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Forelimb structure and function in a new Late Cretaceous parvicursorine theropod dinosaur from Mongolia

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ABSTRACT

A new parvicursorine theropod, *Manipulonyx reshetovi*, gen. et sp. nov., is based on a fragmentary skeleton from the Upper Cretaceous (Maastrichtian) Nemegt Formation at Khermeen Tsav, Gobi Desert, Mongolia. The new taxon differs from other parvicursorines in a unique combination of characters. The skeleton of *Manipulonyx* preserves an articulated and complete forelimb, including rudimentary side fingers, and a complete series of proximal carpals (ulnare, intermedium, and radiale). The proximal carpals were previously unknown for Parvicursorinae. This specimen also shows for the first time the presence of additional dermal ossifications in the carpus, three spikes articulated with (medial and lateral spikes) or attached to (palmar spike) the carpometacarpus. We hypothesize that parvicursorines were egg-eating animals and they used these spikes (covered by a keratinous sheath), as well as rudimentary side fingers, to fix the forelimb on the round and elusive egg surface. After such fixation, the eggshell was punctured by the hypertrophied manual claw. This interpretation is supported by a number of morphofunctional traits of the parvicursorine forelimb discussed in the paper, including the hypertrophied deltopectoral crest of the humerus, keeled sternum, enlarged ectepicondyle of humerus, hypertrophied olecranon of ulna, and lack of the flexor tubercle on the main manual ungual phalanx.
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Key words: carpus anatomy, Dinosauria, forelimb function, Parvicursorinae, Theropoda

Строение и функция передних конечностей у нового позднемелового тероподного динозавра группы парвикурсорин из Монголии

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РЕЗЮМЕ

Новый теропод из группы парвикурсорин, *Manipulonyx reshetovi* gen. et sp. nov., описан по фрагментарному скелету из верхнемеловой (маастрихт) нэмэгэтинской свиты местонахождения Хермин-Цав, пустыня Гоби, Монголия. Новый таксон отличается от других парвикурсорин уникальной комбинацией признаков. Скелет *Manipulonyx* сохранил полную сочлененную переднюю конечность, включая рудиментарные боковые пальцы и полный ряд проксимальных карпальных костей (ulnare, intermedium и radiale). Проксимальные карпальные кости не были ранее известны для Parvicursorinae. Изученный экземпляр также впервые демонстрирует наличие дополнительных дермальных окостенений в запястье, три шипа, сочлененных (медиальный и латеральный шипы) или прикрепленных (пальмарный шип) к карпометакарпусу. Предполагается, что парвикурсорины были яйцеядными животными и использовали эти шипы (покрытые роговым чехлом), а также рудиментарные боковые пальцы, для фиксации передней конечности на круглой и скользкой поверхности яйца. После такой фиксации яичная скорлупа прокалывалась гипертрофированным когтем. В пользу этой интерпретации свидетельствует ряд морфофункциональных признаков передней конечности Parvicursorinae, рассмотренных в статье: гипертрофированный дельтопекторальный гребень плечевой кости, килевидная грудина, увеличенный наружный надмыщелок плечевой кости, гипертрофированный олекранон локтевой кости и отсутствие флексорного бугорка на основной фаланге кисти.
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Ключевые слова: анатомия запястья, Dinosauria, функция передних конечностей, Parvicursorinae, Theropoda

INTRODUCTION

Extinct non-avian dinosaurs provide many examples of bizarre creatures having no analogs among modern animals. Among the weirdest dinosaurs are small, highly specialized parvicursorine theropods that lived in the Late Cretaceous of Asia and North America (Perle et al. 1993; Karhu and Rautian 1996; Chiappe et al. 1998, 2002; Xu et al. 2011; Averianov and Sues 2017; Qin et al. 2021; Averianov et al. 2023). Parvicursorines are characterized by short forelimbs with a robust humerus and a functionally monodactylous manus having an enlarged second digit bearing a very large claw and highly reduced or absent lateral digits. The hind limbs are long and slender, with an arctometatarsal pes, indicating cursorial adaptation. The non-parvicursorine alvarezsauroids are known from the Late Jurassic and Early Cretaceous of Asia and the Late Cretaceous of South America (Bonaparte 1991; Novas 1997; Chiappe et al. 2002; Choiniere et al. 2010; Xu et al. 2018; Qin et al. 2019). They have a non-arctometatarsalian pes, and the Jurassic–Early Cretaceous Asian forms have a manus with three functional digits. The current consensus on the phylogenetic position of Alvarezsauroidea is that they are basal maniraptorans (Clark et al. 2002; Novas and Pol 2002; Xu et al. 2018; Qin et al. 2019).

