

PTEROSAUR AND DINOSAUR REMAINS FROM THE MIDDLE JURASSIC BALABANSAI SVITA IN THE NORTHERN FERGANA DEPRESSION, KYRGYZSTAN (CENTRAL ASIA)

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Abstract: Isolated pterosaur and dinosaur teeth and a sauropod metatarsal I and manual phalanx V-1 from the Middle Jurassic (Callovian) Balabansai Svita in the northern Fergana Valley, Kyrgyzstan, are described and attributed to the pterosaur taxon Rhamphorhynchinae indet., a theropod Tetanurae indet., a sauropod Neosauropoda indet., and a new pachycephalosaurid *Ferganocephale adenticulatum* gen. et sp. nov. The Balabansai theropod is possibly a stem-lineage representative of Dromaeosauridae. The new pachycephalosaurid is the oldest representative of the group and extends its known history by

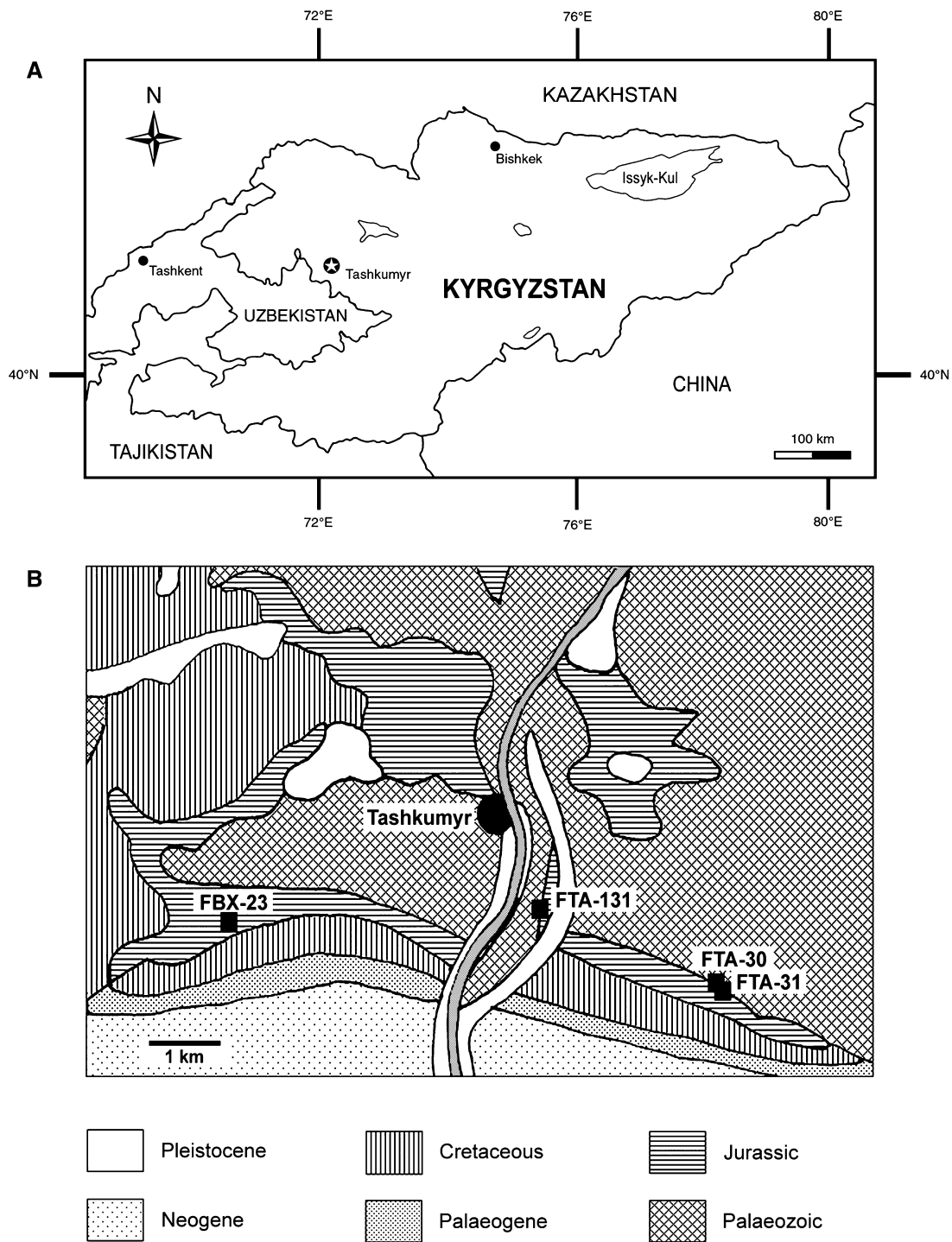
10–20 myr. The Balabansai vertebrate assemblage is most similar to the Callovian assemblages from the Qigu and Upper Shaximiao formations in China, and intermediate in the evolutionary level of the taxa present between the Bathonian assemblages from Wucaiwan and the Lower Shaximiao formations (China) and the Late Jurassic Shar Teg fauna from Mongolia.

Key words: *Ferganocephale* gen. nov., Jurassic, Kyrgyzstan, Neosauropoda, Pachycephalosauridae, Rhamphorhynchinae, Tetanurae.

THE Jurassic Period was the real kingdom of dinosaurs, the ‘Jurassic Park’, dominated by large herbivores such as sauropods, stegosaurs and ornithopods, and diverse carnivores, including ceratosaurs, allosaurids and megalosaurids. However, our current knowledge of Jurassic dinosaurs is based on a few limited locations in western North America, Europe, eastern Africa, India and China (Weishampel 1990). The vast territory of the former Soviet Union was, for a long time, a terra incognita for Jurassic terrestrial life, and especially for dinosaurs. A partial sauropod skeleton was found by N. N. Verzhilina in 1966 in the upper part of the Balabansai Svita (Callovian) west of Tashkumyr city in northern Fergana (Kyrgyzstan) (Text-fig. 1). It was excavated by the Moscow Paleontological Institute team in 1967 (Rozhdestvensky 1968) and recently described by Alifanov and Averianov (2003). In Kyrgyzstan several Middle Jurassic dinosaur localities, most of them in the northern Fergana Depression, were discovered by L. A. Nesov in the 1980s (Nesov 1995; Averianov and Bakirov 2000), but dinosaur remains were not described apart from one sauropod tooth figured by

Kaznyshkin (1990, pl. 10, fig. 22). Nesov (1995, p. 80) established the presence of theropods (cf. Coelurosauria and Megalosauridae or Ceratosauria), camarasaurid sauropods, stegosaurians and ornithopods based on material from several localities within the Middle Jurassic (Callovian) Balabansai Svita, but mostly from one rich fossiliferous lens (FTA-30) at the Sarykamysai 1 locality, 3–4 km east of Tashkumyr (Text-fig. 1). The majority of vertebrate remains were recovered in 1985 and 1992, when Nesov and his team from the Leningrad State University carried out intensive quarrying and screen-washing at the FTA-30 site (see Averianov 2000 for list of vertebrates and bibliography for this site). Recently, remains of Middle and Late Jurassic dinosaurs were reported from Central Russia (Alifanov and Sennikov 2001) and Yakutia (Kurzanov *et al.* 2000, 2003).

In 2000 a joint project of the Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, Freie Universität, Berlin, the Zoological Institute of the Russian Academy of Sciences in St. Petersburg and the Institute of Geology of the National Academy of Science in Bishkek



TEXT-FIG. 1. Geographical map (A) of the region and geological map (B) of the Tashkumyr area, showing position of the main fossil localities in the Middle Jurassic (Callovian) Balabansai Svita.

(Kyrgyzstan) was started in the Republic of Kyrgyzstan to recover Jurassic mammals. In 2000 about 2 tonnes of matrix were screen-washed at the FTA-30 site, which produced about 15 kg of fine fraction. We also picked some 40 kg of fine fraction obtained from the screen-

washing in 1992. In the concentrate, in addition to numerous sharks' teeth, fish scales and other fish remains, and rare crocodile teeth, one lower molar of a docodont mammal was found (Martin and Averianov 2004), but dinosaur teeth were surprisingly absent. In 2001 we dis-

covered a new rich fossiliferous lens at the FTA-30 site, quarrying of which produced some well-preserved dinosaurian and pterosaurian teeth. Some dinosaur teeth were also found during quarrying of the FBX-23 site within the Balabansai Svita on the right bank of the Naryn River, approximately 5 km west of Tashkumyr (Text-fig. 1). Finally, in 2001 we reopened a vertebrate site, FTA-131, on the left bank of the Naryn River, close to Tashkumyr (Text-fig. 1), first discovered by P. V. Fedorov and Nesov in 1992. Quarrying of this site produced one sauropod tooth, a sauropod first metatarsal and a proximal phalanx of the fifth manual digit.

In this paper we describe all available pterosaur and dinosaur material from the Balabansai Svita in the vicinity of Tashkumyr. All of the specimens are housed in the Paleoherpeterological Collection of the Zoological Institute, Russian Academy of Sciences, St Petersburg (abbreviated ZIN PH).

GEOLOGICAL SETTING

In the Tashkumyr area in the northern Fergana valley (Text-fig. 1) continental Jurassic deposits are widely distributed and three svitas can be distinguished (Nikishova and Vinogradova 1964; Aliev *et al.* 1981): the coal-bearing Tashkumyr Svita (70–200 m) containing alternating claystones, clay and coaly shales, siltstones, sandstones and coal layers, which are commercially mined; the Igrysay Svita (40–180 m) comprising greenish and brown sandstones and rare siltstones and claystones; and the Balabansai Svita (up to 250 m) of variegated sandstones, siltstones, claystones, and rare gravels and marls. Above the Jurassic succession is a thick section of Cretaceous red beds, starting with a basal layer of Lower Cretaceous conglomerates. The Tashkumyr and Igrysay svitas are terrestrial deposits containing Early and Middle Jurassic floras, respectively; they accumulated in humid climatic conditions (Sikstel' 1936; Alimov and Kuzichkina 1971). The Balabansai Svita is transitional from terrestrial to marginal marine (Aliev *et al.* 1981; Kaznyshkin 1988).

