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FERGANASAURUS VERZILINI, GEN. ET SP. NOV., A NEW NEOSAUROPOD (DINOSAURIA, SAURISCHIA, SAUROPODA) FROM THE MIDDLE JURASSIC OF FERGANA VALLEY, KIRGHIZIA

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ABSTRACT—A partial sauropod skeleton from the Middle Jurassic (Callovian) Balabansai Formation in Kirghizia, comprising two dorsal and 16 caudal vertebrae, pelvis and limb bones is described and referred to *Ferganasaurus verzilini*, gen. et sp. nov. The manus is known only from drawings as original material has been lost; foot bones, except the astragalus, are unknown. *Ferganasaurus* forms an unresolved polytomy with neosauropods *Jobaria*, Diplodocoidea (Nemegtosauridae, Rebbachisauridae, Diplodocidae, and Dicraeosauridae), and Macronaria (*Camarasaurus*, *Haplocanthosaurus* and Titanosauriformes). The neosauropod characters of *Ferganasaurus* include five coossified sacral vertebra, metacarpal proximal ends subtriangular, composite proximal articular surface of metacarpus U-shaped, tibia with subcircular proximal end, astragalar ascending process extends to the posterior margin of the astragalus, and astragalus wedge-shaped in anterior view. *Ferganasaurus* is one of the oldest known neosauropods, and possesses two primitive characters unusual for a neosauropod (femur shaft with sigmoid curve, and fourth trochanter of the femur blade-like with acuminate apex).

?1 *Ferganasaurus verzilini* gen. & sp. n., *Ferganasaurus Jobaria*, Diplodocoidea (Nemegtosauridae, Rebbachisauridae,
?2 Diplodocidae Dicraeosauridae) Macronaria (*Camarasaurus*, *Haplocanthosaurus* Titanosauriformes). *Ferganasaurus*. *Ferganasaurus*.

INTRODUCTION

In July 1966 the geological team of the Leningrad State University, led by N. N. Verzilin, found a partial sauropod skeleton in the Middle Jurassic rocks of the upper part of the Balabansai Formation at Balabansai in the southern foothills of Chatkal Range, 5 km west of Tashkumyr, northern Fergana Valley, Kirghizia (Fig. 1). This was the first sauropod skeleton found in the USSR (Rozhdestvensky, 1968). It was excavated in August 1966 and July 1967 by a team from the Moscow Paleontological Institute led by A. K. Rozhdestvensky, which recovered an essentially complete skeleton, lacking a skull, cervical and posterior caudal vertebrae, both hind feet and the right manus (Fig. 2). The length of the skeleton was estimated as 18–20 m (Rozhdestvensky, 1968, 1969). Unfortunately, very little was published about this important discovery.

In a preliminary two-page note, Rozhdestvensky (1968) referred this specimen to ''Cetiosauridae,'' meaning Diplodocoidea in current usage, and said that it probably should be referred to a new species or genus. In a popular book, Rozhdestvensky (1969:256) informally called this dinosaur ''ferganasaurus'' and noted that study of this find ''will open a new page in the history of dinosaurs and that this skeleton will serve not only as an original museum specimen, but also as an important scientific standard, necessary for study of known and future sauropod finds.'' Later Rozhdestvensky (1977:108) found that this dinosaur ''may prove to be related to *Apatosaurus* after material is fully studied and identified.'' No reasons for this and previous determinations were given. This important specimen was not studied and this discovery was almost totally unknown to western scientists (e.g., Weishampel, 1990; Hunt et al., 1994).

A set of ink drawings of some bones from the Balabansai skeleton were prepared in the Moscow Paleontological Institute, apparently for publication by A. K. Rozhdestvensky. However, we were not able to find any manuscript by A. K. Rozhdestvensky concerning this skeleton. These drawings are particularly important because they give details of the manus of the Balabansai sauropod, which is now missing. The majority of these illustrations are reproduced here. The complete left femur and the proximal fragment with the femoral head from the right femur of the Balabansai skeleton are now on exhibit at Orlov's Paleontological Museum in Moscow.

In 1967 N. N. Verzilin found in the middle-upper part of Balabansai Formation at Balabansai another partial sauropod skeleton, including pelvis bones, sacrum, partial femur, and some dorsal, sacral, and caudal vertebrae (Nessov, 1995:82). The fate of this skeleton is unknown, and it is possible that it was not excavated. An isolated, broad-crowned sauropod tooth referred to as cf. Camarasauridae was found in the lower-middle part of Balabansai Formation at Sarykamyshsai, 3 km east of Tashkumyr (Nessov, 1995:80). The Balabansai Formation at Sarykamyshsai contains a diverse fauna of Middle Jurassic vertebrates (Averianov, 2000, and references therein). An isolated tooth attributed to Camarasauridae indet. was found also in the lower part of Balabansai Formation at Kamyshbashi, southern Fergana valley, Uzbekistan (Kaznyshkin, 1990:pl. 10, fig. 22; Nessov, 1995:82). Finally, the *Ferganasaurus* site in Balabansai was relocated in September 2001 by the second author, Dr. T. Martin, A. S. Rezvyi and A. Bakirov, and now we can provide GPS coordinates for it. This team found also a spatulate denticulated sauropod tooth and the first metatarsal with a prominent laterodistal process in a new locality within the Balabansai Formation close to Sarykamyshsai. These new materials, which may belong to *Ferganasaurus*, will be described elsewhere.

Here we describe the Balabansai skeleton (PIN N 3042/1), discuss its taxonomic affinities, and assess its phylogenetic relationships. In sauropod systematics we generally follow Upchurch (1998). The sauropod anatomical terminology is after Wilson and Sereno (1998) and Wilson (1999).

Institutional Abbreviation—**PIN**, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

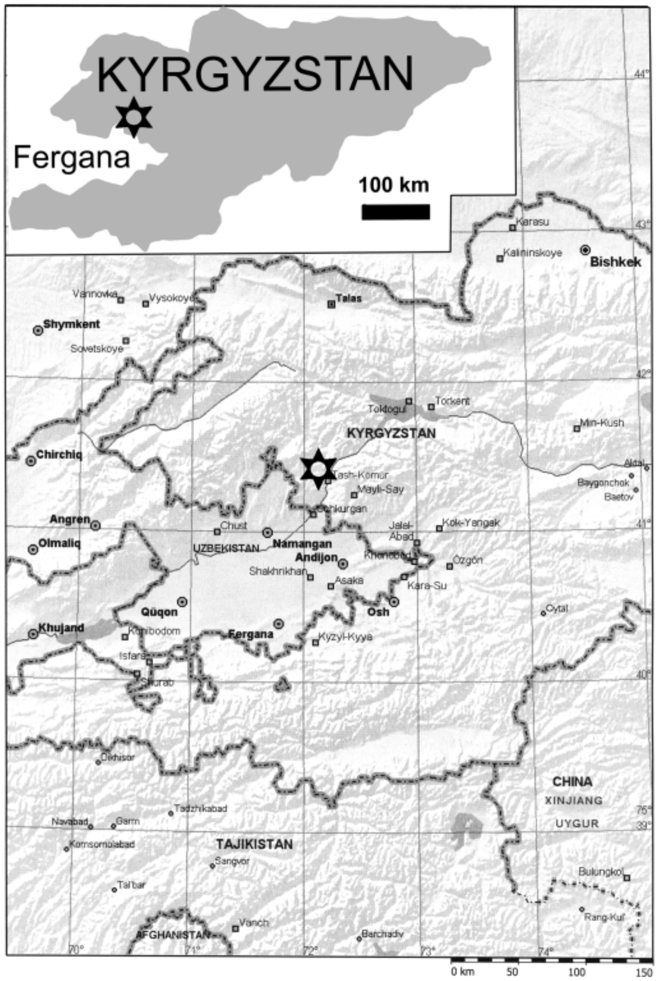

FIGURE 1. Geographic setting of the Balabansai locality (asterisk) in northern Fergana valley, Kirghizia.

Other Abbreviations—**EI**, Elongation index: length of a vertebral centrum divided by the width across its posterior face.

MATERIAL

According to description and photo published by Rozhdestvensky (1968), all sauropod bones excavated at Balabansai belong to a single individual and thus are considered under a common collection number (PIN N 3042/1). The preserved part of the vertebral column was found articulated and the relative position of caudals was marked in the field. We were not able to locate all elements in the collection reported as recovered by Rozhdestvensky (1968) (Fig. 2). At our disposal were the following bones: two incomplete posterior dorsals (possibly penultimate and ultimate), sacrum (majority of sacral ribs are broken off), caudals 1–13, 30, 31 (half of the centrum), and 33 (most of them have a neural arch variably damaged and lacking), left humerus, left ulna, left radius, left and right ilia lacking majority of the dorsal portion, left pubis and proximal portion of right pubis, left ischium and fragments of right ischium, left femur and proximal portion of right femur, left tibia, left fibula, left astragalus, and some unidentified bone fragments. The state of bone preservation is excellent, although the majority of caudals were deformed after death. The description of the manus is based on the preserved drawings only, as the original material is missing.

SYSTEMATIC PALEONTOLOGY

SAUROPODOMORPHA Huene, 1932
SAUROPODA Marsh, 1878
NEOSAUROPODA Bonaparte, 1986, incertae sedis
FERGANASAURUS, gen. nov.

Type Species—*Ferganasaurus verzilini*, sp. nov.

Diagnosis—The new taxon can be diagnosed by a combination of the following primitive (−) and derived (+) characters: (1) posterior dorsals slightly opisthocoelous (+); (2) posterior dorsals with pleurocoels (+); (3) centroparapophyseal lamina on dorsals present (+); (4) single midline lamina supporting hyposphene from below on dorsal neural arches present (+); (5) five co-ossified sacrals (+); (6) sacral spines fused (+); (7) anterior caudals slightly procoelous (+); (8) ''fan''-like caudal ribs on anterior caudals (+); (9) ischiadic peduncle of the ilium is greatly reduced (+); (10) proximal and distal portions of pubis located in the same plane (+); (11) femur shaft with sigmoid curve (−); (12) fourth trochanter blade-like with acu-

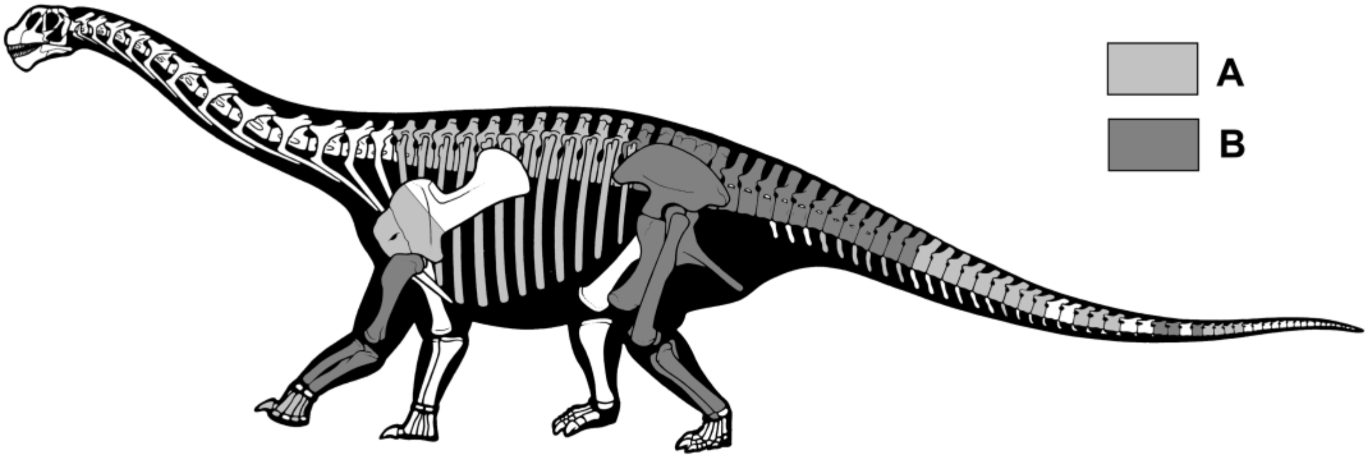

FIGURE 2. Excavated (**A**) and currently preserved in the collection (**B**) skeletal elements of *Ferganasaurus verzilini*, gen. et sp. nov. (PIN N 3042/1). **A** is based on the sketch provided by S. M. Kurzanov and report by A. K. Rozhdestvensky (1968). *Camarasaurus* skeleton (after Wilson and Sereno, 1998:foldout 1) is used for a sauropod outline.