The paradoxical combination of conceivably fossorial forelimbs with evidently cursorial hind limbs makes biological interpretation of these specialized dinosaurs problematic. There are two main hypotheses about their food specialization: eating social insects (Longrich and Currie 2009; Qin et al. 2021; Senter 2023) and feeding on eggs (Lü et al. 2018).

The first parvicursorine described, *Mononykus* from the Maastrichtian of Mongolia, showed a robust forelimb possessing a single stout claw on the second digit. This taxon was considered functionally monodactylous (hence its name meaning “single claw”); however, minute articulation facets on metacarpals 3 and 4 suggested that tiny digits may have been present (Perle et al. 1993, 1994). These tiny digits were subsequently recovered in the Tugriken Shireh parvicursorine from the Campanian of Mongolia (Suzuki et al. 2002). The tiny manual digits 3 and 4 were completely lost in *Linhenykus* from the Campanian of China, which became morphologically monodactylous (Xu et al. 2011, 2013).

So far, only two parvicursorine specimens with tiny manual fingers have been known (Suzuki et al. 2002; Kubo et al. 2023). Here we describe the specimen PIN 3142/364 possessing the most completely preserved manus of these dinosaurs, which includes tiny digits 3 and 4, a full set of proximal carpals previously virtually unknown for the parvicursorines, and enigmatic spikes attached to the carpometacarpus. This manus belongs to a fragmentary skeleton from the Maastrichtian of Mongolia, which is attributed here to a new taxon of Parvicursorinae.

Institutional abbreviations: MPC-D – Institute of Paleontology of the Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; PIN – Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; ZIN PH – Paleoherpetological collection, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

MATERIAL AND METHODS

Geological settings. PIN 3142/364 was found at the northern outcrops of the Khermeen Tsav [=Hermiin Tsav] locality (N 43°29.8', E 99°49.1'; fig. 6 in Gradziński and Jerzykiewicz (1972)) in Govi-Altai Aimag, Transaltai Gobi, Mongolia, by V.Yu. Reshetov in 1979. This locality is confined to the Upper White Beds of Khermeen Tsav of Gradziński and Jerzykiewicz (1972), which were subsequently referred to the Nemegt Formation (Shuvalov and Chkhikvadze 1975; Gradziński et al. 1977).

The Nemegt Formation at the Khermeen Tsav locality produces remains of turtles *Mongolochelys efremovi*, Trionychidae indet., Nanhsiungchelyidae indet., *Mongolemys* sp., *Gravemys barsboldi*, and *Gravemys* sp., crocodylomorphs, sauropods, theropods *Therizinosaurus cheloniformis* and *Tarbosaurus bataar*, ankylosaurs *Tarchia gigantea*, and ornithopods *Saurolophus angustirostris* (Barsbold et al. 1971; Shuvalov and Chkhikvadze 1975; Barsbold 1976; Gradziński et al. 1977; Maryańska 1977; Tumanova 1977, 1987; Sukhanov and Narmandakh 1983; Sukhanov 2000; Danilov 2003; Suzuki and Narmandakh 2004; Danilov and Syromyatnikova 2008; Danilov et al. 2014, 2017).

Computed tomography. PIN 3142/364 was CT scanned at the Borissiak Paleontological Institute of the Russian Academy of Sciences using a high resolution μCT scanner NeoScan N80. The scan parameters were set at voltage 92 kV, current 173 mA, rotation step 0.10 degree, and averaging 6 frames generating a resolution of 10.0 μm (left manus) and 12.5 μm (right manus) of isotropic voxel size and an output of 992 × 768 (left manus) and 1856 x 944 (right manus) pixels per slice. The CT scan data were imported to the software Avizo Lite 2019.1 and 3D Slicer v. 5.6.0, where the model was reconstructed and segmented.