We describe here vertebrates from the following sites (Text-fig. 1): FTA-30, 35 m above the base of the Balabansai Svita at the Sarykamysai 1 locality; FTA-31, stratigraphically several metres above, but hypsometrically just below the previous site because of the steep slope (the sample may be contaminated by materials washed down from FTA-30); FTA-131, 36–37 m above the base of the Balabansai Svita on the left bank of the Naryn River; FBX-23, 9 m below the top of the Balabansai Svita in Dzhidasai (all measurements made by Nesov). The localities FTA-30, FTA-31 and FTA-131 are confined to the lower, variegated but predominantly grey to greenish

coloured part of the Balabansai Svita, which was deposited under a relatively humid climate (Kaznyshkin 1988). The locality FBX-23 is confined to the red coloured upper part of the Balabansai Svita, deposited under conditions of increasing aridity (Kaznyshkin 1988). The increasing aridity of the climate in Central Asia in the Late Jurassic and most of the Early Cretaceous epoch began in the Callovian (Vakhrameev 1991). This climatic event, clearly expressed in the rocks of the Balabansai Svita, further corroborates the Callovian age for this unit.

Detailed study of the microvertebrates from different parts of the Balabansai Svita has not revealed significant differences in the faunal composition between the lower and upper parts of the Svita (Kaznyshkin 1988; Kaznyshkin *et al.* 1990), and therefore we treat here all of the Balabansai vertebrate assemblage as a single unit.

All microvertebrate sites studied were formed by catastrophic mud flows, which transported vertebrate remains from nearshore shallow areas to the basin, more distant from the land; the majority of the presently outcropping rocks of the Balabansai Svita were deposited in this deeper basin (Kaznyshkin 1988). Therefore the microvertebrate remains in this Svita are concentrated in lenses of varying size, from 5–6 m (FTA-30) up to 10 m in width (FBX-23) or even more. Between these lenses the deposits usually lack any vertebrate remains.

The deep-water basin claystones and siltstones of the lower part of the Balabansai Svita are distributed mostly east of the Naryn River (sites FTA-30, FTA-31). West of this river, in the Balabansai ravine, these deposits are replaced by well-sorted fluvial sandstones with numerous silicified logs and locally abundant sauropod bones. The tree trunks are orientated predominantly in a north–south direction (Kaznyshkin 1988). A partial sauropod skeleton was found in this bed in 1966 (Rozhdestvensky 1968; Alifanov and Averianov 2003). This bed is thought to represent a deltaic deposit of a relatively large river ('Palaeo-Naryn River'), entering the Tashkumyr Gulf from the north and running west and parallel to the modern Naryn River. During the increasing aridity this river disappeared. The uppermost part of the Balabansai Svita on the western Naryn River bank is formed by deposits from the deeper basin.

The palaeoenvironmental situation during deposition of the lower Balabansai Svita is similar in many respects to that of the Upper Jurassic Qigu Formation, Shishugou Group in the Junggar Basin, Xinjiang Uygur Autonomous Region of China (McKnight *et al.* 1990; Peng and Brinkman 1994). In the Pingfengshan area the fine-grained lacustrine deposits contain abundant and diverse remains of aquatic and terrestrial vertebrates (fishes, labyrinthodonts, turtles, crocodiles, small

dinosaurs and rare sauropod bones). All these faunal elements are present in the eastern lower Balabansai sites (FTA-30, FTA-31), where the majority of taxa are similar (see Discussion). As in the Pingfengshan area sauropod remains are also very rare. Some 100 km east of Pingfengshan, in the Jiangjunmiao area, the equivalent stratigraphic interval is represented by fluvial beds that contain abundant silicified logs, upright tree stumps, and a vertebrate fauna that is dominated by sauropods and large theropods (McKnight *et al.* 1990). The difference between the two regions is that the 'Palaeo-Jiangjunmiao River' was flowing into a freshwater lake, which filled the Junggar depression in the Late Jurassic – Early Cretaceous (Chen 1987, fig. 1), but the 'Paleo-Naryn River' was flowing into a brackish-water gulf of the Tethys Ocean.

METHODS

Weathered siltstones were taken from the surface and transported to the nearby Sarykamysai Creek and screen-washed using the Henkel process (Henkel 1966). The fraction above 2 mm was picked in the field and the fine fraction between 2 and 0.5 mm was taken to the laboratory for further treatment. In total we screen-washed the following amounts of matrix: about 2 tonnes in 2000 and 4.5 tonnes in 2001 from the FTA-30 site, 1.9 tonnes from the FTA-31 site, 30 kg from the FTA-131 site and 460 kg from the FBX-23 site. Additionally, we collected some 190 kg of matrix from the bone-bed within the FTA-131 site.

About 8.9 tonnes of sediment screen-washed in 2000 and 2001 yielded some 240 kg of fine fraction. In the laboratory, the fine fraction was reduced using 10 per cent acetic acid and 5 per cent hydrogen peroxide. The fine fraction collected in 2000 from the FTA-30 site was additionally treated with heavy liquid, which reduced the content of non-phosphatic particles to less than 10 per cent. The residue was picked under a stereomicroscope.

All pterosaur and dinosaur remains described herein were found during quarrying of the sites or picking of the coarse fraction (above 2 mm) of concentrate, except for a small pterosaur tooth (ZIN PH 37/42), which was found in the fine fraction. The fine fraction did not contain definite dinosaur remains.

Abbreviations for measurements: ACL, anterior carina length; BW, basal width; DSDI, denticle size difference index; FABL, fore-aft basal length; TCH, tooth-crown height (after Currie *et al.* 1990; Farlow *et al.* 1991; Rauhut and Werner 1995; ACL, added here, is measured from the tip of the crown to the mesial end of the anterior denticulated carina). All measurements are in mm.

SYSTEMATIC PALAEOLOGY

PTEROSAURIA Kaup, 1834

RHAMPHORHYNCHOIDEA Plieninger, 1901

RHAMPHORHYNCHIDAE Seeley, 1870

RHAMPHORHYNCHINAE Seeley, 1870

RHAMPHORHYNCHINAE indet.

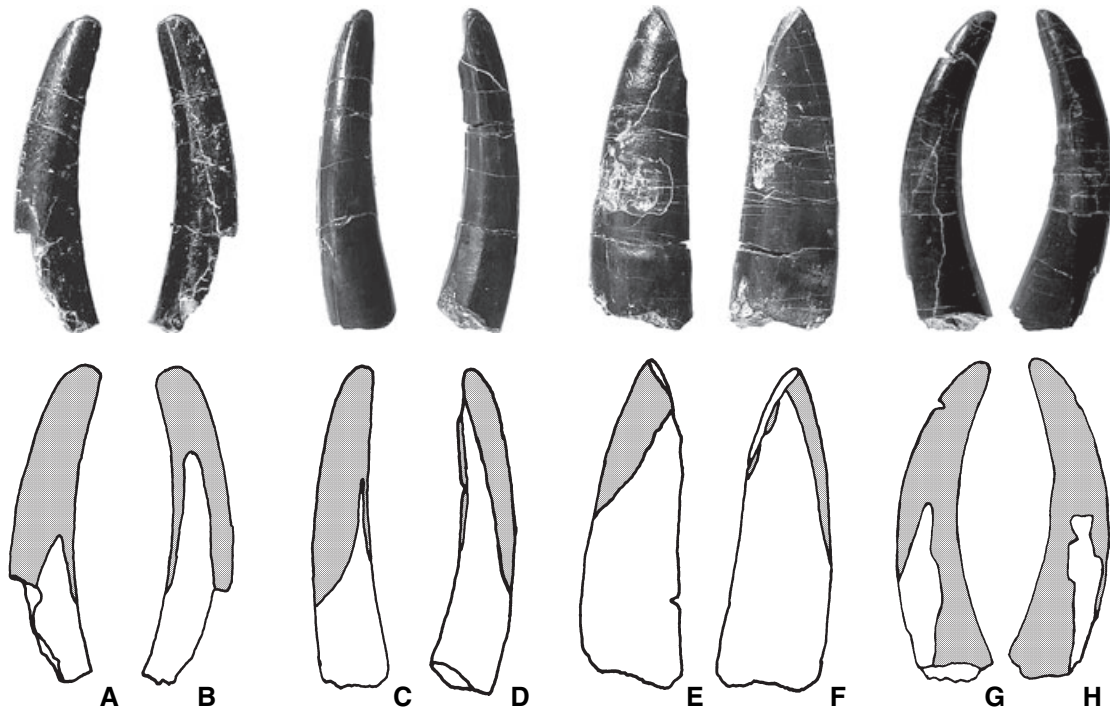
Text-figure 2

Material. Five teeth of different sizes (ZIN PH 1/42–3/42, ZIN PH 23/42, ZIN PH 37/42) and two tooth fragments (ZIN PH 24, ZIN PH 25/42). FTA-30 site.

Description. The teeth are slightly flattened labiolingually (BW/FABL = 0.65, 0.80, 0.88), smooth and tapering towards their tip, gently recurved posteriorly, all exhibiting about the same degree of curvature. The teeth are markedly different in size, the largest measuring nearly 70 mm and the smallest about 4 mm. In two teeth (ZIN PH 1/42 and 3/42) the lingual side of the crown is flattened and the buccal side is gently convex; in ZIN PH 2/42 and 23/42 both lingual and buccal sides are convex. The enamel cap covers about one-half to one-third of the crown height (extending further antapically on the lingual side) in all teeth except ZIN PH 23/42, where the enamel cap occupies more than half of the crown height (Text-fig. 2D). From this enamel cap the enamel bands extend down the anterior and posterior sides of the crown, respectively. The anterior band is much wider than the posterior (except ZIN PH 23/42), and it is noticeably wider from the lingual side. The posterior band is very narrow and follows the posterior carina, except on ZIN PH 23/42, where the posterior enamel band is much wider and longer than the anterior band (Text-fig. 2D). Both anterior and posterior bands terminate somewhat before reaching the tooth base, but in ZIN PH 23/42 the posterior enamel band surrounds much of the tooth base. The enamel surface is smooth, without any sculpture, but covered by numerous longitudinal cracks. In two teeth (ZIN PH 1/42 and 2/42) the apex is considerably worn, with three distinct facets: one on the apex and two longitudinal facets extending onto the anterior and posterior enamel bands. On the third tooth (ZIN PH 3/42) the apex is broken off and the broken surface is polished. Possibly the tooth was broken during life, but continued to function for a certain period. In the smallest specimen (ZIN PH 37/42), the crown is small and triangular, and slightly bent medially. The enamel covers the crown tip and narrow enamel bands extend antapically along the anterior and posterior crown edges, leaving the basal portion of the crown free of enamel on both lateral and medial sides. The enamel surface is smooth.