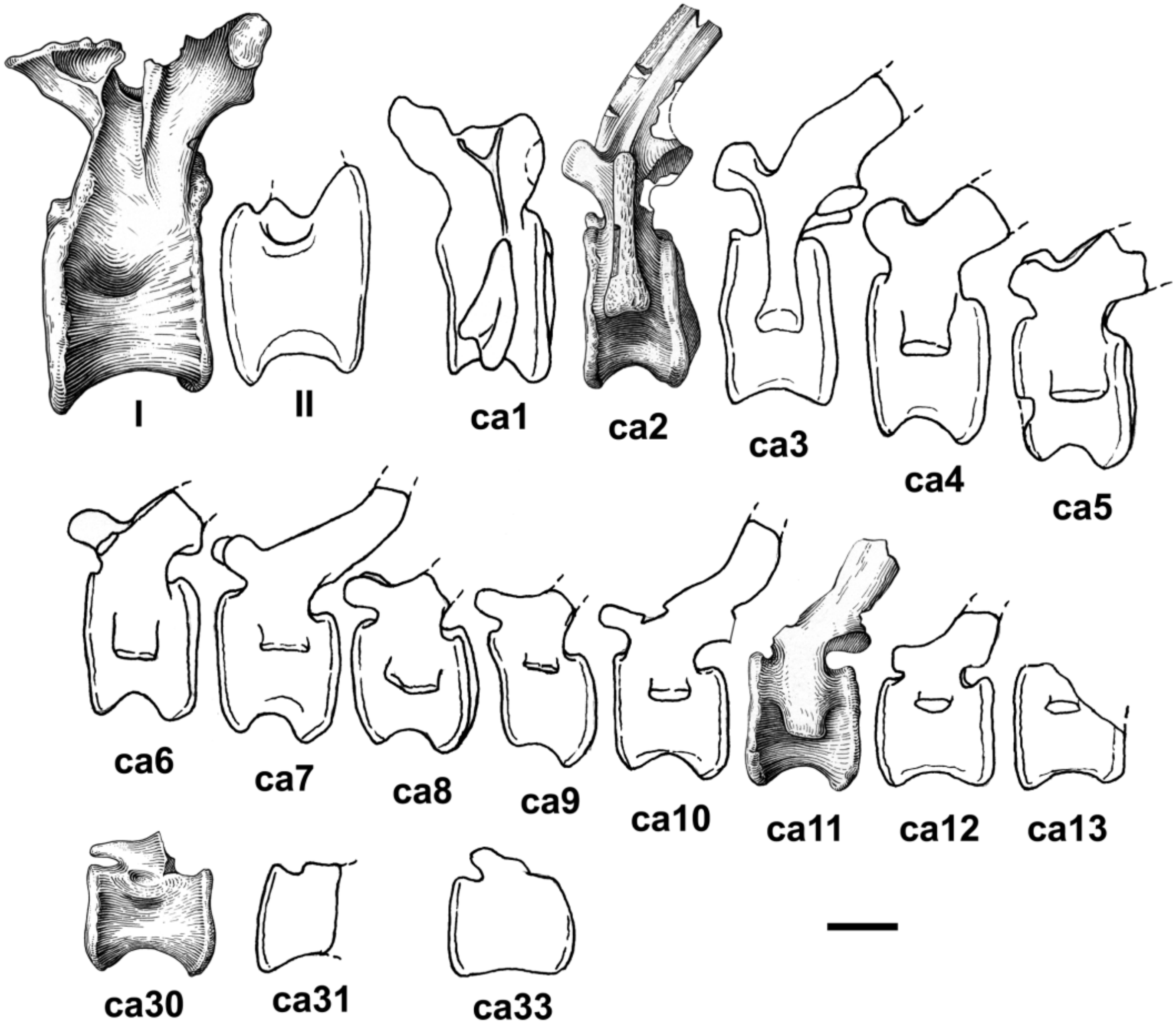

FIGURE 3. Posterior dorsal (I and II) and caudal (ca. 1–13, ca. 30–33) vertebrae of *Ferganasaurus verzilini*, gen. et sp. nov. (PIN N 3042/1) in lateral view. Scale bar equals 10 cm. Anterior end is to the left.

minate apex (−); (13) fourth trochanter situated on posteromedial margin of shaft (+); (14) tibia with subcircular proximal end (+); (15) cnemial crest of tibia laterally projecting (+); (16) fibular lateral trochanter present (+); (17) astragalus tapers medially (+); (18) astragalar ventral surface convex transversely (+).

Etymology—From Fergana valley and Latin ‘‘saurus,’’ a lizard.

Distribution—Middle Jurassic, Middle Asia.

FERGANASAURUS VERZILINI, sp. nov.

(Figs. 3–17)

Holotype—PIN N 3042/1, a partial skeleton.

Type Horizon and Locality—Balabansai Formation; Balabansai [a dried up water creek], N 41° 19′ 59″, E 72° 07′ 30″, southern foothills of Chatkal Range, approximately five km west of Tashkumyr [Tash-Kömür] city, northern Fergana Valley, Dzhalal-Abad [Jalal-Abad] Province, Kirghizia [Kyrgyzstan].

Age—Middle Jurassic (Callovian).

Diagnosis—As for the genus.

Distribution—Middle Jurassic, western border of the ancient Asian landmass, peri-Tethyan coastal plains.

Material—Holotype only.

Etymology—In honor of Prof. Nikita N. Verzilin, who found the holotype in 1966.

OSTEOLOGICAL DESCRIPTION

The Vertebral Column

Dorsal Vertebrae—There are two incomplete dorsals, marked in the field as I and II (Figs. 3, 4). Presumably these are penultimate and ultimate posterior dorsals, because they were found in association with the complete sacrum and a series of anterior caudals. The penultimate dorsal has the base of a neural arch preserved, including the left prezygapophysis. There is only a centrum from the ultimate dorsal. The centra

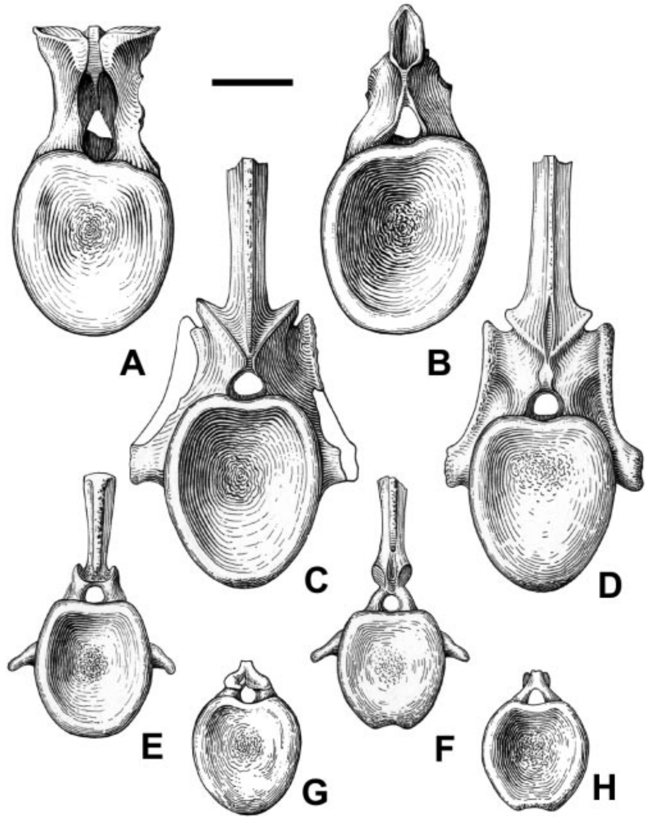

FIGURE 4. Penultimate dorsal (**A** and **B**) and caudal (**C** and **D**—ca. 2, **E** and **F**—ca. 11, **G** and **H**—ca. 30) vertebrae of *Ferganasaurus verzilini,* gen. et sp. nov. (PIN N 3042/1) in anterior (**A**, **C**, **E**, and **G**) and posterior (**B**, **D**, **F** and **H**) views. Scale bar equals 10 cm.