Figs 6–10 were prepared from the virtual three-dimensional model of PIN 3142/364 using the programs Vayu 1.1 (Monkeys Tech Pty Ltd) and MeshLab 2023.12.

Phylogenetic definitions. We employed the phylogenetic definitions of the clades within Alvarezsauroidea that were proposed by Choiniere et al. (2010). Alvarezsauridae Bonaparte, 1991 is the least inclusive clade containing *Alvarezsaurus*, *Mononykus* and their most recent common ancestor. Parvicursorinae Karhu et Rautian, 1996 is the least inclusive clade containing *Parvicursor*, *Mononykus* and their most recent common ancestor. As all alvarezsaurid genera discussed in this paper are monotypic, we use only the generic names in most cases.

Anatomical nomenclature. We use the traditional (“Romerian”) terminology (Wilson 2006) for anatomical structures and directions (e.g., “anterior” and “posterior” instead of “cranial” and “caudal”). We consistently avoid using any terms from avian anatomy (Baumel 1993) for non-avian dinosaurs. In particular, we do not apply the term “scaphoulnare” for the fused radiale and intermedium proposed for non-avian theropods by Botelho et al. (2014).

For the movements in the shoulder joint we adopt the following directional terminology (after Hutson and Hutson 2013): abduction-adduction is movement of the humerus in the frontal plane (forward and backward); flexion-extension is movement of the humerus in the transverse plane (down and up); pronation-supination is rotation of the humerus along its long axis.

We follow here the Frame Shift Hypothesis, postulating that somewhere in the theropod evolution, the genetic programs that regulate development of digit identities 1, 2, and 3 shifted and began to express in embryological positions 2, 3, and 4 (see Young et al. 2011 for review). The three manual fingers with the phalangeal formula 2-3-4 of theropods after the frame shift correspond to fingers 2–4 of the ancestral condition. Consequently, the three manual digits retained in the parvicursorines are fingers 2–4 (Averianov and Sues 2017; Xu et al. 2018).

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Maniraptora Gauthier, 1986

Alvarezsauroidea Bonaparte, 1991

Alvarezsauridae Bonaparte, 1991

Parvicursorinae Karhu et Rautian, 1996

Manipulonyx reshetovi gen. et sp. nov.

(Figs 1–11)

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Etymology. The generic name is derived from Latin verb manipulare, to manipulate, to handle, and Greek noun ὄνυξ, claw. The species is named after Soviet palaeontologist V.Yu. Reshetov, who found the holotype.

Holotype. PIN 3142/364, fragmentary skeleton, including parts of vertebral column, forelimbs, pelvis, and hind limbs (see description for details).

Type locality and horizon. Khermeen Tsav, Gobi Desert, Mongolia. Nemegt Formation (=Upper White Beds of Khermeen Tsav), Upper Cretaceous (Maastrichtian).

Diagnosis. A parvicursorine theropod dinosaur characterized by the following unique combination of characters: humerus short and robust; internal tuberosity of humerus projects proximal to humerus head; notch between humeral head and deltopectoral crest absent; deltopectoral crest of humerus enlarged; single distal condyle of humerus for articulation with radius and ulna; ectepicondyle of humerus hypertrophied and projects distally; olecranon process of ulna hypertrophied; manual digit 2 hypertrophied with very large and robust ungual phalanx; proximodorsal process of manual phalanx II-1 large; ventral canals of manual phalanx II-2 closed laterally; manual digits 3 and 4 greatly reduced; supraacetabular crest of ilium arcuate and does not extend anteriorly beyond pubic peduncle; entocondylar tuber of femur present; popliteal fossa of femur open distally; entocondylar tuber of femur directed posteriorly; and metatarsal 4 with lateral flexor ridge.

Comparison. Differs from *Dzharaonyx eski* from the Turonian Bissekty Formation at Dzharakuduk, Uzbekistan (Averianov and Sues 2017, 2022) in internal tuberosity of humerus projecting more proximally than humeral head, large proximodorsal process of manual phalanx II-1, and larger ilium facet on pubis.