Measurements. ZIN PH 1/42: FABL, ?, BW, 4.45; ZIN PH 2/42: FABL, 4.30, BW, 3.80; ZIN PH 2/42: FABL, 8.05, BW, 5.20; ZIN PH 23/42: FABL, 5.00, BW, 4.00.

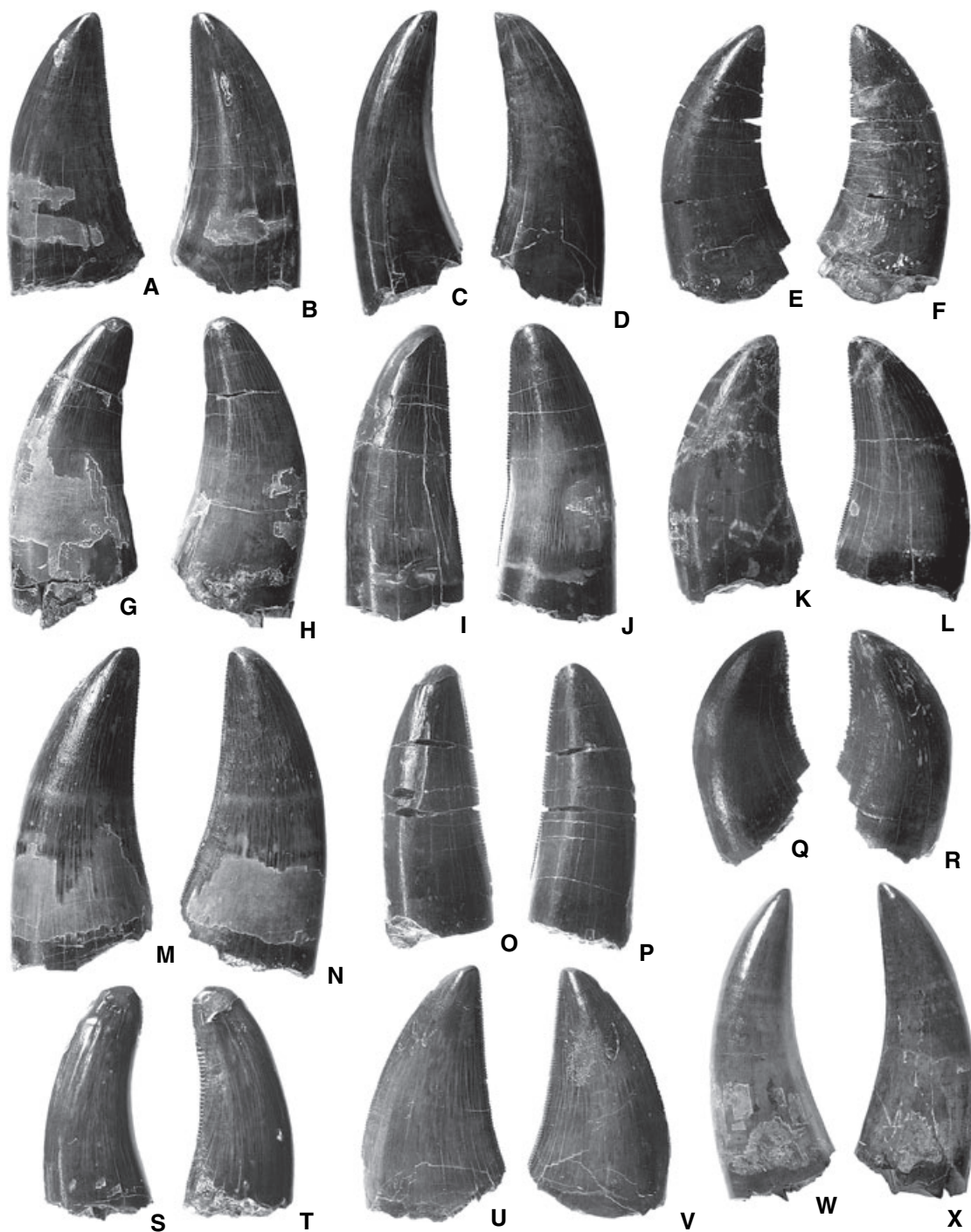
Discussion. Pterosaurs were tentatively reported from the FTA-30 site (e.g. Nesov and Kaznyshkin 1988,



TEXT-FIG. 2. Pterosaur teeth, Rhamphorhynchinae indet., from the Middle Jurassic (Callovian) Balabansai Svita, northern Fergana Valley, Kyrgyzstan, in two side views; photographs and schematic drawings showing distribution of enamel (shaded). All teeth are from the FTA-30 site. A–B, ZIN PH 1/32; $\times 0.85$. C–D, ZIN PH 2/32; $\times 1.05$. E–F, ZIN PH 3/32; $\times 0.85$. G–H, ZIN PH 23/32; $\times 1.95$.

p. 161) based on fragments of hollow bones. Nesov (1990, p. 7) reported from FTA-30 a fragmentary mandibular symphysis of a small pterosaur with small, closely spaced teeth slanting anteriorly and outwards, and referred this specimen to Anurognathidae(?). Bakhurina and Unwin (1995, p. 217) questioned the anurognathid nature of this specimen and proposed that it should be attributed to the Rhamphorhynchidae. Unfortunately, we currently cannot trace this specimen in the collection. The pterosaur teeth described above were collected in the 1980s and early 1990s, but their pterosaur nature was not recognized until our study. We refer these teeth to the Rhamphorhynchidae because of a unique combination of the following characters: the teeth are slender, tapering, slightly posteriorly curved with one lateral side convex and the other more flattened, while the enamel is restricted to the apical portion of the crown with an anterior and a posterior asymmetrical enamel band. Among tetrapods, this combination of characters is found only in rhamphorhynchid pterosaurs (e.g. Wellnhofer 1978, p. 5). The rhamphorhynchid teeth from Sarykamyshtsai 1 belong to a rather large animal (except for ZIN PH 37/42). Two rhamphorhynchids of comparable size have been described so far: *Angustinaripterus* He *et al.*, 1983 from

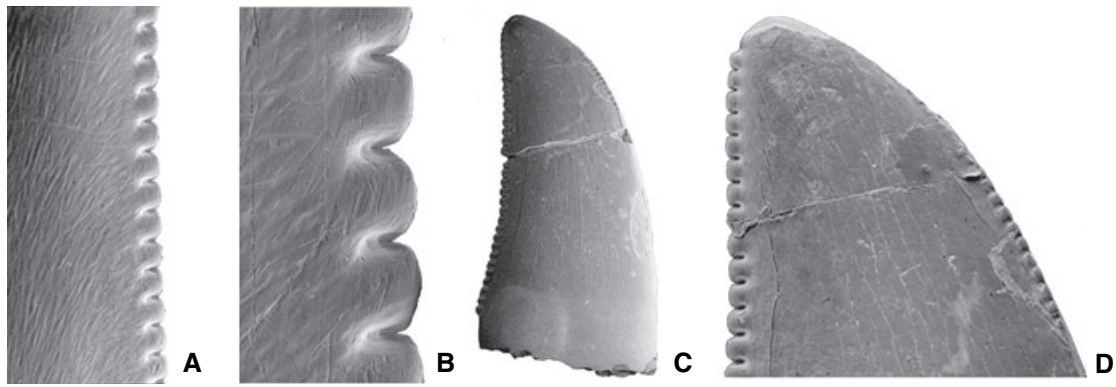
the lower Callovian Shaximiao [= Xiashaximiao] Formation in Sichuan Province, China (He *et al.* 1983) and *Rhamphocephalus* Seeley, 1880 with two species from several Bathonian localities in England (Unwin 1996). The tooth morphology of *Rhamphocephalus* is generally similar to that of the teeth from the Balabansai Svita (D. Unwin, pers. comm. 2001). The teeth of *Angustinaripterus* have not been described in detail but, judging from the published photograph (Wellnhofer 1991, text-fig. on p. 80), the enamel on its anterior enlarged teeth was distributed exactly as on the teeth from FTA-30. In spite of the great similarity in the tooth morphology of *Angustinaripterus* and the Balabansai rhamphorhynchoid, we attribute the latter only to Rhamphorhynchinae indet. because a more precise determination is not possible based on isolated teeth. ZIN PH 37/42 differs from the other rhamphorhynchoid teeth by its smaller size and by the curvature in the medial–lateral plane instead of in the anterior–posterior plane. In this regard it is similar to the pterodactyloid teeth from the Bathonian Forest Marble Formation of England (Evans and Milner 1994, text-fig. 18.6A–B) and teeth of the Cretaceous Anhangueridae (Wellnhofer 1985, text-fig. 7). However, teeth with a triangular crown that is relatively short and wide are also typical



TEXT-FIG. 3. Tetanurae indet., teeth from the Middle Jurassic (Callovia) Balabansai Svita, northern Fergana Valley, Kyrgyzstan, in two side views. All teeth are from the FTA-30 site. A–B, ZIN PH 7/42; $\times 0.8$. C–D, ZIN PH 8/42; $\times 0.75$. E–F, ZIN PH 9/42; $\times 0.78$. G–H, ZIN PH 10/42; $\times 0.78$. I–J, ZIN PH 12/42; $\times 1.05$. K–L, ZIN PH 13/42; $\times 1.18$. M–N, ZIN PH 11/42; $\times 1.02$. O–P, ZIN PH 14/42; $\times 1.15$. Q–R, ZIN PH 15/42; $\times 1.35$. S–T, ZIN PH 16/42; $\times 1.3$. U–V, ZIN PH 28/42; $\times 2.32$. W–X, ZIN PH 26/42; $\times 1.0$.

for the posterior end of the tooth row of rhamphorhynchoids (Wellnhofer 1991). Unwin (1996) reported teeth with the same morphology for the

Middle Jurassic rhamphorhynchoid *Rhamphocephalus*. Therefore we interpret ZIN 37/42 as a posterior tooth of a juvenile rhamphorhynchoid.



TEXT-FIG. 4. Tetanurae indet., teeth from the Middle Jurassic (Callovian) Balabansai Svita, northern Fergana Valley, Kyrgyzstan, SEM micrographs. All teeth are from the FTA-30 site. A–B, ZIN PH 19/42, posterior denticles; A, $\times 150$; B, $\times 500$. C–D, ZIN PH 18/42; C, $\times 6.1$; D, $\times 17.5$.

