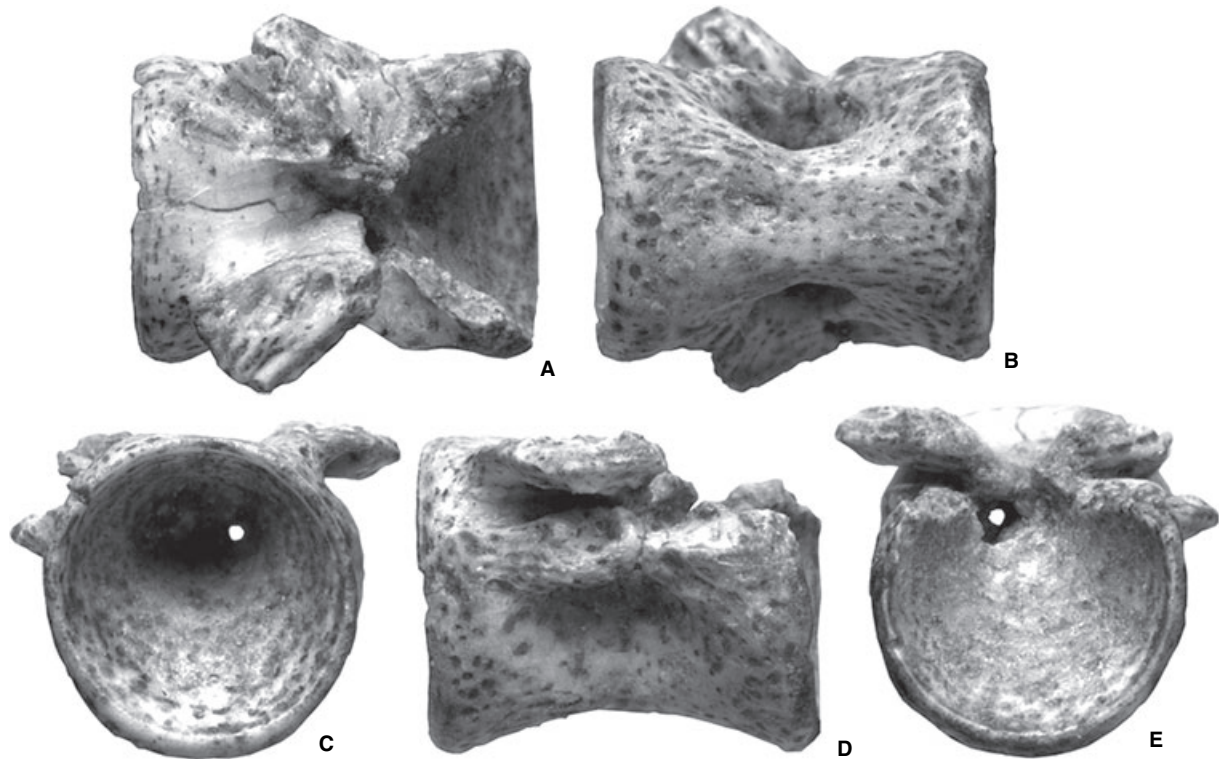
Description. The centrum is elongate (length 6.8 mm) and deeply amphicoelous with the notochordal canal open just below the dorsal margin of the cotyle rim. On the left lateral surface there are two deep circular depressions, a smaller one anterodorsally in front of the transverse processes and a larger one more posteroventrally below the ridge-like transverse process. On the right side, these depressions are slit-like and larger, and separated by a ridge. The ventral depression connects interiorly with the notochordal canal. The ventral centrum surface is concave, without a keel or lateral ridges, and with a small, round, medial fossa located posterior to the middle of the centrum. The external surface of the centrum is sculptured by small pits, including the surface of the cotyles.

Remarks. ZIN PH 2/47 is similar to *Kokartus honorarius* in its pitted sculpture, deeply amphicoelous centrum, and comparable lateral and ventral depressions on the centrum, but differs in having a notochordal perforation. Attribution of this vertebra to a larva of *Kokartus* is not likely because of its large size, which is comparable to that of the largest available trunk vertebrae of *Kokartus*. ZIN PH 2/47 might belong to a neotenous caudate similar to *Kokartus* or to a metamorphosed karaurid with a larger body than *Kokartus*.