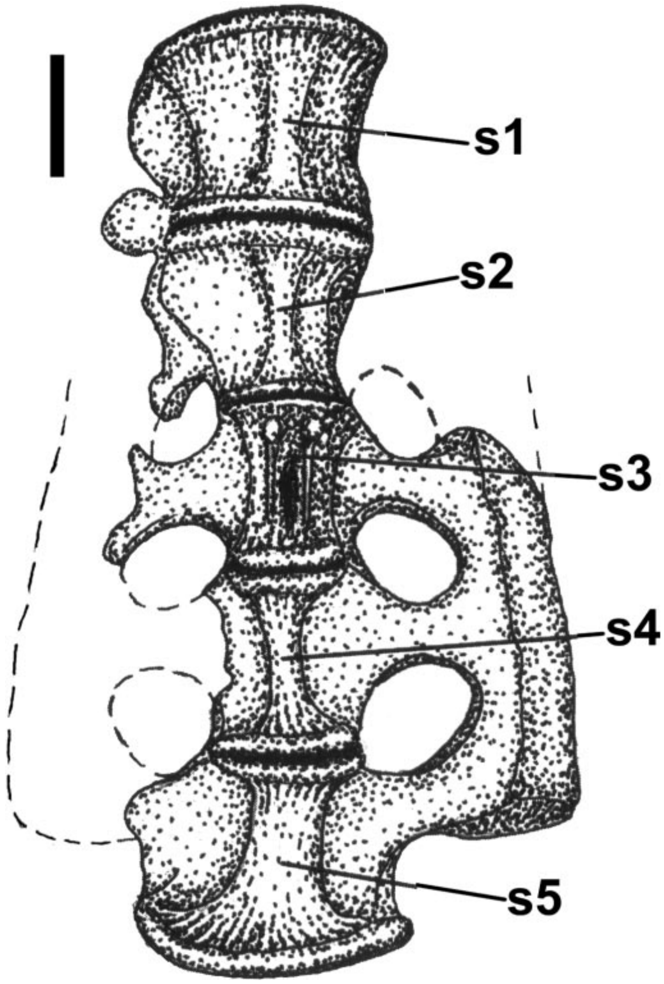

FIGURE 5. Sacrum of *Ferganasaurus verzilini,* gen. et sp. nov. (PIN N 3042/1) in ventral view. s1–s5—sacral vertebrae. Scale bar equals 10 cm.

of the posterior dorsals are only slightly opisthocoelous, the anterior end is not developed as a prominent ''ball,'' and the posterior end is only shallowly concave. The centra are relatively short anteroposteriorly, EI = 0.81 and 0.74 respectively. There is a moderately deep pleurocoel just below the neural arch on both posterior dorsals. It is a rather simple pit (''pseudopleurocoel'') which is not extensively ramified within the centrum. The neural canal is relatively large and laterally compressed. The prezygapophysis is relatively large, with a horizontally oriented articular facet, and does not protrude anteriorly beyond the level of the centrum. The medial margin of the prezygapophysis comes very close to the vertebral midline (probably due, in part, to postmortem deformation), and thus the presence of a hypantrum is unlikely. There is a distinct ridge (lamina) running posteriorly from the prezygapophysis towards the diapophysis (transverse process). The parapophysis is not preserved, and it was placed apparently relatively high on the neural arch. There is a single weakly defined lamina, running anterodorsally from the posterior margin of the neurocentral joint. The postzygapophysis is lacking, but a distinct centropostzygapophyseal lamina is preserved which runs posterodorsally from the posterior margin of the neurocentral joint towards the postzygapophysis. On the posterior face of the neural arch there is a ''hyposphenal'' ridge, extending from the ventral midline junction of the postzygapophyses to the top of the neural canal. The hyposphene area is missing and its presence cannot be established.

Sacrum—The sacrum is not coossified with the ilia (Fig. 5). The coossified sacrum (synsacrum) consists of five vertebrae. The first two are apparently dorsosacrals, the last one is a sacrocaudal, and the sacrals three and four are primordial sacrals (Wilson and Sereno, 1998). Alternatively, they may consists of a dorsosacral, three primary sacrals, and a caudosacral (Upchurch, 1998). The anterior face of the first centrum sacral and the posterior face of the fifth centrum sacral are oval in outline and slightly convex, not truly opisthocoelous. The maximum centrum width of the anterior face of the first sacral and the posterior face of the fifth sacral are 23 and 22 cm, respectively. The third sacral centrum is biconvex. It is the shortest centrum in the series: the centrum length decreases gradually from sacral vertebra one to sacral vertebra three and then gradually increases towards sacral vertebra five (16.5, 15.5, 14, 14.5, and 16.5 cm respectively, measured from the ventral side). The third sacral centrum is also the most narrow ventrally in the series. The ventral surfaces of the sacral centra are convex transversely and concave anteroposteriorly. All sacral centra except the third bear a weakly defined longitudinal ventral ridge. The third sacral centrum has two parallel ventral ridges, bordering a shallow groove. Pleurocoels are not present in any sacral vertebrae.

The sacral neural spines are preserved, but are not attached to centra. The neural spines of at least three middle sacrals (2–4) are coossified. The sacral neural spines are not bifid.

The sacral ribs are fused to the centra. The first sacral rib is directed posterolaterally, the fifth anterolaterally, and the remaining sacral ribs are directed laterally. All sacral ribs are

TABLE 1. Measurements (cm) of caudal vertebrae of *Ferganasaurus verzilini,* gen. et sp. nov. (PIN N 3042/1).

Caudal #	Centrum length	Maximum anterior centrum width	Maximum posterior centrum width
1	13.0	19.5	19.0
2	11.0	18.5	20.5
3	14.0	20.0	16.5
4	14.0	19.0	16.0
5	14.0	19.0	16.0
6	14.0	17.5	16.0
7	14.0	18.0	15.0
8	14.5	17.5	17.0
9	12.0	?	14.5
10	14.0	15.5	14.0
11	14.0	14.5	13.5
12	14.5	13.0	12.0
13	15.0	12.0	?
30	15.0	12.5	?
33	?	11.0	?
35	15.0	12.0	?

approximately equally robust. Distal ends of at least three sacral ribs (3–5) are fused with one another and form a sacricostal yoke.

Caudal Vertebrae—There were at least 33 caudals found in the articulation (Figs. 3, 4). The last preserved centrum (33) has a mid-caudal morphology, suggesting that the animal apparently possessed not fewer than 10–15 more distal caudals. This suggests that the minimum number of caudals in *Ferganasaurus* was 45–50.

All the caudal centra have shallowly concave anterior faces and almost flat or slightly convex posterior faces. The caudal centra articulations can be classified as slightly procoelous. The height of the caudal centra diminish posteriorly. The lengths of the caudal centra remain relatively uniform for the first 13 vertebrae (Table 1), and possible further distally, because the centra of the mid-caudals (30 and 33) have a similar length. The caudal centra become more compressed posteriorly (Table 1). Pleurocoels are not present in any of the known caudals. In all known caudals the ventral surface of the centrum is deeply concave anteroposteriorly and bears a distinct longitudinal ridge on the ventral mid-line. This ridge is bordered laterally by shallow excavations. On the seventh caudal, a short longitudinal ridge is present just below the caudal rib facet. This ridge becomes more pronounced on caudal centra eight and nine. On caudal centra 10–13, this ridge extends to near the margins of anterior and posterior articular surfaces, migrates ventrally, and borders the ventral centrum surface, which become more flat in these vertebrae. On the mid-caudals (30, 31, 33) the ventral mid-line ridge is absent and the two parallel longitudinal lateral ridges migrate toward the mid-line of the centrum.

Caudal centra one to four bear no distinct chevron facets. Caudal centrum five has a double chevron facet only on its posterior margin. Starting with caudal 6, all the centra bear chevron facets on their anterior and posterior margins. It is not clear whether chevrons were lacking on caudals 1–4, or if their attachments are not marked on the centra. All the ridges for the chevron facets are comparatively low and faint.

The caudal rib facets are present on caudals 1–13. They were possibly also present further distally, judging by the relatively large size of the rib facet on the last preserved proximal caudal. In the known mid-caudals (30, 31, 33) the rib facets are absent. The first caudal rib is linked to the lateral surface of the neural arch and the prezygapophyses by a stout ridge, and has a ''wing''-like shape in anterior and posterior views. The ''wing''-like rib is present also on the second caudal (Fig. 4C, D). On caudals three to nine, the caudal rib facet is connected to the neural arch by a stout ridge that gradually increases in height so the caudal rib facets become placed more dorsally on the centrum. This stout ridge disappears after the ninth caudal vertebra.

The neural arches decrease in height posteriorly. The postzygapophyses are placed relatively lower than the prezygapophyses on caudals 1–10, suggesting that the proximal portion of the tail was not held horizontally but slanted downwards (Fig. 3). On caudals 11 and 12 the zygapophyses are at the same level, suggesting that from this region posteriorly the tail was held more horizontally. The neural spines of the proximal caudals are simple, laterally compressed plates lacking laminae, with strongly developed attachment surfaces for the interspinal tendons. The most complete neural spines (caudals 7, 10) are slightly transversely inflated at their dorsal apices. On caudal three, the neural spine is aligned dorsoposteriorly at its base and than curves more posteriorly. On caudals 7–12 the neural spine is directed first dorsoposteriorly at a lower angle and than curves more dorsally. The neural arches on the mid-caudals are situated over the middle of the centrum. The proximal caudals (1–4) have a ''hyposphenal'' ridge on the posterior face of the neural arch, running from the ventral midline junction of the postzygapophyses to the top of the neural canal. The neural canal in all caudals is rounded and relatively small.

Forelimb

Humerus—The humerus (Fig. 6) has a laterally constricted and anteroposteriorly flattened shaft that is expanded proximally and distally. The proximal end is wider (Table 2). Unlike most sauropods, the humerus has a noticeably sigmoid curvature in a parasagittal plane: the proximal and distal ends respectively, are deflected posteriorly and anteriorly from the humerus shaft at an angle of about 25–30°. The head of the humerus is rounded and not distinctly separated from the shaft. The deltopectoral crest is prominent, extending from the proximal end along the anterolateral border. The posterior surface of the lower one-third of the humerus is broadly concave. This depression is bordered by two subvertical ridges, converging dorsally into a single ridge, that runs along the mid-line of the shaft. The radial and ulnar condyles are very weakly separated and subequal in size.

Ulna—Compared to most sauropods, the ulna (Fig. 7) is a relatively gracile and elongated bone (Table 2). The proximal end is roughly triangular. The triangle is formed by the olecranon process, the long craniomedial process, and the shorter craniolateral process. There is a deep radial fossa between the craniomedial and craniolateral processes for the reception of the proximal end of the radius. The craniolateral, craniomedial, and olecranon processes have flat articular surfaces. There are sharp ridges running along the shaft and starting from the craniomedial and craniolateral processes. These ridges merge at the distal one-fourth of the ulna. There is a marked depression on the medial part of the proximal ulna. The depression is bordered by two ridges that converge distally near the center of the bone. The middle of the shaft is triangular in cross section. The ulna gradually tapers towards the distal end, which is oval in outline and smaller than the proximal end. The distal one-fourth of the ulna is deflected posteriorly in a parasagittal plane at an angle of approximately 20–22°. On the anterior surface of the distal ulna shaft, distal to this curvature, there is a marked depression for the reception of the distal end of the radius.