DINOSAURIA Owen, 1841
 SAURISCHIA Seeley, 1888
 THEROPODA Marsh, 1881
 TETANURAE Gauthier, 1986
 TETANURAE indet.

Text-figures 3–4

Material. 18 teeth (ZIN PH 7–20, ZIN PH 26/42–29/42), and over 20 uncatalogued teeth or tooth fragments. FTA-30 site.

Description. The shape of the teeth ranges from moderately laterally compressed to almost rounded in cross-section

(BW/FABL ratio between 0.39 and 0.97; M, 0.64; Table 1). The more laterally compressed teeth possibly derive from more posterior tooth loci. A posterior tooth position is also indicated by a posterior inclination of the crown tip (Text-fig. 3Q–R). The teeth from anterior positions have straighter crowns (Text-fig. 3O–P). The most posterior teeth have relatively small, D-shaped crowns in lateral view, with the crown tip shifted strongly distally. There is no constriction between crown and root. The posterior carina is serrated along the entire crown height. Along the anterior carina denticles occur at about one-half of the crown height (ACL/TCH, 0.39–0.89; M, 0.54), only in ZIN PH 28/42 do they occupy almost the entire crown height (Text-fig. 3U–V). There is a significant difference in height between the anterior and posterior denticles, the latter being at

TABLE 1. Measurements of teeth of Tetanurae indet. from the FTA-30 site, Sarykamysai 1, Kyrgyzstan; Balabansai Svita, Middle Jurassic (Callovian).

Specimen ZIN PH	ACL	TCH	FABL	BW	Anterior denticles per 1 mm	Posterior denticles per 1 mm	ACL/TCH	BW/FABL	DSDI
7/42	19.75	31.50	17.00	11.45	4.5	4.0–4.5	0.63	0.67	1.000–1.125
8/42	15.85	31.15	11.85	10.00	– *	4.0	0.51	0.84	–
9/42	12.70	26.75	11.95	5.95	5.0	4.5	0.48	0.50	1.111
10/42	16.35	30.05	12.25	11.90	– *	– *	0.54	0.97	–
11/42	12.95	24.20	10.85	5.95	– *	4.0	0.54	0.55	–
12/42	– **	21.05	8.65	6.70	– *	3.5–4.0	–	0.78	–
13/42	15.75	– **	– **	– **	5.0	4.5	–	–	1.111
14/42	7.95	18.65	7.00	5.05	5.0	4.5	0.43	0.72	1.111
15/42	6.85	13.00	6.60	3.65	5.0	4.5	0.53	0.55	1.111
16/42	5.15	13.20	6.70	4.30	– *	4.5	0.39	0.64	–
17/42	– **	– **	5.95	2.95	5.5	4.5	–	0.50	1.222
18/42	5.40	9.15	3.25	3.00	7.0	5.0	0.59	0.92	1.400
19/42	9.95	16.95	8.00	4.30	5.0	4.0–4.5	0.59	0.54	1.111–1.250
20/42	– **	10.20	6.75	3.55	– *	4.5	–	0.53	–
26/42	17.10	44.40	17.50	8.85	– *	3.5–4.5	0.39	0.51	–
27/42	– **	– **	21.80	13.40	– **	3.0	–	0.62	–
28/42	15.10	16.95	9.70	3.75	5.0	4.5–5.0	0.89	0.39	1.111
29/42	2.60	4.85	3.50	2.15	– *	5.0–5.5	0.54	0.61	–

*Denticles completely worn down. **The crown is not complete.

least twice as high, but the difference in length is not great: there are 4.5–7.0 anterior denticles per 1 mm and 3.0–5.5 posterior denticles per 1 mm (DSDI, 1.0–1.4; M, 1.139). The posterior denticles are rectangular in shape; some are slightly hooked apically, and have relatively deep blood grooves orientated perpendicularly to the tooth edge (Text-fig. 4A). The anterior denticles are rounded, with the main axis orientated perpendicular to the tooth edge, and with very shallow blood grooves (Text-fig. 4B). In ZIN PH 26, 28/42, and in other teeth with better preserved crown surfaces, there are very faint transverse wrinkles on the enamel next to the serrations, visible only in oblique light. In none of the teeth do the blood grooves extend to the crown surface. Two teeth have the anterior carina slightly shifted inwards to the lingual surface. One of these teeth, ZIN PH 14/42, with a straighter and somewhat rounded crown (BW/FABL, 0.72), less lingually deflected anterior carina and sigmoidally bent posterior carina, could be an anterior dentary tooth. Another tooth, ZIN PH 18/42 (Text-fig. 4B), with an almost rounded crown cross-section (BW/FABL, 0.92) and more posteriorly inclined crown tip, more lingually deflected anterior carina, and straight posterior carina, could be a premaxillary tooth. The tooth ZIN PH 16/42, with a relatively straight crown, BW/FABL, 0.64, sigmoidally curved posterior carina, and a very short and not lingually displaced anterior carina (ACL/TCH, 0.39; anterior denticles completely worn down), could also be an anterior dentary tooth from a somewhat more distal position than ZIN PH 14/42. One tooth, ZIN PH 28/42 (Text-fig. 3U–V), is unusual in having an elongate anterior carina that extends to the crown–root boundary and is not displaced lingually. This tooth also differs from the other teeth from FTA-30 in having a relatively narrow crown, with the lowest value for BW/FABL (0.39).

Measurements. See Table 1.

Discussion. The teeth described above represent the typical plesiomorphic dinosaurian type ('ziphodont' teeth; Sander 1997) and do not show modifications characteristic for some theropods with more specialized dentition (e.g. Spinosauridae, Carcharodontosauridae, Troodontidae, *Richardoestesia* Currie *et al.*, 1990). Identification of such isolated teeth is quite difficult, especially for teeth from Jurassic deposits. The current basis for identifying isolated teeth (e.g. Zinke 1998; Rauhut 2000; Alifanov and Sennikov 2001) is largely influenced by data on much better known teeth of Late Cretaceous theropods (Currie *et al.* 1990; Farlow *et al.* 1991), while dentitions of diverse Jurassic theropods, known from complete skulls and skeletons, are still poorly described. Nesov (1995, p. 80) identified from FTA-30 teeth of small cf. 'Coeluridae' and medium-sized Megalosauridae. It is not clear what he meant by 'Coeluridae', possibly basal Coelurosauria in current usage (Hutchinson and Padian 1997). Both identifications seem doubtful. Some small teeth from FTA-30 (Text-fig. 4) can be compared with the posterior teeth of the Compsognathidae (Zinke 1998, text-fig. 2D–G), but they are not especially diagnostic because the

plesiomorphic dinosaurian type is also characteristic for many other small theropods. The lack of compsoognathid-like anterior teeth in FTA-30, with sharp-edged but unserrated anterior carinae, or cone-shaped crowns lacking serrations at all (first and second morphotypes of Zinke 1998), advocates against the presence of this taxon in the assemblage. It is more likely that the small teeth from FTA-30 with fewer and proportionally larger denticles (Text-fig. 4) belong to juvenile individuals, as is the case in other theropods (Currie *et al.* 1990). Thus, we have no evidence for the presence of more than one theropod taxon in FTA-30. All variations in tooth shape and size, described above, can be attributed to variation within the ontogenetic age or position in the jaw. Attribution of this taxon to 'Megalosauridae' is not supported, because *Megalosaurus* Buckland, 1824 itself cannot be unequivocally diagnosed and 'suprageneric taxa based on *Megalosaurus* are to date questionable' (Padian 1997, p. 416).

The lack of downpointing blood grooves extending onto the crown surface, which are present in some allosaurids (Zinke 1998, p. 186; Azuma and Currie 2000, fig. 4), prevents the attribution of the teeth from FTA-30 to the Allosauridae. These teeth resemble isolated teeth from the Upper Jurassic of Guimarota, Portugal, referred to as 'probable allosaurid teeth' (Zinke 1998, text-fig. 8E–I; Rauhut 2000, text-fig. 11.8a) in that they have an FABL/BW ratio of 2 : 1, anterior carinae covering about one-half of the crown height, and anterior and posterior denticles of similar basal width, with the posterior denticles distinctly longer. They differ, however, in the lack of blood grooves extending onto the crown surface and a median ridge on the lingual crown side bordered by longitudinal depressions.

The most distinctive character of the theropod teeth from the Balabansai Svita is the short anterior carina, extending to only about half of the crown height. This character is not typical for large theropods, such as the Carcharodontosauridae, Allosauridae or Tyrannosauridae, but is found in the Dromaeosauridae. This, together with a slightly lingually deflected anterior carina in some teeth (ZIN PH 18/42), and incipient disparity in size between anterior and posterior denticles, may suggest affinities of the Balabansai theropod with Dromaeosauridae. Moreover, the tooth morphotype of the Balabansai theropod exhibits characters more explicitly present in the Cretaceous velociraptorines (anterior carina not lingually displaced in most teeth, some teeth considerably laterally compressed, with BW/FABL ratio of about 0.5) and dromaeosaurines (lingual shift of the anterior carina in some anterior teeth). In *Dromaeosaurus* all teeth have a lingually displaced anterior carina (Currie *et al.* 1990). In *Saurornitholestes* the teeth are more laterally compressed, with a greater size disparity between anterior and

posterior denticles, and posterior denticles that are more apically hooked, with wider blood grooves compared with the Balabansai theropod (Currie *et al.* 1990). The Balabansai theropod teeth possibly represent a morphotype that may be plesiomorphic compared with more derived Cretaceous dromaeosaurids. Thus, the Balabansai theropod might be a taxon belonging to a stem-group of the Dromaeosauridae that branched off prior to the splitting of the clade into the Dromaeosaurinae and Velociraptorinae. A similar stem-group dromaeosaurid is possibly present in the Upper Jurassic (Kimmeridgian) Guimarota locality in Portugal. Zinke (1998) referred one premaxillary tooth to *cf. Dromaeosaurus* sp. and 28 teeth to a velociraptorine dromaeosaurid, from a sample of 440 isolated theropod teeth from the Guimarota coal mine. It seems more probable that one dromaeosaurid-like taxon is present in the fauna and the tooth morphotype with lingually displaced anterior carina, referred to as '*cf. Dromaeosaurus* sp.', is a premaxillary or anterior dentary tooth of this theropod; its more posterior teeth lack a lingual displacement of the anterior carina, as in the Balabansai theropod.