DISCUSSION

Three (possibly four) amphibian groups are present in the Balabansai Svita: brachyopoid temnospondyls, karaurid caudates and anurans. Nesov (1988; see also Gardner and Averianov 1998) reported the presence of an albanerpetontid, based on isolated fused frontal bones from a site near the Sarykamyshsai 1 locality, and an anuran, represented by a humerus fragment, from the Kugart River (Nesov *et al.* 1994). Unfortunately, neither of these specimens has been located in the collection, but the drawing of the frontals in Nesov's 1981 field notebook suggests its attribution to the Albanerpetontidae.

The distribution of brachyopoids and caudates varies among the Balabansai localities. In Sarykamyshsai 1 and Tashkumyr 1 in northern Fergana only rare remains of brachyopoids are present. A previous report of Caudata indet. for the Sarykamyshsai 1 locality (Averianov *et al.* 2005, table 3) is not confirmed by our study. At Dzhiddasai brachyopoids and caudates are present but very rare. At the Kyzylsu 1 and Kugart 1 localities in southern Fergana caudates are quite common but brachyopoids are extremely rare. This distribution might reflect a shift in environments from estuarine in northern Fergana towards predominantly freshwater conditions in the south. There is only one Juras-



TEXT-FIG. 8. Caudal vertebra of *Karauridae* indet. from the Middle Jurassic (Callovian) Balabansai Svita, Fergana Depression, Kyrgyzstan; FBX-23a site. ZIN PH 2/47, in A, dorsal, B, ventral, C, posterior, D, left lateral, and E, anterior views. All $\times 7.2$.

sic locality elsewhere with non-lissamphibian temnospondyls and caudates, namely the Middle Jurassic (Bajocian–Bathonian) Peski Quarry near Moscow (Shishkin 2000a; Alekseev *et al.* 2001; Gambaryan and Averianov 2001). Among other Jurassic Laurasian localities there are sites with a dominance of non-lissamphibian temnospondyls (Shar Teg in Mongolia and the Junggar Basin in the Xinjiang Uigur Autonomous Region in China), anurans (some levels at Dinosaur National Monument and Garden Park in USA), albanerpetontids (Guimarota in Portugal), albanerpetontids and salamanders (Kirtlington in England), and salamanders (Skye in Scotland, Daohugou in Inner Mongolia, and Fengshan in Hebei Province, China) (Hecht and Estes 1960; Evans *et al.* 1988, 2005; Shishkin 1991; Evans and Milner 1993; Evans and Waldman 1996; Wiechmann 2000; Gao and Shubin 2001, 2003; Maisch *et al.* 2001, 2003).

In the Balabansai Svita there are at least two taxa of caudates: *Kokartus* from the Kyzylsu 1 and Kugart 1 localities and *Karauridae* indet. from the Dzhiddasai locality. This faunal difference may be correlated with the different geologic ages and/or geographic position of these localities, because sites with *Kokartus* are confined to the lower Bathonian part of the formation in southern Fergana, whereas Dzhiddasai is located in the uppermost Callovian part in northern Fergana. In the Bathonian sites of England and Scotland there are more contemporaneous taxa of stem caudates: *Marmorerpeton* and a more primitive,

hitherto undescribed, ‘Kirtlington salamander A’ (Evans *et al.* 1988; Evans and Waldman 1996; Milner 2000). This modest diversity of Middle Jurassic caudates could be an artefact of collecting, as very few microvertebrate localities of this age have been thoroughly explored.

Karauridae were widely distributed during the Middle–Late Jurassic in Europe, Central Asia, North America (see above) and Siberia (Skutschas *et al.* 2005). The wide distribution of this plesiomorphic and possibly paraphyletic group can undoubtedly be linked to the large, consolidated Laurasian landmass (e.g. Golonka *et al.* 1996) at this time. Bathonian records of *Karauridae* in Great Britain, Kyrgyzstan and Siberia are the oldest indisputable occurrences for Caudata. Curtis and Padian (1999, figs 11–12) reported two caudate atlantes from the Early Jurassic Kayenta Formation in Arizona, USA. These are short and have a very deeply concave posterior cotyle (seemingly notochordal), a foramen for the first spinal nerve, and a broad intercotylar tubercle flanked by shallow concave and weakly expanded laterally anterior cotyles. According to this complex of characters, they are more likely to belong to Albanerpetontidae than to Caudata.

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