Differs from *Xixianykus zhangi* from the upper Coniacian–Santonian Majiacun Formation at Zhoujiagou, Henan Province, China (Xu et al. 2010), in popliteal fossa of femur open distally and entocondylar tuber of femur directed posteriorly.

Differs from *Shuvuuia deserti* from the Campanian Djadokhta Formation at Ukhaa Tolgod, Mongolia (Chiappe et al. 1998, 2002), in greater angle of scapular blade to scapulocoracoid suture and in lack of notch between humeral head and deltopectoral crest.

Differs from *Ceratonykus oculatus* from the Campanian Barungoyot Formation at Khermeen Tsav (=Red Beds of Khermeen Tsav), Mongolia (Alifanov and Barsbold 2009), in more prominent medial tab on carpometacarpus and deeper extensor and flexor fossae on manual phalanx II-1.

Differs from *Parvicursor remotus* from the Campanian Barungoyot Formation at Khulsan, Mongolia (Karhu and Rautian 1996; Averianov and Lopatin 2021), in arcuate supraacetabular crest of ilium, not extending anteriorly beyond pubic peduncle, transversely wider posteromedial condyle of tibia, which is similar in size with fibular condyle, and deeper incisura tibialis.

Differs from *Ondogurvel alifanovi* from the Campanian Barungoyot Formation at Nemegt, Mongolia (Averianov and Lopatin 2022), in smaller central proximal facet of carpometacarpus, less exposure of central and medial proximal facets of carpometacarpus on extensor side, lack of common articular surface between condyles for phalanx II-1 on carpometacarpus, metacarpal 4 condyle smaller than metacarpal 3 condyle, proportionally longer manual phalanx II-1, large proximodorsal process of manual phalanx II-1, and convex extensor surface of manual phalanx II-1.

Differs from *Jaculinykus yaruui* from the Campanian Barungoyot Formation at Nemegt, Mongolia (Kubo et al. 2023), in lack of epipophyses on cervical vertebrae, in fused cervical ribs, in lack of notch between humeral head and deltopectoral crest, large proximodorsal process of manual phalanx II-1, more distinct obturator notch on pubis, and much larger fibular condyle of tibia.

Differs from *Linhenykus monodactylus* from the Campanian Wulansuhai Formation at Bayan Mandahu, Inner Mongolia, China (Xu et al. 2011, 2013), in more pronounced medial tab on carpometacarpus, presence of manual digits 3 and 4, laterally closed ventral canals of manual phalanx II-2, and having a distinct entocondylar tuber of femur.

Differs from *Mononykus olecranus* from the Maastrichtian Nemegt Formation at Bugin Tsav, Mongolia (Perle et al. 1994), in lack of notch between humeral head and deltopectoral crest, smaller central proximal articular facet of carpometacarpus, lack of common articular surface between condyles for phalanx II-1 on carpometacarpus, proportionally longer manual phalanx II-1, convex extensor margin of manual phalanx II-1, less pronounced size disparity between flexor ridges and distal condyles of manual phalanx II-1, short and proximally wide ventral sulcus of manual phalanx II-2, and entocondylar tuber of femur present.

Comments. *Trierarchuncus prairiensis* from the Maastrichtian Hell Creek Formation of Montana, USA (Fowler et al. 2020; Freimuth and Wilson 2021), was not included in the phylogenetic analysis of Kubo et al. (2023), but was recovered as a parvicursorine by Fowler et al. (2020). *Manipulonyx* differs from *Trierarchuncus* in the short and proximally wide ventral sulcus of manual phalanx II-2.