Recently, dromaeosaurid-like teeth were described from a number of Middle and Upper Jurassic localities in Europe (Metcalf and Walker 1994; Zinke 1998; Rauhut 2000) and North America (Chure 1995). Diverse Lower Cretaceous dromaeosaurids are known from North America (Ostrom 1969; Kirkland *et al.* 1993; Brinkman *et al.* 1998), Europe (Zinke and Rauhut 1994; Rauhut and Zinke 1995), Siberia (Averianov and Skutschas 2000; Leshchinskiy *et al.* 2000) and China (Dong 1997). The almost pan-Laurasian distribution of dromaeosaurids in the Lower Cretaceous, together with their relatively good Middle and Upper Jurassic fossil record and their sister-group relationships with the Upper Jurassic Archaeopterygidae, suggests that this group had a relatively long and complex Jurassic evolutionary history.

Theropod teeth quite similar to those from the Balabansai Svita, in particular having a short anterior carina and a rounded anterior crown face below it, are known from the Lower Cretaceous of Japan (Manabe and Barrett 2000, pls 41–42) and Mongolia (Osborn 1924, text-figs 5–6; the holotype and paratype of *Prodeinodon mongoliense* Osborn, 1924, *nomen dubium*).

SAUROPODOMORPHA Huene, 1932

SAUROPODA Marsh, 1878

NEOSAUROPODA Bonaparte, 1986

NEOSAUROPODA indet.

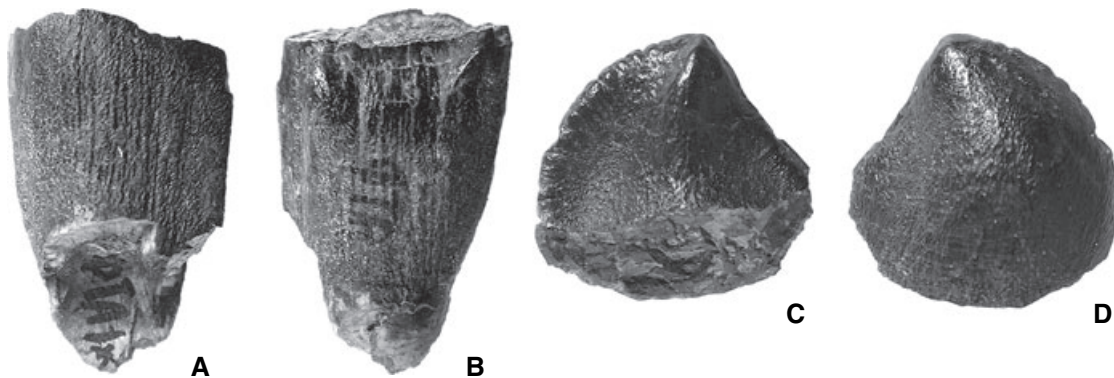
Text-figures 5–6

1990 *cf.* Camarasauridae Kaznyshkin, pl. 10, fig. 22.

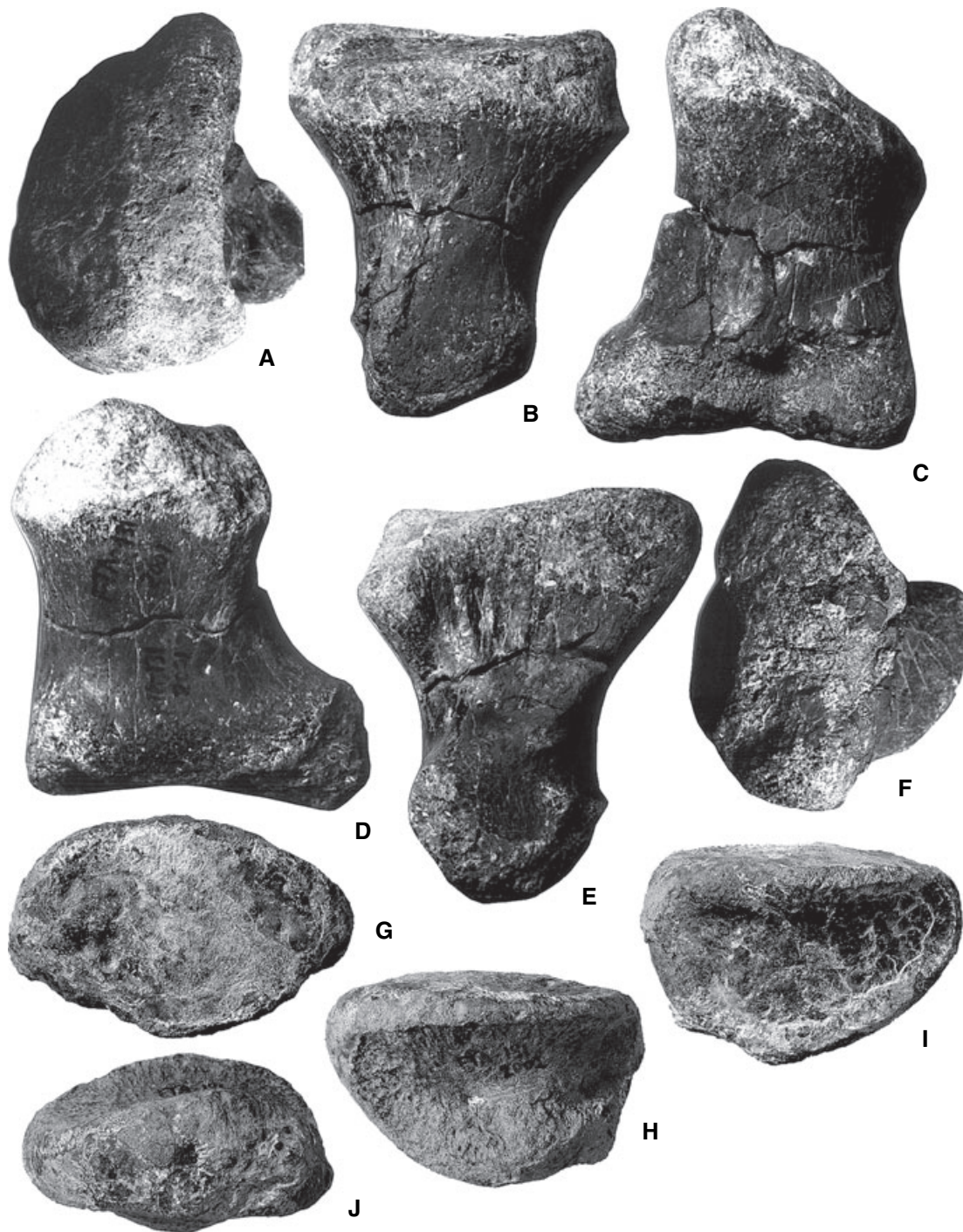
1995 *cf.* Camarasauridae Nesov, p. 80.

Material. A heavily worn tooth (ZIN PH 6/42), FTA-1zh site; the apex of a tooth crown (ZIN PH 21/42), FTA-131 site; a left metatarsal I (ZIN PH 22/42) and a right manual phalanx V-1 (ZIN PH 38/42), FTA-131 site.

Description. ZIN PH 21/42 represents the most apical portion of the tooth crown. The crown is evidently broad, spatulate and asymmetrical, with the apex distally deflected, mesial carinae greatly convex, and distal carina concave at the apex and convex more distally. The mesial carina bears coarse, poorly differentiated denticles 0.7–1.0 mm in size. The distal carina bears much smaller, almost indistinguishable denticles, and two small wear facets, one near the apex and another near the preserved distal end. The labial crown face is convex. On the lingual crown face there is a gently convex and oblique ridge leading to the crown apex and bordered by mesial and distal depressions. The crown enamel is wrinkled, with an irregular texture of short subvertical branching striae (Text-fig. 5).



TEXT-FIG. 5. Sauropod teeth, Neosauropoda indet., from the Middle Jurassic (Callovian) Balabansai Svita, northern Fergana Valley, Kyrgyzstan, in two side views. A–B, ZIN PH 6/42, heavily worn tooth, FTA-1zh site; $\times 1.3$. C–D, ZIN PH 21/42, apex of the tooth crown, FTA-131 site; $\times 2.7$.



TEXT-FIG. 6. Sauropod isolated limb bones, Neosauropoda indet., from the Middle Jurassic (Callovian) Balabansai Svita, northern Fergana Valley, Kyrgyzstan. All bones from the FTA-131 site. A–F, ZIN PH 22/42, left metatarsal I, in proximal (A), medial (B), posterior (C), anterior (D), lateral (E) and distal (F) views. G–J, ZIN PH 38/42, right manual phalanx V-1, in proximal (G), anterior (H), posterior (I) and distal (J) views. All $\times 0.54$.

The crown in ZIN PH 6/42 is relatively broad mesiodistally and narrow buccolingually, tapering towards the root. More than half of the crown is removed by wear. The single wear facet is perpendicular to the long axis of the crown and asymmetric-

ally lenticular in shape (somewhat D-shaped), with a more convex labial side. The lingual crown side bears a prominent depression in the centre and is generally concave; the labial crown side is slightly convex. There are no denticles preserved in

the remaining part of the crown. The crown is considerably constricted near the root, which is about half the length of the preserved part of the crown. The crown enamel is wrinkled, with an irregular texture of subvertical striae and pits (Text-fig. 5).

The metatarsal I is a relatively short, massive bone with the articular surfaces not fully ossified. Its proximal condyle is crescent-shaped, with a slightly concave lateral margin and convex medial margin. The proximal condyle is markedly elongated anteroposteriorly and its long axis is perpendicular to that of the distal condyle. The preserved (ossified) portion of the proximal articular surface faces dorsomedially. The medial and anterior bone surfaces are gently concave (dorsoventrally) and the lateral and posterior surfaces are more deeply concave. On the lateral surface at the anterior and posterior ends of the proximal margin there are two small, poorly defined (not well ossified) articulation surfaces for the second metatarsal. The laterodistal portion of the bone bears a prominent laterodistal process, which forms up to one-third of the distal transverse breadth of the condyle. On the anterior surface, close to the root of the laterodistal process, there is a distinct vascular foramen. The distal end is elongated mediolaterally, kidney-shaped, and not fully ossified.