Radius—The radius (Fig. 8) is a rather slender bone: the maximum width of the proximal end is only 28% of the greatest radius length (Table 2). The radius shaft is considerably curved in a frontal plane: proximal and distal ends meet together at an angle of about 160–162° somewhat above the center of the bone. The radius is also moderately curved in a parasagittal plane. At the proximal one-third on the posterior surface there

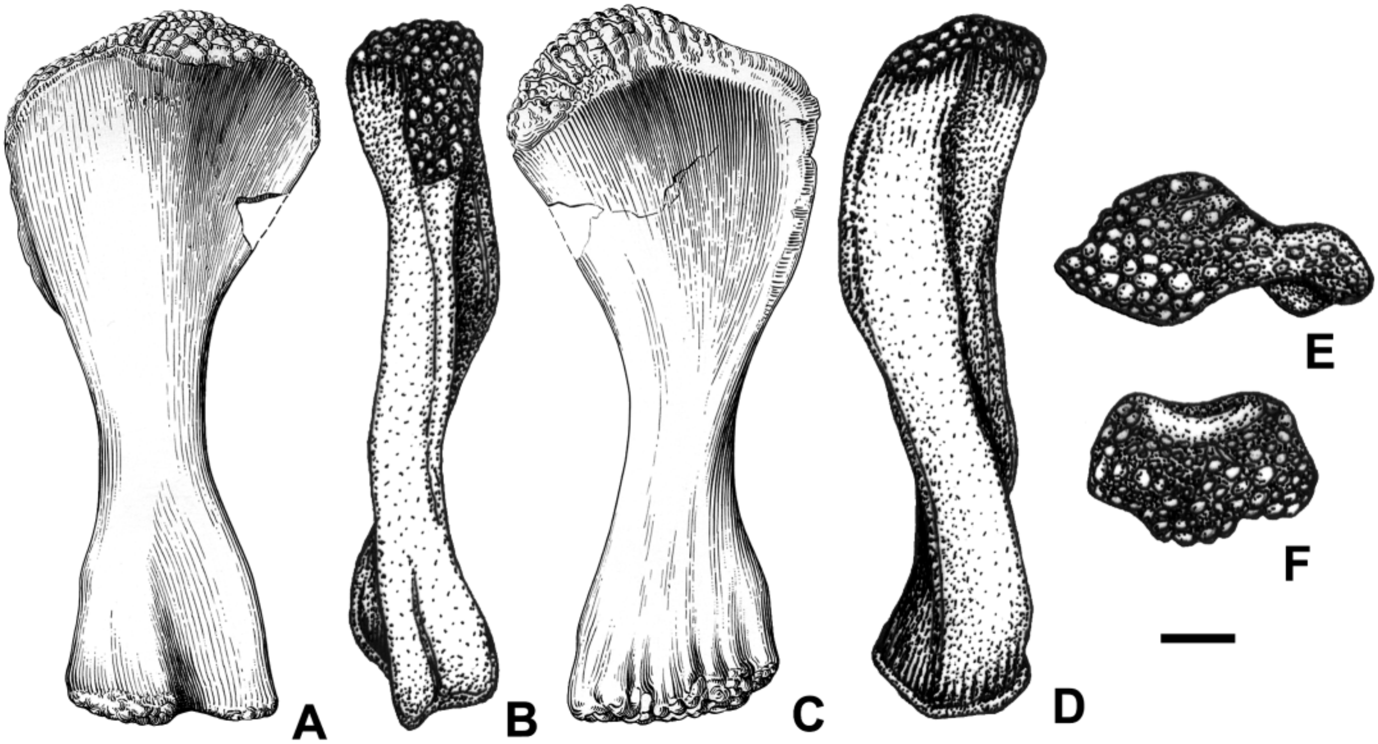

FIGURE 6. Left humerus of *Ferganasaurus verzilini,* gen. et sp. nov. (PIN N 3042/1) in posterior (**A**), medial (**B**), anterior (**C**), lateral (**D**), proximal (**E**), and distal (**F**) views. Scale bar equals 10 cm.

is a marked tuberosity of triangular shape, the ulnar articular surface, placed in a deep depression bordered by low ridges. Along the posterolateral border of the distal portion of the radius there is a greatly developed longitudinal ridge, starting from the distal end and occupying about one-fourth of the radial length. The proximal end of the radius is subrectangular in shape, flattened anteroposteriorly, and transversely wider than the distal end, with convex anterior and almost flat posterior surfaces. The distal end of the radius is weakly globular and oval in outline.

TABLE 2. Measurements of limb and pelvic girdle bones of *Ferganasaurus verzilini,* gen. et sp. nov. (PIN N 3042/1).

Measurement	cm
Humerus, greatest length	89
Humerus, proximal end maximum width	35
Humerus, distal end maximum width	26
Ulna, greatest length	63
Ulna, proximal end maximum width	28
Ulna, distal end maximum width	16.5
Radius, greatest length	58
Radius, proximal end maximum width	16.5
Radius, distal end maximum width	14
Pubis, greatest length	63
Ischium, greatest length (estimated)	63
Femur, greatest length	108
Femur, proximal end maximum width	34
Femur, distal end maximum width	29
Tibia, greatest length	71
Tibia, proximal end maximum width	22
Tibia, distal end maximum width	15
Fibula, greatest length	74
Fibula, proximal end maximum width	17
Fibula, distal end maximum width	17
Astragalus, maximum transverse width	25

Manus—The metacarpals have a semicircular arrangement (Fig. 9A) and were apparently oriented vertical or subvertical, except the metacarpal I, which was more obliquely oriented (Fig. 9B). Metacarpals I–IV are similar in length, and metacarpal V is distinctly smaller (62% from the metacarpal III length). All metacarpals are rather gracile bones with subtriangular (metacarpals I, III, and V) or trapezoid (metacarpal II) proximal articular surfaces. Metacarpals IV and V are interlocked such that the proximal articular surface of the fifth metacarpal fits deeply in a concavity on the proximal articular surface of the fourth metacarpal. The proximal and distal ends are subequal in all the metacarpals and their long axes are oriented in the

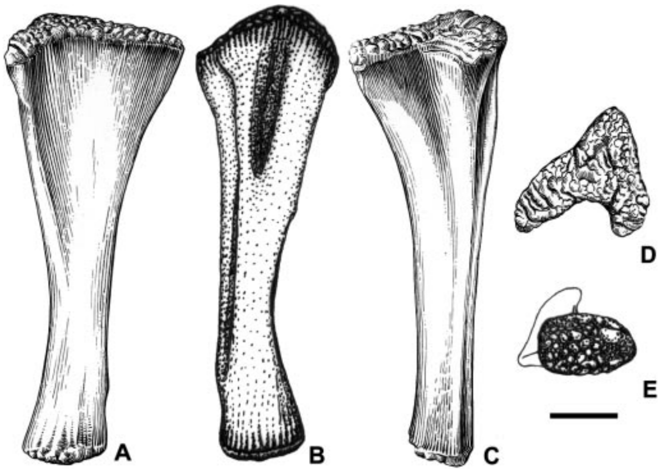

FIGURE 7. Left ulna of *Ferganasaurus verzilini,* gen. et sp. nov. (PIN N 3042/1) in posteromedial (**A**), lateral (**B**), anterolateral (**C**), proximal (**D**), and distal (**E**) views. Scale bar equals 10 cm.

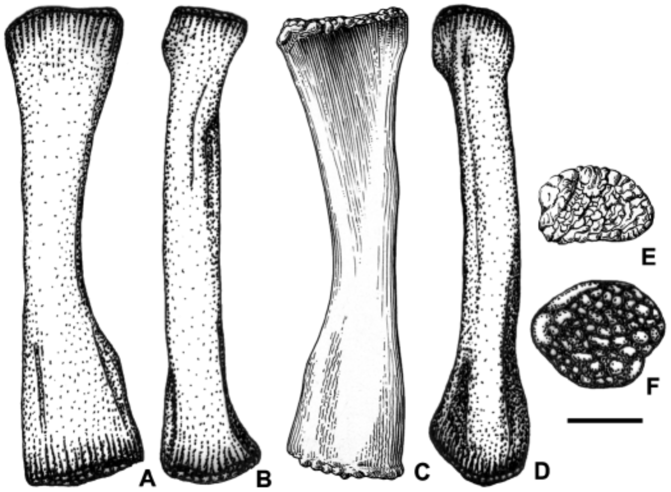

FIGURE 8. Left radius of *Ferganasaurus verzilini*, gen. et sp. nov. (PIN N 3042/1) in anterior (**A**), medial (**B**), posterior (**C**), lateral (**D**), proximal (**E**), and distal (**F**) views. Scale bar equals 10 cm.

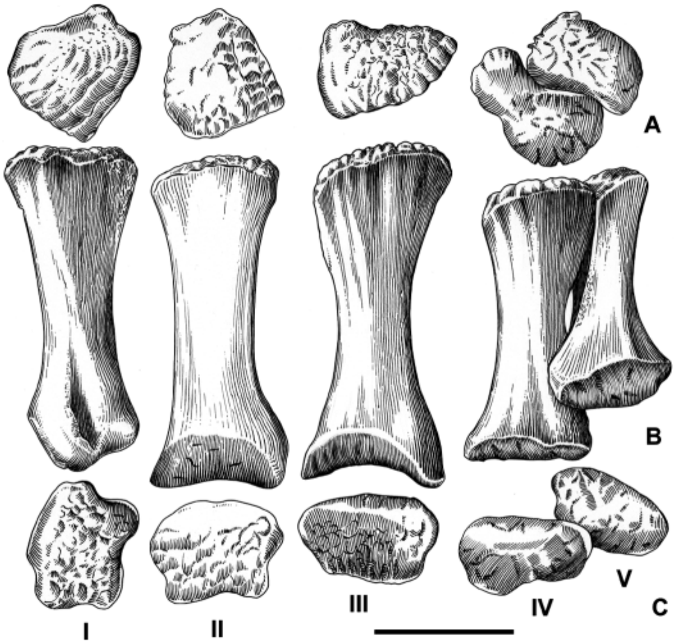

FIGURE 10. Left metacarpals (I–V) of *Ferganasaurus verzilini*, gen. et sp. nov. (PIN N 3042/1) proximal (**A**), anterior (**B**), and distal (**C**) views. Scale bar equals 10 cm.

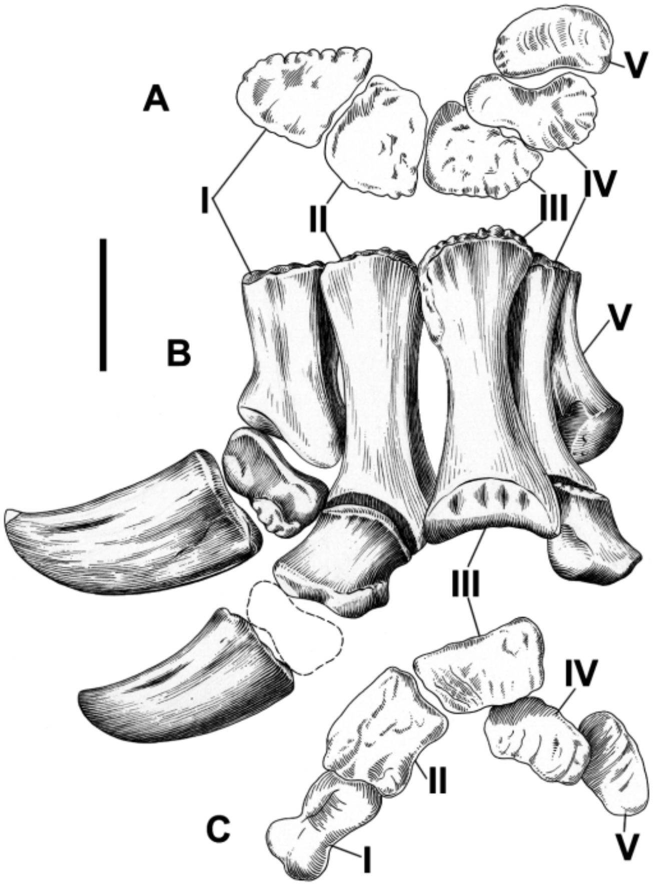

FIGURE 9. Left manus of *Ferganasaurus verzilini*, gen. et sp. nov. (PIN N 3042/1) in proximal (**A**) and anterior (**B**) views. **C**—distal view of metacarpals (I–V). Scale bar equals 10 cm. Note: the figured ungual phalanges were referred to the first and second manual digit by A. K. Rozhdestvensky. However, one of the alternative interpretations seems more possible: at least one of these phalanges is actually a pedal claw, or these are right and left pollex unguals, see discussion in the text.

same plane, except in metacarpal V where the distal end has the long axis oriented almost perpendicularly to the proximal end long axis. Metacarpals II and III have more robust, trapezoidal distal ends. In metacarpals I, IV, and V, the distal ends are more compressed anteroposteriorly. The distal ends are ventrally concave in anterior view in the second and third metacarpals and straight in the remaining metacarpals. The somewhat long intermetacarpal articulations could be between fifth and fourth, and, to a lesser extent, between fourth and third metacarpals, but not between the more medial metacarpals.