The two Asian Late Cretaceous alvarezsaurids, *Qiupanykus zhangi* from the Maastrichtian Qiupa Formation at Guanping, Henan Province, China (Lü et al. 2018), and *Nemegtonykus citus* from the Maastrichtian Nemegt Formation at Altan Uul III, Mongolia (Lee et al. 2019), and the North American *Albertonykus borealis* from the Maastrichtian Horseshoe Canyon Formation of Alberta, Canada (Longrich and Currie 2009), were found outside Parvicursorinae in the most recent phylogenetic analysis (Kubo et al. 2023). This may be due to insufficient knowledge of these taxa. With addition of more material on these taxa, they may be included in Parvicursorinae. The validity of *Qiupanykus* is uncertain. Its original diagnosis (Lü et al. 2018) lists mostly characters common to all parvicursorines. The only character that appears to be unique to *Qiupanykus* is the presence of a small pneumatic foramen inside shallow depressions on the lateral surface of the posterior caudal centra. There is no such foramen on the posterior caudals of *Manipulonyx*. *Manipulonyx* differs from *Nemegtonykus* in transversely narrower popliteal fossa of femur and entocondylar tuber of femur present; from *Albertonykus*, in short and proximally wide ventral sulcus of manual phalanx II-2.

DESCRIPTION

Two posterior cervical and the first dorsal vertebrae are preserved in articulation (Fig. 1). The ultimate cervical vertebra is distinctly smaller than the penultimate cervical vertebra. The cervical centra are opisthocoelous, constricted in the middle, and lack pleurocoeles. There are lateral tubercles (="carotid processes") on the ventral side of the centrum at the anterior condyle (Fig. 1B). On the penultimate cervical the postzygapophyses diverge posterolate-

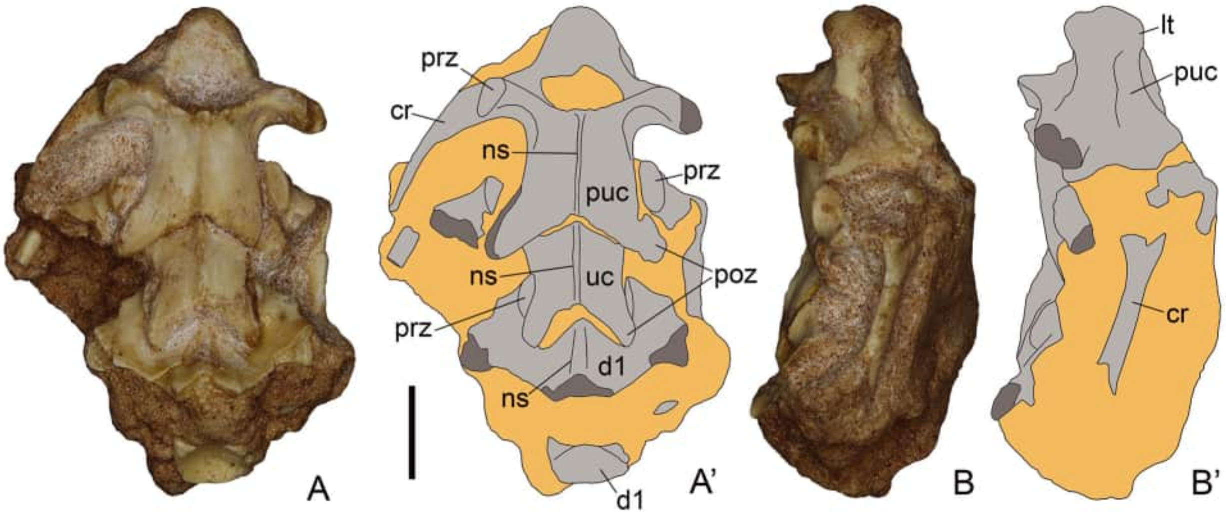

Fig. 1. *Manipulonyx reshetovi* gen. et sp. nov., PIN 3142/364, two posterior cervical and first dorsal vertebrae. A. Dorsal view. B. Right lateral view. Photographs (A, B) and explanatory drawings (A', B'). *Abbreviations:* cr, cervical rib; d1, first dorsal vertebra; lt, lateral tubercle; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; puc, penultimate cervical vertebra; uc, ultimate cervical vertebra. Scale bar: 5 mm.

rally, while on the posterior cervical they are directed posteriorly. The neural spine is very low, ridge-like, and extends for the entire length of the neural arch. There are no epipophyses. The cervical rib is fused with the anteriorly placed parapophysis/diapophysis (Fig. 1A).