The proximal phalanx of the fifth manual digit is short (almost twice as wide as it is long) and massive with fully ossified articulation surfaces. The proximal articulation facet is oval and has an almost flat surface that is orientated vertical to the long axis (proximo-distal) of the bone; it represents the anteroposteriorly widest part of the bone. The distal articulation facet is slightly convex and orientated somewhat medially. The dorsal (anterior) surface of the phalanx is concave with a small oval foramen in the middle (longitudinal diameter of the foramen about 5.5). Owing to the medial orientation of the distal articulation facet, the bone is somewhat wedge-shaped with a broadly rounded lateral side and a much shorter medial side. The posterior (palmar) surface of the phalanx is almost flat, but becomes slightly convex towards the proximal articulation facet.

Measurements. The maximum preserved lengths of the tooth crowns are 11.05 (ZIN PH 6/42, measured along the wear surface) and 12.9 (ZIN PH 21/42). ZIN PH 22/42, metatarsal I: maximum length 135, proximal end maximum width 80, proximal end anteroposterior (= ?dorsopalmar) diameter 118, distal end maximum width 108, distal end anteroposterior diameter 56. ZIN PH 38/42, right manual phalanx V-1: maximum length 65, proximal end maximum width 100, proximal end anteroposterior diameter 60, distal end maximum width c. 60, distal end anteroposterior diameter 37.

Discussion. The teeth described display three eusauropod synapomorphies: (1) spatulate tooth crown, with lingual side concave and labial side convex; (2) enamel with wrinkled surface; and (3) precise crown-to-crown occlusion, suggested by the well-developed wear facet in ZIN PH 6/42 (characters 32:1, 33 and 35 of Wilson and Sereno 1998). The presence of another eusauropod

synapomorphy, V-shaped wear facets (character 36:1 of Wilson and Sereno 1998), cannot be demonstrated with certainty. The wear facet in ZIN PH 6/42 could have been formed by unified mesial and distal wear facets. In any case, this wear facet is different from the elliptical wear facets on the teeth of diplodocids and the narrow-crowned teeth of titanosaurs. The absence of tooth denticles was cited as a synapomorphy of Neosauropoda (Wilson and Sereno 1998, character 78), in spite of their presence in at least some teeth of the neosauropods *Camarasaurus* Cope, 1877 and *Brachiosaurus* Riggs, 1903. Teeth similar to ZIN PH 21/42, with a convex and coarsely denticulated mesial margin and a concave posterior margin with finer and fewer denticles, are present in the Middle–Late Jurassic Chinese euhelopodids *Datousaurus* Dong and Tang, 1984, *Omeisaurus* Young, 1939, and *Mamenchisaurus* Young, 1954 (Dong and Tang 1984, pl. 2, figs 1–2; He *et al.* 1988, text-figs 16–17; Zhang and Chen 1996, text-fig. 11). This tooth morphology is apparently primitive for Eusauropoda and probably does not indicate any special relationships of the Balabansai sauropod with the euhelopodids.

A well-developed laterodistal process on the first metatarsal is considered to be diagnostic for the Diplodocidae (e.g. McIntosh *et al.* 1992), but this character seems to be more widely distributed in sauropods (Upchurch 1998; Averianov *et al.* 2002). The detailed structure of the laterodistal process in ZIN PH 22/42 and diplodocids is different; in the former its anterior surface is confluent with the anterior surface of the bone shaft, in diplodocids the anterior surfaces of both structures are separated by the antero-lateral margin of the bone (McIntosh 1990, text-fig. 16.19; McIntosh *et al.* 1992, text-fig. 5). ZIN PH 22/42 further differs from the first metatarsal in diplodocids in that it is more elongate and less massive.

The proximal phalanx of the fifth manual digit (ZIN PH 38/42; Text-fig. 6G–J) is quite similar in proportions and absolute dimensions to that of *Brachiosaurus brancai* Janensch, 1914, preserved in the right hand MB R 2249 (Janensch 1961, pl. 18, fig. 13). The well-developed distal articular surface indicates the presence of a functional phalanx V-2. The corresponding phalanges of the mounted skeleton of *Brachiosaurus brancai* are about 20 per cent wider and 60 per cent longer than the specimen from Kyrgyzstan. A more precise systematic position of the Balabansai sauropod cannot be determined based on the materials described, but they may belong to the new basal neosauropod taxon that has been described on the basis of a partial skeleton without a skull from the Balabansai ravine west of Tashkumyr (Alifanov and Averianov 2003).

ORNITHISCHIA Seeley, 1888

MARGINOCEPHALIA Sereno, 1986

PACHYCEPHALOSAURIA Maryanska and Osmolska, 1974

PACHYCEPHALOSAURIDAE Sternberg, 1945

Genus *FERGANOCEPHALE*, gen. nov.

Derivation of name. From the Fergana Valley and Greek κεφαλή, head, the common suffix for the pachycephalosaurid genera; gender neutral.

Type species. *Ferganocephale adenticulatum* sp. nov.

Diagnosis. (1) Teeth with both lingual and labial crown sides covered by enamel (-)*; (2) tooth crowns asymmetrical in side view, with one crown side (mesial?) being more convex than the opposite side (+)*; (3) main crown ridge poorly differentiated or not distinguishable (+)**; (4) vertical crown ridges leading to the marginal denticles very weak or absent (+)**; (5) marginal crown denticles absent or so small that they are eliminated by the slightest wear (+)**; (6) basal crown cingulum present (+)*; (7) basal cingulum more prominent on one crown side compared with the opposite side (on the lingual side in the maxillary teeth and on the labial side in the mandibular teeth) (+)*; (8) basal crown cingulum interrupted at the centre of the labial side in the maxillary teeth and of the lingual side in the mandibular teeth (+)**; (9) vertical wrinkled ornamentation could be present on the less concave crown side, adjacent to the basal cingulum interruption, at least in some teeth (+)**; (10) dentition monognathically heterodont, with the posterior teeth having lower and more asymmetrical crowns than the anterior teeth (+)* ('-' primitive character, '+' derived character, * character typical for Pachycephalosauria, ** autapomorphy).

Comparison and comments. Differs from all known pachycephalosaurian taxa by the autapomorphies (**) listed in the diagnosis. The weakness or absence of marginal denticles on the teeth described is possibly due partially to their preservational state. All teeth look water-worn, but it is more likely that they were swallowed and subsequently became slightly corroded when passing the digestive system (it can be assumed that pachycephalosaurs, as with many other herbivorous dinosaurs, frequently swallowed shed teeth). The sampled sediment bodies in the Balabansai Svita represent mudflows rather than fluvial deposits; therefore abrasion of the teeth by long-term transport in water is unlikely. However, the digestive corrosion cannot have been very strong because in none of the teeth has the thin enamel cover been removed. Therefore characters (4) and (5) can be used to diagnose the taxon even if they are somewhat influenced by corrosion. One of the teeth, referred here to *Ferganocephale adenticulatum* gen. et sp.

nov. (ZIN PH 4/42), was attributed by Nesov to a stegosaur according to his original label. This and other similar teeth from the Balabansai Svita cannot be attributed to Stegosauria because all stegosaurs, even the most basal taxa such as *Kentrosaurus* Hennig, 1915, *Huayangosaurus* Dong *et al.*, 1982, and *Tuojiangosaurus* Dong *et al.*, 1977, have well-developed marginal crown denticles supported by prominent ridges approximating the basal cingulum (e.g. Galton 1990, text-fig. 21.4; pers. obs.). In ankylosaurs the crown denticles and ridges are also very prominent and the enamel is usually characteristically wrinkled on both sides (e.g. Coombs 1990; Baszio 1997, pl. 11; pers. obs.). This precludes the attribution of the Balabansai ornithischian teeth to the Ankylosauria, which are now known from the approximately contemporaneous Toutunhe Formation in Junggar Basin, Xinjiang Uygur Autonomous Region of China (Dong 1993). These teeth also are not attributable to basal ornithopods, such as Fabrosauridae and Hypsilophodontidae, because of the lack of crown denticles and the presence of a prominent basal cingulum. The only dinosaurs that have teeth with weak vertical crown ridges and marginal denticles easily eliminated by wear at least from one crown side are the Pachycephalosauria (Maryanska 1990, p. 570, text-fig. 27.3B–H; Baszio 1997, pp. 42–43, pl. 8; Sereno 2000, text-fig. 25.1). Furthermore, the tooth crowns in pachycephalosaurs are asymmetrical with a prominent basal cingulum, and monognathically heterodont dentition with the crown asymmetry increasing posteriorly. This supports the attribution of the new Balabansai ornithischian taxon to that group.

Ferganocephale adenticulatum gen. et sp. nov. is the oldest known member of the Pachycephalosauria and the Marginocephalia, extending the known fossil record of the Marginocephalia (Sereno 2000, pp. 480, 508) by some 10–20 myr, depending on the exact age, Late Jurassic or Early Cretaceous, for the neoceratopsian *Chaoyangsaurus* Zhao *et al.*, 1999, the previous oldest marginocephalian.

Distribution and stratigraphical range. Balabansai Svita around Tashkumyr, northern Fergana valley. Late Middle Jurassic (Callovian).