Proximal phalanges from digits I to IV and two ungual phalanges were found (Fig. 11). Rozhdestvensky reconstructed an ungual phalanx and a phalanx between the proximal and ungual phalanges for the second digit (Fig. 9B), possibly by analogy with prosauropods, for which the typical manual phalangeal formula is 2-3-4-3-2 (Upchurch, 1997:603). According to Wilson and Sereno (1998:39; character 43), in all eusauropods the second digital ungual is absent, and thus the very reduced ossicle-like phalanx found in some sauropods distal to the II-1 phalanx (e.g., Gilmore, 1936:figs. 15, 17C) would be the II-2 phalanx. No known sauropod has three phalanges in the manual second digit (Upchurch, 1994). Even the archaic eusauropod *Shunosaurus* has the typical eusauropod manual phalangeal formula 2-2-2-2-1? (Upchurch, 1994:fig. 1C) or 2-2-2-2-2 (Wilson and Sereno, 1998:40). Therefore, we doubt the reconstruction made by Rozhdestvensky and present in Figures 9 and 11. One of these ungual phalanges may be the pollex ungual phalanx of the left hand and another of the right hand (in some sauropods right and left manual claws may differ in size, pers. comm. from Dr. M. F. Bonnan), or one of these phalanx (a larger one?) may be actually a pedal claw, mixed with the manus bones.

The proximal phalanges in the second to fourth digits have divided distal articular surfaces (condyles; Fig. 11C), suggesting presence of at least vestigial terminal elements (unguals?). Similarly, metacarpal V has a distal articular surface for a phalanx. Thus, the minimum estimation of the manual phalangeal formula for *Ferganasaurus* would be 2-2-2-2-1.

The proximal manual phalanges (Fig. 11A–C) are stout

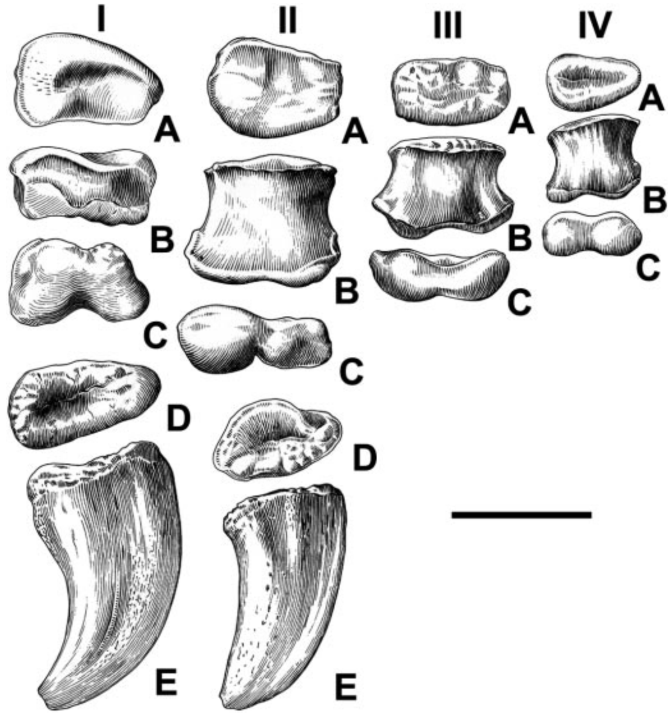

FIGURE 11. Left proximal (A–C) phalanges of manual digits I–IV and ungual phalanges of unknown attribution (**D**, **E**; see note to the Fig. 9 and discussion in the text) of *Ferganasaurus verzilini*, gen. et sp. nov. (PIN N 3042/1) in proximal (**A** and **D**), anterior (**B**), distal (**C**), and medial (**E**) views. Scale bar equals 10 cm.

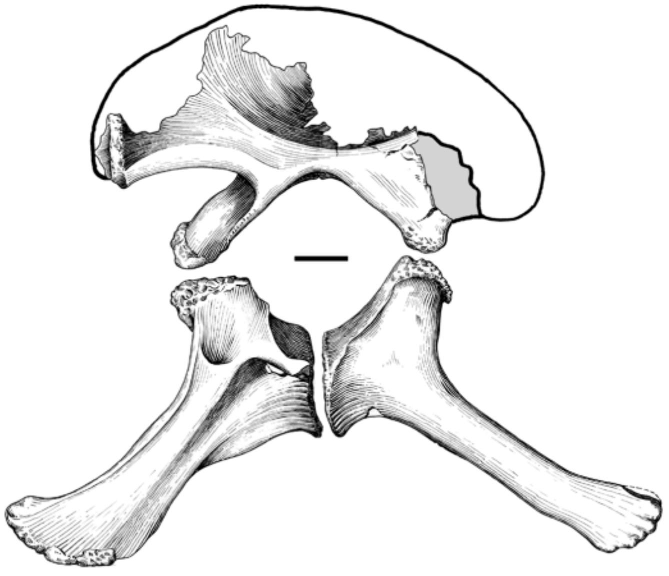

FIGURE 12. Left pelvis of *Ferganasaurus verzilini*, gen. et sp. nov. (PIN N 3042/1) in lateral view. Scale bar equals 10 cm. The shaded area indicates ilium part reconstructed from the reserved part of the right ilium.

bones, broader than long, with oval shaped proximal articular surfaces and figure-eight shaped distal articular surfaces. Phalanx I-1 is shortest but relatively broad, with a concave proximal articular surface. The phalanges II-1, III-1, and IV-1 are similar is shape, gradually decreasing in size from the phalanx II-1 towards phalanx IV.

Both figured unguals (Figs. 9B, 11D, E) are sickle-shaped, similar in form and size, one being somewhat larger and more curved. The proximal articular surface is oval in shape, relatively wider in the second claw. As noted above, the attribution of these phalanges is unclear, they may belong to different side hands, or at least one of them may be a pedal claw.

Pelvic Girdle

Ilium—The acetabulum and peduncles of both ilia are completely preserved, but the majority of the iliac blade is missing (Fig. 12). Each acetabulum is anteroposteriorly wide, but not dorsoventrally high. The pubic peduncle is long, approximately three times longer than the ischiadic peduncle, and directed anteroventrally. The ischiadic peduncle is greatly reduced and directed posteroventrally. The angle between the ventral border of the preacetabular (anterior) process and the pubic peduncle is about 63–65°. The angle between the ventral border of the postacetabular (posterior) process and the ischiadic peduncle is about 138–140°. At the summit of the pubic peduncle and the acetabulum there is a marked swelling. A similar, but smaller swelling can be seen at the base of the ischiadic peduncle. Both swellings apparently served for securing the femoral head in the acetabular cavity. Although the preacetabular process of the ilium is almost completely lacking, the preserved portion of the iliac blade suggests that the preacetabular process was not turned outwards and lay in a near vertical plane. The preserved portion of the iliac blade has no sufficient external depressions and oriented dorsally.

Pubis—The pubis is a stout bone with expanded ends, especially proximally (Fig. 12). The shaft of the pubis is relatively thin along the posterior and medial margins but quite stout along the lateral margin. The dorsal pubic surface is deeply concave. The iliac peduncle is broad and oval in shape, anteroposteriorly expanded, with a slightly concave surface. The acetabular embayment is a flat triangular surface lacking rugosities and is located anteroventrally on the iliac peduncle. The ischial peduncle is deeply concave and formed by two thin plates meeting at an angle of 118°. Anterior to this juncture, close to the pubic margin, there is the obturator (pubic) foramen, completely enclosed in bone. The pubic symphysis is quite long, 67% from the pubic length, and is convex dorsally. There is a small ‘‘hook’’-shaped ambiens process at the anterior border of the iliac peduncle developed to a much lesser extent than in *Diplodocus*. The distal pubic margin is oval in shape.

Ischium—The better preserved left ischium (Fig. 12) consists of two parts. The ischium is a flat, triradiate bone. One of the three parts is formed by the iliac peduncle, which is directed anterodorsally. The iliac peduncle surface is oval in shape and its greatest diameter is about 19% of the ischial length. Another part of the ischium is formed by the pubic peduncle. The angle between the two peduncles is about 100°. The pubic peduncle surface is elongated and triangular in shape, twice as narrow as the iliac peduncle surface, and about 27% of the ischium length. The acetabular embayment is shallowly concave and lacks rugosities. The third part of the ischium is formed by a long ischial shaft, which is slightly expanded at the distal end. The ischial shaft is thin along the ventromedial margin and stout along the dorsolateral margin. The ischial shaft is relatively narrow, about 19% of the ischium length. The symphysis between the ischia is quite long, exceeding 50% of the ischium length (the exact length of the symphysis cannot be determined because of damage). The surface of the distal end of the ischium is elongated, and its long axis was apparently directed dorsolaterally.

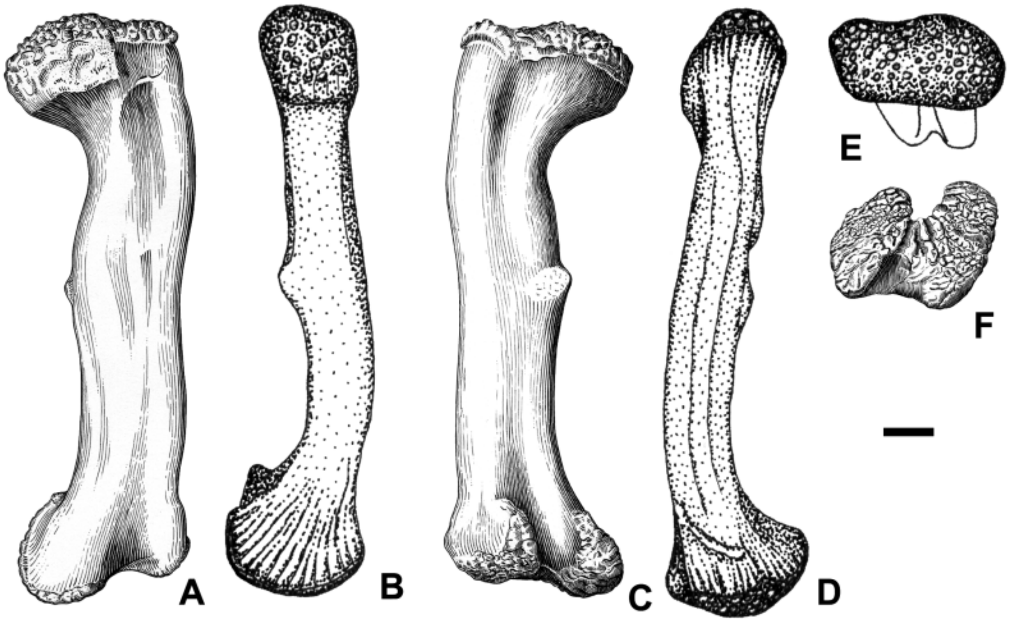

FIGURE 13. Left femur of *Ferganasaurus verzilini,* gen. et sp. nov. (PIN N 3042/1) in anterior (**A**), medial (**B**), posterior (**C**), lateral (**D**), proximal (**E**), and distal (**F**) views. Scale bar equals 10 cm.

Hindlimb

Femur—The femur is unique for sauropods in retaining a partial sigmoid curvature (Fig. 13B, D). The distal portion is more strongly curved in a parasagittal plane than the proximal portion. The shaft is compressed anteroposteriorly. The horizontal cross-section through the femoral shaft is subrectangular. The lateral femoral margin is almost straight, except a slight ''bulge'' near the proximal end. The femoral head is confluent with the greater trochanter and is oriented to the femoral shaft at almost a right angle. In proximal view, the femoral head is separated from the greater trochanter by a shallow anteroposteriorly oriented depression. The fourth trochanter is situated on the posteromedial margin of the shaft, about 45% of the length from the distal end. The fourth trochanter is a blade-like structure, about 13 cm in length, and with an acuminate apex. Distally, the femoral shaft is only slightly expanded transversely, being more thick to the medial side than to the lateral side. The tibial (medial) condyle is distinctly larger than the fibular (lateral) condyle. The long axis of both condyles is oriented posteromedially, at an angle of approximately 25° to a parasagittal plane. The intercondylar groove is relatively narrow and long, and oriented at an angle of 20° to the femoral shaft midline.

Tibia—The tibia is a relatively gracile bone with a wide (both transversely and anteroposteriorly) proximal end and shaft distally tapering (Table 2). The tibial shaft is relatively narrow anteroposteriorly (Fig. 14B, C), being only one third that of the anteroposterior diameter of the proximal end. The distal end is expanded anteroposteriorly, but to a lesser extent than the proximal end. The proximal end has a nearly flat surface. The cnemial crest is very short in proximal view and is separated by a very shallow notch (Fig. 14E). The cnemial crest is relatively weak, not protruding far laterally, and extends along approximately 40% of the tibial shaft. The fibular articular surface is a deep, well-defined excavation in the proximal one-third of the tibia. The articular surface for the ascending process of the astragalus is almost flat and occupies more than a half of the surface of the distal end. It is separated from the posteroventral process by a shallow groove, and is located in the same plane as the latter process.

Fibula—The proximal end of fibula is widened anteroposteriorly and bent posteriorly (Fig. 15). The fibular shaft at the middle is also gently curved posteriorly. The proximal end of the medial surface bears a wide tibial articular surface. Above the fibular mid-shaft, there is a prominent muscle scar (''lateral trochanter'') of oval shape on the lateral surface, oriented along the long axis of the bone. The distal end bears a distinct astragalar articular facet on the medial surface. As in other sauropods (Bonnan, 2000), there is not a facet for the calcaneum on the lateral surface. The distal fibular end is narrow mediolaterally and of oval outline.

Astragalus—The astragalus is a stout bone of rhomboid shape (Fig. 16). The ascending process is small, located at the middle of the posterior margin, and its surface is in the same plane as the remaining astragalar proximal surface. The ascending process is separated from the remaining proximal surface by a relatively long but shallow groove. The proximal surface is gently concave, and the distal surface is considerably convex. Again, as in other sauropods, there is no distinct facet for the calcaneum and the posterior astragalar fossa is not developed.

PHYLOGENETIC POSITION OF *FERGANASAURUS*

For the phylogenetic analysis we used the data matrix by Upchurch (1998), with the addition of *Datousaurus* (from Dong and Tang, 1984), *Jobaria* (from Sereno et al., 1999), and *Tehuelchesaurus* (from Rich et al., 1999), and with reduction of the six titanosaurian genera to the Titanosauria and the seven diplodocoid genera to the families Dicraeosauridae, Diplodocidae, and Nemegtosauridae (see Appendix). Dental and metatarsal I characters for *Ferganasaurus* were coded from the isolated sauropod teeth and the first metatarsal from the Balabansai Formation. The taxa added to the data matrix of Upchurch (1998) are archaic sauropods that potentially could help to resolve the position of *Ferganasaurus* on the cladogram. We did not include in the analysis some recently discovered sauropod genera which belong to the well defined monophyletic groups (brachiosaurids, titanosaurids, diplodocoids). These taxa should not emend the topology of the cladogram significantly. We

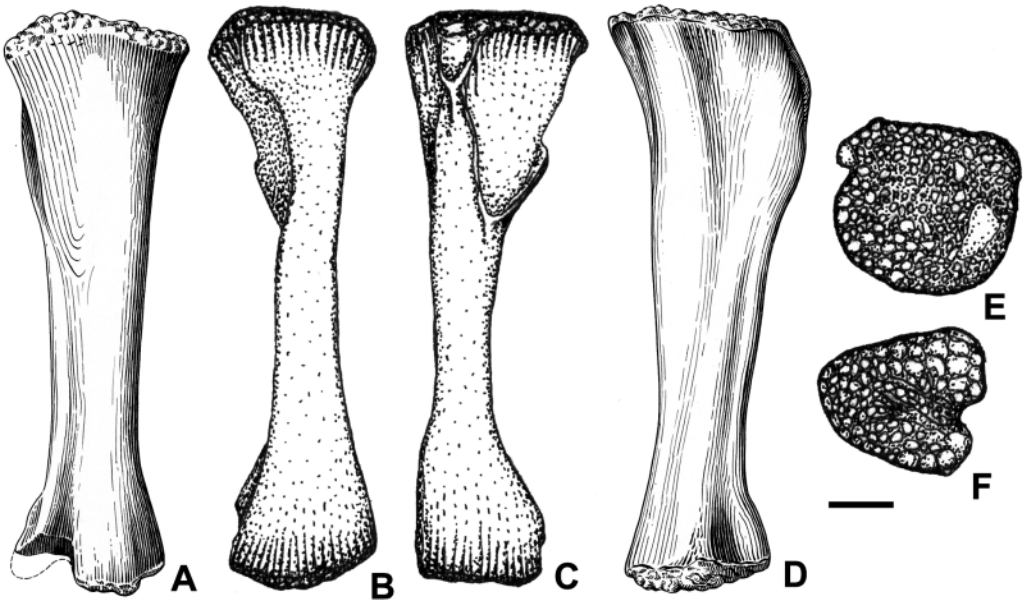

FIGURE 14. Left tibia of *Ferganasaurus verzilini,* gen. et sp. nov. (PIN N 3042/1) in posterior (**A**), lateral (**B**), medial (**C**), anterior (**D**), proximal (**E**), and distal (**F**) views. Scale bar equals 10 cm.

emended the data matrix by Upchurch (1998) for the following characters: C20—derived state scored for *Shunosaurus*; C121—derived state scored for *Euhelopus* and *Mamenchisaurus*; C122—derived state scored for *Euhelopus*; C187—derived state scored for *Mamenchisaurus* and *Euhelopus*. Some of these emendations are explained further in the text.

The data matrix was analyzed using PAUP 3.1.1 (Swofford, 1993). The heuristic search option found 36 most parsimonious trees. A strict consensus tree based on these trees, with relevant statistics, is shown in Figure 17. On this cladogram *Ferganasaurus* forms a polytomy with *Jobaria* and the clades F (Diplodocoidea) and G (Macronaria), thus attributing to the Neosauropoda incertae sedis. A bootstrap analysis (300 replicates) showed support (bootstrap values of 50% or higher) for only four nodes: A (Eusauropoda, 66%), F (Diplodocoidea, 76%), Diplodocoidea excluding Nemegtosauridae (56%), and Diplodocidae + Dicraeosauridae (83%). In the strict consensus tree based on 540 fundamental trees of length 378 and 379 steps only the nodes F, H, and Titanosauria + *Lapparentosaurus* + *Phuwiangosaurus* were revealed. The majority rule consensus tree based on the same fundamental trees showed that the node E (Neosauropoda, including *Ferganasaurus*) is present in 96% of trees. This result may be considered as evidence of a relatively firm position of *Ferganasaurus* within the Neosauropoda, taking into account the overall unstability of the Upchurch's

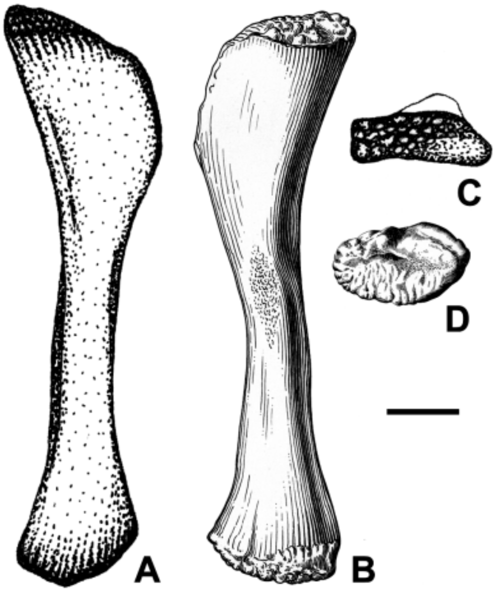

FIGURE 15. Left fibula of *Ferganasaurus verzilini*, gen. et sp. nov. (PIN N 3042/1) in medial (**A**), lateral (**B**), proximal (**C**), and distal (**D**) views. Scale bar equals 10 cm.