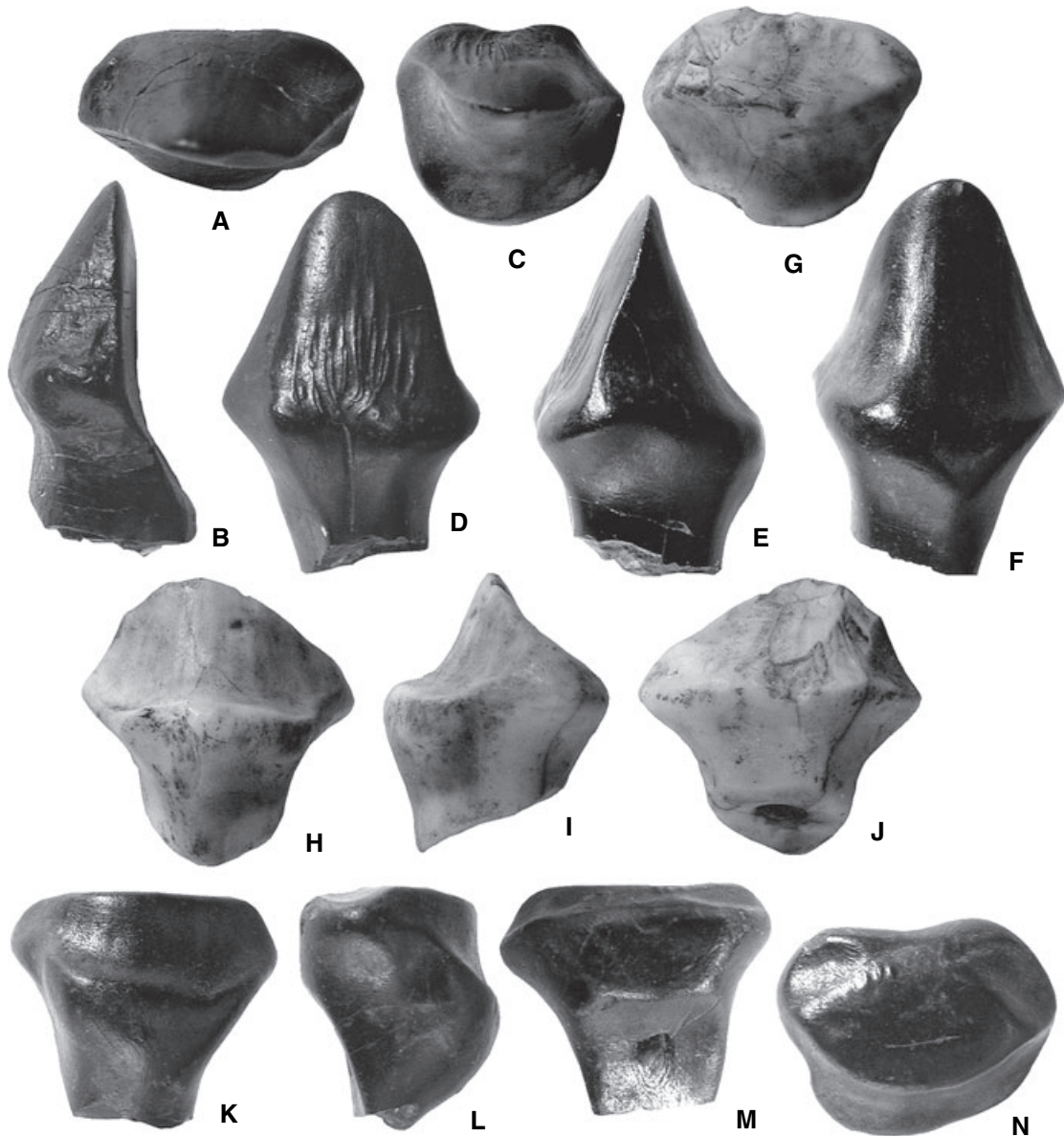
Ferganocephale adenticulatum sp. nov.

Text-figures 7–8

Derivation of name. Greek *a*, denoting absence, and *denticulum*, denticle, meaning absence or easy loss of vestigial marginal crown denticles by wear.

Holotype. ZIN PH 34/42, isolated unworn adult tooth.

Referred material. ZIN PH 5/42, possible juvenile tooth. ZIN PH 4, 30–33/42, four isolated adult teeth. Site FTA-30. ZIN PH



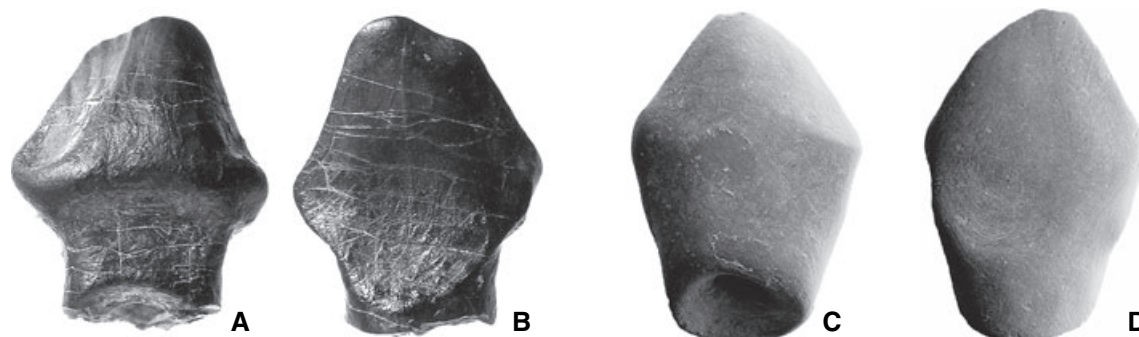
TEXT-FIG. 7. Teeth of the pachycephalosaurid *Ferganocephale adenticulatum* gen. et sp. nov. from the Middle Jurassic (Callovian) Balabansai Svita, northern Fergana Valley, Kyrgyzstan. A–B, ZIN PH 31/42, adult tooth, FTA-30 site, in occlusal (A) and anterior or posterior (B) views. C–F, ZIN PH 34/42, holotype, unworn adult tooth, FTA-30 site, in occlusal (C), side A (D), anterior or posterior (E) and side B (F) views. G–J, ZIN PH 36/42, adult posterior tooth, FBX-23 site, in occlusal (G), side B (H), anterior or posterior (I) and side A (J) views. K–N, ZIN PH 33/42, worn adult tooth, FTA-30 site, in side B (K), anterior or posterior (L), side A (M) and occlusal (N) views. All $\times 5-8$.

35/42, isolated heavily worn adult tooth. Site FTA-31. ZIN PH 36/42, isolated adult posterior tooth. Site FBX-23.

Description. The holotype is the best preserved specimen (Text-fig. 7C–F). It has a high and slightly asymmetrical crown, with one crown edge (mesial?) more convex than the opposite one. No marginal crown denticles or vertical crown ridges leading to the denticles are preserved, although the crown is not worn at all. The crown side A (labial for maxillary teeth and lingual for mandibular teeth) is almost flat and bears distinct and regular subver-

tical enamel wrinkles at the centre, radiating from the cingulum hiatus. The opposite crown side B is slightly concave vertically and convex horizontally. The basal crown cingulum is more prominent on side B. On this side the middle part of the basal cingulum extends somewhat antapically and on the opposite side (A) it is interrupted. This interruption continues into a shallow vertical groove along the root surface. The root is narrower than the crown and oval in cross-section.

The remaining teeth correspond to the holotype morphology except that some have weak vertical crown ridges, possibly



TEXT-FIG. 8. Teeth of the pachycephalosaurid *Ferganocephale adenticulatum* gen. et sp. nov. from the Middle Jurassic (Callovian) Balabansai Svita, northern Fergana Valley, Kyrgyzstan. A–B, ZIN PH 4/42, worn adult tooth, FTA-30 site, in side A (A) and side B (B) views; $\times 4.4$. C–D, ZIN PH 5/42, possible juvenile tooth (SEM micrograph), FTA-30 site, in side A (C) and side B (D) views; $\times 12.8$.

leading to marginal crown denticles, but which are not preserved in any of the specimens examined. The teeth also show variation in the crown height and asymmetry, which can be interpreted as monognathic heterodonty. In the holotype and ZIN PH 31/42 the crown is high and the crown asymmetry is very weak. These teeth apparently derive from the anterior portion of the jaw. In ZIN PH 31/42 the crown is heavily worn, with the cingulum almost removed by wear from side B, but any distinct wear facet is not elaborated. The opposite morphotype is represented by ZIN 36/42 (Text-fig. 7G–J), where the crown is noticeably lower and more asymmetrical. The crown side B is vertically and horizontally concave. This tooth, with an apparently little-worn crown, bears very faint vertical crown ridges on side A. It most probably comes from the posterior part of the jaw.

In ZIN PH 4/42 (Text-fig. 8A–B) the basal cingulum is weakened at the centre of side A, but not interrupted. This is the only specimen attributed to this species that has a poorly differentiated median crown ridge on side A. This ridge is surrounded by shallow depressions mesially and distally, one of which (mesial?) bears faint parallel vertical crown ridges. The crown side B in ZIN PH 4/42 is deeply excavated by wear and the basal cingulum is almost eliminated. In ZIN PH 33/42 (Text-fig. 7K–N) the crown is almost completely worn down by wear, but on side A the remnants of the vertical wrinkled ornamentation can be seen. At the same time the basal cingulum on side B is almost untouched by wear in contrast to other specimens. In ZIN PH 33/42 the root is also resorbed from side B with a narrow pulp cavity opening into the resorption depression (Text-fig. 7M). Possibly this tooth was displaced by a replacement tooth. As a result its crown was turned towards side B, which led to the formation of an abnormal wear facet and prevented the basal cingulum on side B from becoming worn. In ZIN 33/42 there are very faint subvertical ridges preserved on the crown surface B.

One tooth (ZIN PH 5/42; Text-fig. 8C–D) is smaller than the other teeth and has a very faint basal cingulum. It is interpreted as a tooth of a juvenile individual.

Measurements. See Table 2.

TABLE 2. Measurements of teeth of *Ferganocephale adenticulatum* gen. et sp. nov. from FTA-30, FTA-31 and FBX-23 sites, near Tashkumyr, Kyrgyzstan; Balabansai Svita, Middle Jurassic (Callovian).

Specimen ZIN PH	TCH	FABL	BW
4/42	6.70	6.40	3.10
5/42	2.65	2.20	0.90
30/42	–	5.30	3.35
31/42	6.00	5.10	3.05
32/42	–	5.65	4.30
33/42	–	6.45	4.85
34/42	6.75	5.70	5.20
35/42	–	6.10	5.00
36/42	4.20	6.25	4.75

PALAEOBIOGEOGRAPHICAL ASPECTS

The Balabansai vertebrate assemblage can be compared with various Middle–Upper Jurassic vertebrate assemblages in China and Mongolia (Table 3). It is distinctly younger than the Lower Shaximiao assemblage of the Sichuan Basin, which contains more primitive cryptodiran turtles that retain mesoplastra: *Chengyuchelys* Young and Chow, 1953 and *Sichuanochelys* Ye and Pi, 1997 (Chengyuchelyidae: Yeh 1990; Ye and Pi 1997). The latter taxon is possibly not valid and based on juvenile specimens of *Chengyuchelys*. The Lower Shaximiao Formation is apparently contemporaneous with the Wucaiwan Formation in the northern Junggar Basin, as suggested by the presence of the common tritylodontid *Bienotheroides zigongensis* Sun, 1986 in both formations (Table 3). However, the vertebrate assemblages from these formations differ significantly in the composition of the dinosaur fauna, which can be at least partially explained by palaeo-zoogeographical factors.