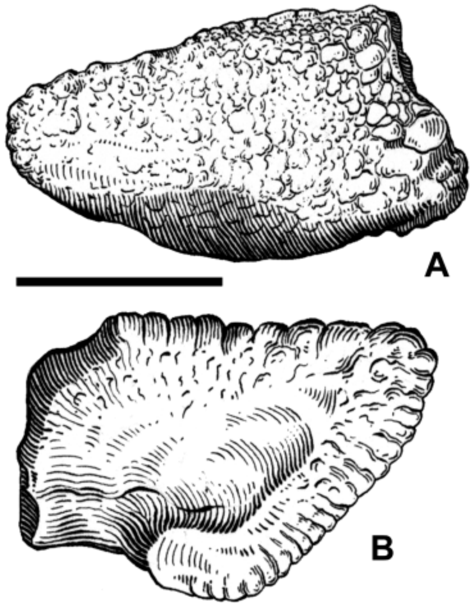

FIGURE 16. Left astragalus of *Ferganasaurus verzilini,* gen. et sp. nov. (PIN N 3042/1) in anterior (**A**) and proximal (**B**) views. Scale bar equals 10 cm.

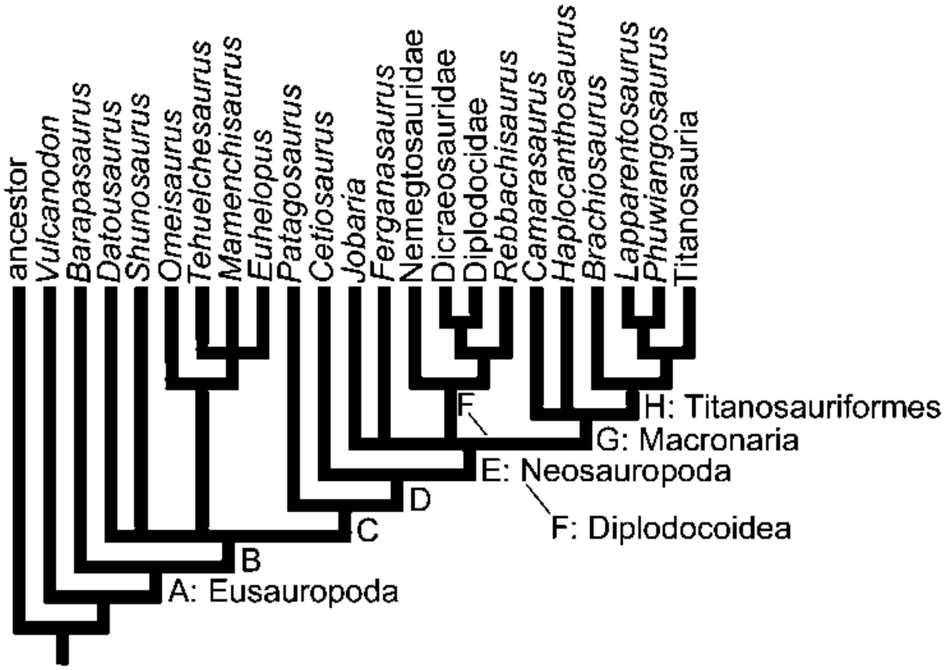

FIGURE 17. Strict consensus tree based on 36 most parsimonious trees (TL = 378 steps, CI = 0.616, RI = 0.594, RC = 0.366). Only nodes relevant to discussion in the text are labeled.

data matrix, caused mostly by a high amount of missing data and by presence of some unstable taxa (Upchurch, 1998).

Ferganasaurus is included in the Eusauropoda (node A) in our analysis by one synapomorphy (character numbers in quadrate brackets are from Upchurch's (1998) data matrix; DELTRAN optimization): middle and distal portion of pubis lies in approximately the same plane as the proximal end [C179]. Although the pubic structure in *Ferganasaurus* meets the criterion of Eusauropoda (pubic apron canted posteromedially, character 46 of Wilson and Sereno, 1998), it remains quite primitive. The pubic symphysis in *Ferganasaurus* is relatively long (67% of the pubic length). In this respect *Ferganasaurus* is similar to *Vulcanodon*, which also has a ratio of about 67% (Upchurch, 1995:fig. 9b). In other eusauropods the pubic symphysis is distinctly shorter, e.g., about 54% in *Patagosaurus fariasi* (Bonaparte, 1986:fig. 53), or 47% in *Camarasaurus lentus* (Wilson and Sereno, 1998:fig. 28).

The cnemial crest of tibia in *Ferganasaurus* is laterally projecting, as in other eusaropods (character 47 of Wilson and Sereno, 1998:40), although it is relatively weakly developed compared to other eusauropods. Other eusauropod characters found in *Ferganasaurus* are posteroventral process of tibia reduced and fibular lateral trochanter present (characters 48 and 49 of Wilson and Sereno, 1998:40).

In our analysis *Barapasaurus* lies outsides the clade B (Euhelopodidae, ''Cetiosauridae,'' and Neosauropoda). In the cladogram by Wilson and Sereno (1998:fig. 49) and Sereno et al. (1999:fig. 4A), *Barapasaurus* is placed between *Shunosaurus* and *Omeisaurus*. One of the characters putting *Shunosaurus* outside of the clade *Barapasaurus* + *Omeisaurus* + Neosauropoda in the analysis by Wilson and Sereno is a sacricostal yoke absent (character 61). However, the specimen upon which the state of this character was determined in *Shunosaurus* is likely immature (Wilson and Sereno, 1998:43, fig. 38), and thus adult animals may have had the derived state. In our analysis clade *Barapasaurus* + Euhelopodidae + ''Cetiosauridae'' + Neosauropoda constitute Eusauropoda, and thus presence of a sacricostal yoke, is another eusauropod synapomorphy of *Ferganasaurus*. Similarly, fibula with broad triangular scar for tibia (character 62 of Wilson and Sereno, 1998:43), is also an eusauropod synapomorphy present in *Ferganasaurus*.

There are four synapomorphies for *Ferganasaurus* at the node B (all eusauropods except *Barapasaurus*):

(1) Centrum length divided by centrum width in the most anterior caudals is 0.5–0.6 [C132; unknown for *Barapasaurus*]. The character is reversed in Titanosauridae, except *Opisthocoelicaudia*.

(2) First caudal rib is linked to the lateral surface of neural arch and prezygapophysis by a stout ridge [C142; unknown for *Vulcanodon*, *Datousaurus*, and *Barapasaurus*]. This character was supposed as a synapomorphy for the Eusauropoda (Upchurch, 1998:99).

(3) Semicircular or ''tubular'' arrangement of metacarpals [C169; unknown for *Vulcanodon*, *Datousaurus*, and *Barapasaurus*].

(4) Manual phalangeal formula is reduced to 2-2-2-2-1 [C170; unknown for *Vulcanodon*, *Datousaurus*, and *Barapasaurus*, hypothesized for *Ferganasaurus*, see above].

Both of the first two characters may become synapomorphies for Eusauropoda when they become known for *Barapasaurus*. Both of latter two characters may be sauropod synapomorphies.

Ferganasaurus is included in the node C (Eusauropoda except *Barapasaurus* and euhelopodids) by one synapomorphy: five coossified sacral vertebra [C121]. Supposed synapomorphy for the Neosauropoda (Upchurch, 1995:375), but present also in *Omeisaurus* and *Mamenchisaurus*. In the analysis by Wilson and Sereno (1998:45; character 2:2) this character is a synapomorphy for the clade *Omeisaurus* + Neosauropoda. In *Euhelopus* there are six sacral vertebrae (Wilson and Sereno, 1998: 45, fig. 47; this taxon was erroneously coded as having four sacrals by Upchurch, 1998), which was considered as one of the synapomorphies of their Somphospondyli (*Euhelopus* + Titanosauria).

There are two synapomorphies for *Ferganasaurus* at node D (*Cetiosaurus*, *Ferganasaurus*, *Jobaria*, Diplodocoidea, and Macronaria):

(1) Accessory lamina in the infrapostzygapophyseal cavity (=centropostzygapophyseal lamina of Wilson, 1999) of the dorsals present [C107].

(2) Fourth trochanter on the femur is situated on the posteromedial margin of the shaft [C189]. The state of this character is unknown for *Barapasaurus*, primitive in *Patagosaurus* and Euhelopodidae, and convergently(?) derived in *Vulcanodon*.

Synapomorphies at the node E (Neosauropoda) for *Ferganasaurus* are the following:

(1) Centroparapophyseal lamina on dorsals present [C105]. The derived state is convergently acquired in Euhelopodidae, reversed in *Camarasaurus*.

(2) Ischiadic peduncle of the ilium is greatly reduced [C176; unknown for *Cetiosaurus*].

(3) Ventral surface of the astragalus is broadly convex transversely [C194]. The state of this character is not known for *Jobaria*, *Cetiosaurus*, *Patagosaurus*, and *Barapasaurus*. *Vulcanodon*, *Ohmdenosaurus* and Euhelopodidae possess a primitive state.

(4) Astragalus tapers medially [C195]. The distribution of this character is the same as the previous one, except the derived state is present in *Euhelopus* and *Vulcanodon*.

(5) Calcaneum absent or fails to ossify [C196] (convergently acquired in *Opisthocoelicaudia* and *Omeisaurus*). This character cannot be definitely demonstrated for *Ferganasaurus*, but it is quite likely because the fibula is distinctly longer than the tibia, recalling the condition of diplodocids, which may indicate absence of the ossified calcaneum.

Ferganasaurus has four derived characters, cited as synapomorphies for the Neosauropoda sensu Wilson and Sereno (1998:48–49; characters 81, 83, 84, and 85): metacarpal proximal ends subtriangular, composite proximal articular surface U-shaped (Fig. 9A), tibia with subcircular proximal end (Fig. 14E), astragalar ascending process extends to the posterior margin of astragalus, and astragalus wedge-shaped in anterior view (Fig. 16A). Wilson and Sereno (1998:48; character 80) cited also long intermetacarpal articulations, leading to a bound metacarpus, as a neosauropod synapomorphy.

Ferganasaurus is excluded from the Diplodocoidea (node F) by the following characters:

(1) Height of neural spines on posterior dorsals, sacrals, and anterior caudals is less than or equal to 1.5 times the height of the centrum [C125]. The derived state for this character, neural spines at least 2.0 times the height of the centrum, is an apomorphy for Diplodocoidea and convergently acquired in *Shunosaurus* and *Andesaurus*.

(2) ‘‘Dorsalization’’ of the neural spine of the anterior caudals absent [C140]. The derived state, the dorsalization of anterior caudals neural spines, is occur in Diplodocoidea and some Titanosauridae.

(3) Neural spines of anterior caudals are transversely compressed [C141]. The distribution of the derived state (neural spines anteroposteriorly compressed) is similar with the previous character.

(4) Forelimb/hindlimb length ratio is 0.75 or more [C159; reversal in Diplodocoidea]. Although the limbs are not completely known for *Ferganasaurus*, the high value of the humerus + ulna/femur + tibia ratio (0.85) in this taxon indicate the derived state of this character (adding of foot and manus will only increase this value, because the manus should be definitely longer than the foot).

Ferganasaurus is excluded from the node G (Macronaria) by two characters:

(1) Length of the longest metacarpal divided by the length of the radius is more than 0.45 [C167]. In *Ferganasaurus* this ratio is 0.41.

(2) Long-axis of the distal end surface of ischiadic shaft is directed dorsolaterally [C184]. The derived state, long axis directed laterally, is convergently acquired at the node G and in *Rebbachisaurus*.

There are also two derived characters shared by *Camarasaurus* and titanosauriforms, but not *Haplocanthosaurus* and *Ferganasaurus*. The first one is posterior dorsals strongly opisthocoelous, with well-marked, hemispherical convexity on the anterior surface of the centrum (character 92 of Wilson and Sereno, 1998:51). *Ferganasaurus* has only slightly opisthocoelous posterior dorsals (Fig. 3A, B), with slightly convex anterior face and concave posterior face of the centrum. The second character (95 of Wilson and Sereno, 1998:51) is puboischial contact deep dorsoventrally. In *Camarasaurus* and titanosaurs the puboischial contact constitute nearly half the total length of the pubis. In *Ferganasaurus* it is only 24% from the pubis length, which is similar to the condition of more primitive eusauropods (Wilson and Sereno, 1998:51).

There are two characters that exclude *Ferganasaurus* from the Titanosauriformes (node H):

(1) Neural arches of middle caudals are situated over the middle of the centrum [C138], on the anterior half of the centrum in Titanosauria.

(2) Length of the ischiadic articular surface of the pubis divided by pubis length is less than 0.33 (estimated as 0.25–0.29 in *Ferganasaurus*) [C180], is 0.45 or more in Titanosauriformes (character reversed in *Opisthocoelicaudia*).

Possible Affinities with Titanosauriformes—Although two characters mentioned above [C138 and C180] clearly set *Ferganasaurus* apart from the Titanosauriformes, there are two other characters that may indicate some kind of relationships of *Ferganasaurus* to this group:

(1) Articulations between anterior caudal centra are mildly procoelous (at least) [C129]. This derived state also occur in advanced Titanosauridae, Diplodocidae, Dicraeosauridae taxa, as well as in *Mamenchisaurus*. As the derived state is not known for *Haplocanthosaurus*, *Camarasaurus*, and Brachiosauridae, it was apparently convergently acquired by Titanosauridae, *Mamenchisaurus* and *Ferganasaurus*. According to Bonaparte at al. (2000) this character is of little systematic value.

(2) Forelimb/hindlimb length ratio is 0.75 or more [C159; unknown in *Haplocanthosaurus*]. The derived state is present in Titanosauriformes, *Camarasaurus*, *Jobaria*, *Omeisaurus*, and *Vulcanodon*.

Possible Affinities with the Euhelopodidae—Upchurch (1995, 1998) argued for a monophyletic Euhelopodidae, an endemic clade of Middle Jurassic–Early Cretaceous Chinese sauropods, containing *Shunosaurus*, *Omeisaurus*, *Mamenchisaurus*, and *Euhelopus*. Unfortunately, all but one of the characters listed as synapomorphies for Euhelopodidae cannot be checked in *Ferganasaurus* because of its incompleteness. There is only a single character that was once considered as a synapomorphy for Euhelopodidae (Upchurch, 1995:373) and this is present in *Ferganasaurus*: ‘‘wing’’ or ‘‘fan’’-like caudal ribs present on first caudals [C143]. In *Ferganasaurus*, such ribs present are on at least the first two caudals. The derived state is also characteristic for Dicraeosauridae and Diplodocidae. However, in a later paper, Upchurch (1998) coded *Shunosaurus*, *Omeisaurus*, and *Mamenchisaurus* as lacking this character, in spite of its indication for *Omeisaurus* (Sun et al., 1992:145) (the tail is not known for *Euhelopus*). This character may be significant.

According to our phylogenetic analysis, *Ferganasaurus* is clearly more derived from euhelopodids in possessing the derived states for the following characters: C121 (node C), C107 and C189 (node D), C105, C176, C194, C195, and C196 (node E). However, at least some euhelopodids also possess derived states for some of these characters: C121 (*Omeisaurus* and *Mamenchisaurus*), C105 (*Shunosaurus*, *Omeisaurus*, *Euhelopus*, unknown for *Mamenchisaurus*), C195 (*Euhelopus*), C196 (*Omeisaurus*).

Ferganasaurus is also similar to *Omeisaurus*, *Mamenchisaurus*, and *Euhelopus* in having fused (co-ossified) neural arches of at least three sacrals. This character was not included in any numerical phylogenetic analysis of sauropods, but may be potentially important. It is present also in *Datousaurus*, *Haplocanthosaurus*, *Brachiosaurus*, and *Opisthocoelicaudia*. *Patagosaurus*, *Diplodocus*, and *Apatosaurus* have fused neural arches of two sacrals. The fusion of sacral neural arches is apparently a homoplasy, possibly correlated with neck elongation. If so, fusion of sacral neural arches in *Ferganasaurus* may indicate presence of a long neck in this animal and this would increase its similarity with *Mamenchisaurus*. *Ferganasaurus* additionally shares with *Mamenchisaurus* proximal caudals slightly procoelous [C129], neural spines in proximal caudals directed first dorsoposterior at a lower angle and then curved dorsally (Young, 1958:figs. 3, 4). The other compatible postcranial elements in *Ferganasaurus* and *Mamenchisaurus* are also basically similar. Affinities of *Ferganasaurus* with the Euhelopodidae should be seriously considered when more materials of this taxon becomes available, taking into account the similarities mentioned above and close temporal and geographic position of *Ferganasaurus* and Chinese taxa.

The idea of a monophyletic Euhelopodidae was criticized by Wilson and Sereno (1998:60), who considered *Shunosaurus* as the most primitive eusauropod, *Omeisaurus* as a sister taxon for the Neosauropoda, and *Euhelopus* as a sister taxon for the Titanosauria. The monophyly of the Euhelopodidae was confirmed by a new set of synapomorphies (Upchurch, 1998:99). The Euhelopodidae sensu stricto is characterized by the enormously long neck, even by the sauropod standards, consisting of 17–19 vertebrae, and is likely a monophyletic group.

Primitive characters of *Ferganasaurus*—There are two characters of *Ferganasaurus* that are remarkably primitive and not consistent with the position of this taxon within the Neosauropoda, as found by the phylogenetic analysis.

(1) Femur shaft has a sigmoid curve [C186]. Derived state, a straight femoral shaft, is characteristic for all known sauropods except *Ferganasaurus*.

(2) Fourth trochanter of the femur is a blade-like structure with an acuminate apex [C190]. In the majority of sauropods the fourth trochanter is a low rounded ridge (synapomorphy at the node B). The primitive state, except *Ferganasaurus*, is known also *Barapasaurus*, *Datousaurus*, and *Vulcanodon*. In the earliest, Late Triassic sauropod *Isanosaurus* the fourth trochanter is also blade-like and possibly secondarily exaggerated (Buffetaut et al., 2000).

DISCUSSION

The Early–Middle Jurassic history of sauropods is still inadequately known. In the Early Jurassic basal sauropods (‘‘vulcanodontids’’) were distributed in Gondwana (South African *Vulcanodon* and Indian *Kotasaurus*) and Europe (*Ohmdenosaurus*). Possibly a sauropod from the Early Jurassic Lower Lufeng Formation in southern China belongs to this group (‘‘*Kunmingosaurus*’’ [nomen nudum]; see also Barrett, 1999). The poorly known taxa from the Early Jurassic Ziliujiang Formation in Sichuan Province, China (*Sanpasaurus*, *Zizhongosaurus*) may also belong to the ‘‘Vulcanodontidae’’ (Upchurch, 1995: 371). The only Early Jurassic non-‘‘vulcanodontid’’ sauropod is an eusauropod *Barapasaurus* from the Kota Formation of India, which shares with the South American Middle Jurassic *Patagosaurus* a unique chambered structure of the dorsal neural arches (Bonaparte, 1986). Both taxa may represent currently little known radiation of basal eusauropods. The Middle Jurassic is dominated by two groups of more specialized eusauropods: ‘‘cetiosaurids’’ (*Cetiosaurus* and *Cetiosauriscus* in Europe, undescribed taxon in Morocco, and *Amygdalodon* in Argentina) and euhelopodids and related forms (*Datousaurus*, *Shunosaurus*, *Omeisaurus* in Sichuan Province, China and *Tehuelchesaurus* in Argentina). This wide geographic distribution of both groups is consistent with the recent paleogeographic reconstruction, showing land connection between all the continents in Bajocian–Bathonian (Golonka et al., 1996:fig. 2). The systematic position of *Bellusaurus* and *Klamelisaurus* from the Middle Jurassic Wucaiwan Formation in Xinjiang Uygur Autonomous Region of China is not clear, but possibly they are related to the Euhelopodidae (Upchurch, 1995:374). Additional to ‘‘cetiosaurids’’ and euhelopodids, in the Middle Jurassic there is also a number of neosauropod taxa. The recently described *Atlasaurus* from the Bathonian–Callovian Tilougguit Formation in Morocco clearly shows affinities with brachiosaurids (Monbaron et al., 1999). The other Middle Jurassic brachiosaurid-like taxa are *Volkheimeria* from Argentina, *Bothriospondylus* from England and France, and *Lapparentosaurus* from Madagascar (Bonaparte, 1986; Upchurch, 1995). The latter taxon is closer to Titanosauria than to *Brachiosaurus* on our cladogram (Fig. 17). *Rhoetosaurus* from the Early or Middle Jurassic of Australia may be another neosauropod (Upchurch, 1995:374); anterior caudal chevrons with open proximal articulation in this taxon may suggests affinities with macronarians (character 87 of Wilson and Sereno, 1998:49). This variety of Middle Jurassic Neosauropoda and possibly presence of its sister taxon Euhelopodidae (Fig. 17) in the Early Jurassic suggests that origin of this group may take place in the Early Jurassic. Development of neosauropods may be confined to Gondwana, North America, and Europe and at least partly may be explained by vicariance with Euhelopodidae, confined mostly to Asia. All previously known Middle Jurassic neosauropods belong to or show affinities with the Macronaria. On the contrary, *Ferganasaurus* may be more closely related to Diplodocoidea than to the Macronaria. Although it obviously lacks important diplodocoid synapomorphies, as discussed above (mostly connected with the ‘‘dorsalization’’ of anterior caudals, e.g., characters C125, 140, 141), it shows some similarities with diplodocids and dicraeosaurids, but not with *Rebbachisaurus*, like mildly procoelous anterior caudals with ‘‘wing’’-like caudal ribs (characters C129, 143). A recently found first metatarsal from the Balabansai Formation at a new site near Sarykamyshsai is clearly diplodocid-like, short, massive and with very prominent laterodistal process. If this metatarsal indeed belongs to *Ferganasaurus*, which is likely, it may future advocate for closer affinities of this taxon with the Diplodocoidea. *Ferganasaurus* may be potentially important for understanding the place and time of origin of diplodocoid sauropods.

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APPENDIX

Taxa added to data matrix by Upchurch (1998, characters C1-C205).

Ferganasaurus

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Jobaria

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Datousaurus

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Tehuelchesaurus

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Nemegtosauridae

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Diplodocidae

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Dicraesauridae

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Titanosauria

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