TABLE 3. Selected Middle and Late Jurassic vertebrate assemblages from Fergana, Junggar and Sichuan basins, and Transaltai Gobi (compiled after Su 1974; Chow and Rich 1982, 1984; Dong *et al.* 1982; Dong and Tang 1983, 1984; He *et al.* 1983, 1988; Efimov 1988a, b, 1989, 1996; Zhang 1988; Barsbold *et al.* 1989; Dong 1989, 1990, 1992; Russell and Zheng 1990, 1994; Gao 1993, 2001; Zhao 1993; Currie and Zhao 1994; Peng and Brinkman 1994; Zhao and Currie 1994; Peng 1995, 1996; Gubin and Sinitza 1996; Lucas 1996; Wu *et al.* 1996; Zhang and Chen 1996; Ye and Pi 1997; Averianov 2000 and literature cited therein; Efimov *et al.* 2000; Sukhanov 2000; Maisch *et al.* 2001; Kurzanov *et al.* 2003; this report).

Sarykamyshsai 1, Fergana Basin, Kyrgyzstan;
 Balabansai Svita
 Pisces:
Polyacrodus balabansaiensis
Polyacrodus prodigialis
Palaeobates verzilini
 ?Ptycholepididae indet.
Ferganamia verzilini
 cf. Lepidotidae indet.
 Ichthyodectiformes indet.
Ferganoceratodus jurassicus
 Amphibia:
Ferganobatrachus riabinini
 Caudata indet.
 Testudinata:
Xinjiangchelys tianshanensis
 Choristodera:
 Choristodera indet.
 Squamata:
 Lacertilia indet.
 Crocodylomorpha:
Sunosuchus sp.
 Thalattosuchia indet.
 Pterosauria:
 Rhamphorhynchinae indet.
 Dinosauria:
 Theropoda:
 Tetanurae indet.
 Sauropoda:
 Neosauropoda indet.
 Pachycephalosauria:
Ferganocephale adenticulatum gen. et sp. nov.
 Mammalia:
 Docodonta:
Tashkumyrodon desideratus
 ‘Triconodonta’
 ?Amphilestidae indet.
 Several localities in Jiangujnmiao and Kelamaili areas
 in northern Junggar Basin, Xinjiang Uygur AR, China;
 Wucaiwan Formation
 Pisces:
 Pisces indet.
 Amphibia:
 ‘*Superstogyrinus ultimus*’, *nomen nudum*?

TABLE 3. (Continued).

Testudinata:
 Testudinata indet.
 Squamata:
 ‘*Archovaranus klameliensis*’, *nomen nudum*?
 Crocodylomorpha:
 Crocodylomorpha indet.
 Dinosauria:
 Theropoda:
 Coelurosauria indet.
Monolophosaurus jiangi
 Sauropoda:
Bellusaurus sui
Klamelisaurus gobiensis
Tianshanosaurus sp.
 Ornithopoda:
 Hypsilophodontidae indet.
 Ankylosauria:
 Ankylosauria indet.
 Theromorpha:
Bienotheroides zigongensis
 Several localities in Pingfengshan, Jiangujnmiao and
 Kelamaili areas in northern Junggar Basin, Xinjiang
 Uygur AR, China; Shishugou Group, Qigu Formation
 Amphibia:
 Temnospondyla indet.
 Testudinata:
Xinjiangchelys latimarginalis
Xinjiangchelys sp.
 Squamata:
 Lacertilia indet.
 Crocodylomorpha:
Sunosuchus junggarensis
 Dinosauria:
 Theropoda:
Sinraptor dongi
 Theropoda indet.
 Sauropoda:
Tianshanosaurus chitaiensis
Mamenchisaurus sinocanadorum
 Ornithopoda:
Gongbusaurus wucaiwanensis
 Theromorpha:
 Tritylodontidae indet.
 Mammalia:
 ‘Triconodonta’:
Klamelia zhaopengi
 Several localities in southern Junggar Basin,
 Xinjiang Uygur AR, China; Toutunhe Formation
 Pisces:
 Hybodontoidae indet.
 Ptycholepididae indet.
 Amphibia:
 cf. *Gobiops* sp.
 Testudinata:
Xinjiangchelys radiplicatus

TABLE 3. (Continued).

Crocodylomorpha:
Sunosuchus sp.
 Crocodylomorpha indet.

Dinosauria:
 Theropoda:
 Carnosauria indet.
 Ankylosauria:
Tianchisaurus nedegoapeferima

Several localities in southern Junggar Basin,
 Xinjiang Uygur AR, China; Qigu Formation

Amphibia:
 ?Capitosauroida indet.

Testudinata:
Xinjiangchelys sp. nov.

Crocodylomorpha:
 Crocodylomorpha indet.

Dinosauria:
 Sauropoda:
 Sauropoda indet.

Dashanpu quarry in Sichuan 'red bed' Basin, Sichuan, China;
 Lower Shaximiao Formation

Pisces:
 Hybodontidae indet.
 Ceratodontidae indet.
 Semionotidae indet.

Amphibia:
Sinobrachyops placenticephalus

Testudinata:
Chengyuchelys baenoides
Chengyuchelys zigongensis
Sichuanchelys chowi

Crocodylomorpha:
Hsisosuchus dashanpuensis
 Telesauridae indet.

Pterosauria:
Angustinaripterus longicephalus

Dinosauria:
 Theropoda:
Gasosaurus constructus
Xuanhanosaurus qilixiaensis
Szechuanosaurus zigongensis

Sauropoda:
Protognathosaurus oxyodon
Shunosaurus lii
Abrosaurus gigantorhinus
Datousaurus bashanensis
Omeisaurus tianfuensis
Omeisaurus junghsiensis
Abrosaurus gigantorhinus

Ornithopoda:
Agilisaurus louderbacki
Xiaosaurus dashanpuensis

Stegosauria:
Huayangosaurus taibaii

TABLE 3. (Continued).

Theromorpha:
Bienotheroides zigongensis
Polistodon chuannanensis

Wujiaba quarry and numerous other localities in
 Sichuan 'red bed' basin, Sichuan, China;
 Upper Shaximiao Formation

Pisces:
Yuchoulepis szechuanensis
 Ptycholepididae indet.
Ceratodus szechuanensis

Testudinata:
Xinjiangchelys chungkingensis
Xinjiangchelys radiplicatus

Sauropterygia:
 pliosaurs

Crocodylomorpha:
Sichuanosuchus huidongensis
Hsisosuchus chungkingensis

Dinosauria:
 Theropoda:
Sinocoelurus fragilis
Szechuanosaurus campi
Yangchuanosaurus shangyouensis
Yangchuanosaurus magnus
Sinraptor hepingensis

Sauropoda:
Mamenchisaurus constructus
Mamenchisaurus hochuanensis
Omeisaurus junghsiensis
Omeisaurus fuxiensis

Ornithopoda:
Gongbusaurus shiyii
Yandusaurus hounghensis

Stegosauria:
Chialingosaurus kuani
Toujiangosaurus multispinus
Chungkingosaurus jiangbeiensis

Theromorpha:
Bienotheroides wansiensis

Mammalia:
 Symmetrodonta:
Shuotherium dongi

Shar Teg, Altai Gobi Desert, Mongolia; Shar Teg Beds*,
 Ulan Malgait Beds** or both***

Pisces:
 Hybodontidae indet.*
 Paleonisciformes***
*Ceratodus shartegensis**
*Ceratodus temporarius**
*Ceratodus porrectus**

Amphibia:
*Gobiops desertus**

Testudinata:
*Shartegemys laticentralis**
*Shartegemys elegans**

TABLE 3. (Continued).

<i>Annemys latiens</i> **
<i>Annemys levensis</i> **
<i>Annemys</i> sp.*
Crocodylomorpha:
<i>Sunosuchus shartegensis</i> *
<i>Shartegosuchus asperopalatum</i> *
<i>Nominosuchus matutinus</i> *
<i>Nominosuchus arcanus</i> **
<i>Adzhosuchus fuscus</i> **
Dinosauria:
Theropoda indet.*?
a sauropod, allied to <i>Mamenchisaurus</i> **
Mammalia:
Docodonta:
<i>Tegotherium gubini</i> *

The Balabansai vertebrate assemblage is most similar to that from the Qigu Formation in the northern and southern Junggar Basin (Table 3), as indicated by the presence in both of the more derived (lacking mesoplastra) cryptodiran turtle *Xinjiangchelys* Yeh, 1986, the goniopholidid crocodile *Sunosuchus* Young, 1948, and similar temnospondyl amphibians, but differs by the presence of dipnoans and pachycephalosaurs and absence of ankylosaurs and tritylodontids. These differences, however, may be a result of environmental factors. A similar vertebrate assemblage has been collected from the Toutunhe Formation, underlying the Qigu Formation, in the southern Junggar Basin (Maisch *et al.* 2001). The Toutunhe Formation is dated on the basis of palynoflora as Bathonian and the Qigu Formation as Callovian (Wang 2001). This strengthens a close correlation between the latter and the Balabansai Svita, which has also been dated on the basis of palynoflora as Callovian (Aliiev *et al.* 1981). Eberth *et al.* (2001, text-fig. 2) dated the Qigu Formation as Oxfordian and the Toutunhe Formation as Bathonian–Callovian, but the reasons for this are not evident from their paper. The famous vertebrate assemblage from the Upper Shaximiao Formation (so-called *Mamenchisaurus* fauna), sharing *Xinjiangchelys* with the Qigu and Balabansai assemblages (Table 3), may be Callovian. The age of the Upper Shaximiao Formation was considered to be Middle Jurassic based on invertebrates and fishes, or as early Late Jurassic based on dinosaurs (Su 1974; Chow and Rich 1982; Sun and Li 1985; Dong 1992). A Middle Jurassic (Callovian) age seems to be more acceptable because the mostly endemic *Mamenchisaurus* dinosaur fauna does not invite any comparison with well-known Late Jurassic dinosaur faunas of North America and Africa (Lucas 1996; contra Dong 1992). On the other hand, this fauna has at least one similar element with the Middle Jurassic (Callovian) fauna of South America: the sauropod *Tehuelchesaurus* Rich *et al.*, 1999 resembles the Chinese *Omeisaurus* Young, 1939 from

the *Mamenchisaurus* fauna (Rich *et al.* 1999). The Shar Teg vertebrate assemblage from the Transaltai Gobi in Mongolia, comprising more derived xinjiangchelyid turtles (Sukhanov 2000) and a docodont (Tatarinov 1994), is distinctly younger than the Balabansai assemblage and can be confidently placed within the Late Jurassic.

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