The first dorsal vertebra is slightly transversely wider than the penultimate cervical vertebra and about twice as wide as the ultimate cervical vertebra (Fig. 1). The centrum is opisthocoelous. The neural arch is short anteroposteriorly. The diapophysis is located at the middle of the neural arch. The neural spine is low as in the posterior cervical vertebrae.

Three complete and one fragmentary sacral vertebrae are preserved in articulation with the ilium (Fig. 2). The sacral vertebrae are incompletely fused with open suturae between the centra. The anterior of these sacral vertebrae, located at the level of acetabulum, has a low heterocoelous anterior centrum articular surface and a flat ventral centrum surface. In the next sacral vertebrae, the centrum is triangular in cross section and bears a prominent ridge confined to the posterior half of the centrum (Fig. 2A, B). In the posterior of these three sacral vertebrae, the centrum is triangular, but the ridge is lacking. The neural arch increases in transverse width posteriorly. The neural spine is very low and fused between the adjacent vertebrae (Fig. 2C).

The centrum of the possible last sacral vertebra (Fig. 3A, B) is not fused with the neural arch and the adjacent vertebrae. The centrum is procoelous, with the anterior articular surface about half as large as the posterior articular surface. The centrum is triangular in cross section, with a sharp ridge along the entire ventral surface.

Numerous caudal vertebrae (Fig. 3C–P) have elongate, laterally compressed, and deeply procoelous centrum with a ventral groove, which is deeper on the posterior caudals. The first caudal vertebra has a sharp ventral ridge, and the second caudal vertebra lacks the ventral groove (Fig. 3E, G). The neural spine is very low.

The left scapulocoracoid is unfused (Fig. 4A–C). The acromion is very small, not protruding. There is no biceps (coracoid) tubercle.

The left humerus is represented by proximal (Fig. 4D–F) and distal fragments. The right humerus is known only from a distal fragment (Fig. 4G–I). On the proximal humerus there are hypertrophied and proximally projecting internal tuberosity, humeral head oblique to the shaft, and elongate deltopectoral crest, which is continuous with the humeral head (Fig. 4D–F). The large and round distal condyle is a common condyle for articulation with the radius and ulna. There are a hypertrophied and distally positioned ectepicondyle and a small ridge-like entepicondyle (Fig. 4G–I).

The almost complete right ulna and radius are coossified proximally with a distinct suture delimiting these bones (Figs 5, 6A, C). The bones are dorsoventrally compressed. The proximal part of the ulna, including the mostly missing olecranon process, is especially flat dorsoventrally. The articular facet for the humeral condyle is crescentic in flexor/extensor view and slightly exposed in extensor view (Figs 5A, 6A, C). Two-thirds of this facet are formed by the ulna and one-third by the radius, as in *Mononykus* (Perle et al. 1994). The distal part of the ulna becomes triangular in cross-section proximally and terminates in a carpal trochlea, which is roughly triangular in distal view. The radius shaft is short and stout. It extends distinctly more distally than the ulna. On the lateral side of the radius there is a large aponeurosis tubercle (Figs 5A, 6A), which does not approach the ulna, in contrast with *Mononykus*. The radial trochlea is bulbous and larger than the ulnar trochlea.

There are three proximal carpals articulating with ulna and radius and identified as ulnare, intermedium and radiale (Figs 5–7). On the right manus, the intermedium is partially fused with the ulnare and articulates with the ulna (Figs 5B, 6A). This bone is missing on the left manus (Fig. 7), where it apparently was not fused with the ulnare. This may represent individual variation between the left and right hand in fusion of the intermedium and ulnare that echoes individual or ontogenetic variation in fusion of these bones in *Coelophysis* (Barta et al. 2018). The ulnare is a button-like bone contacting by a narrow globular part with the central proximal articular surface of the carpometacarpus formed by metacarpals 2 and 3. The proximal surface of ulnare, contacting the ulna, is flat. The intermedium is a wedge-like bone tapering medially towards the radiale. On the right manus it is apparently displaced proximally from its original contact with the radiale (Figs 5B, 6A). The radiale is a bean-shaped bone with slightly concave proximal surface contacting the radius and more deeply concave distal surface contacting the medial proximal articular facet of carpometacarpus (Figs 5–7).

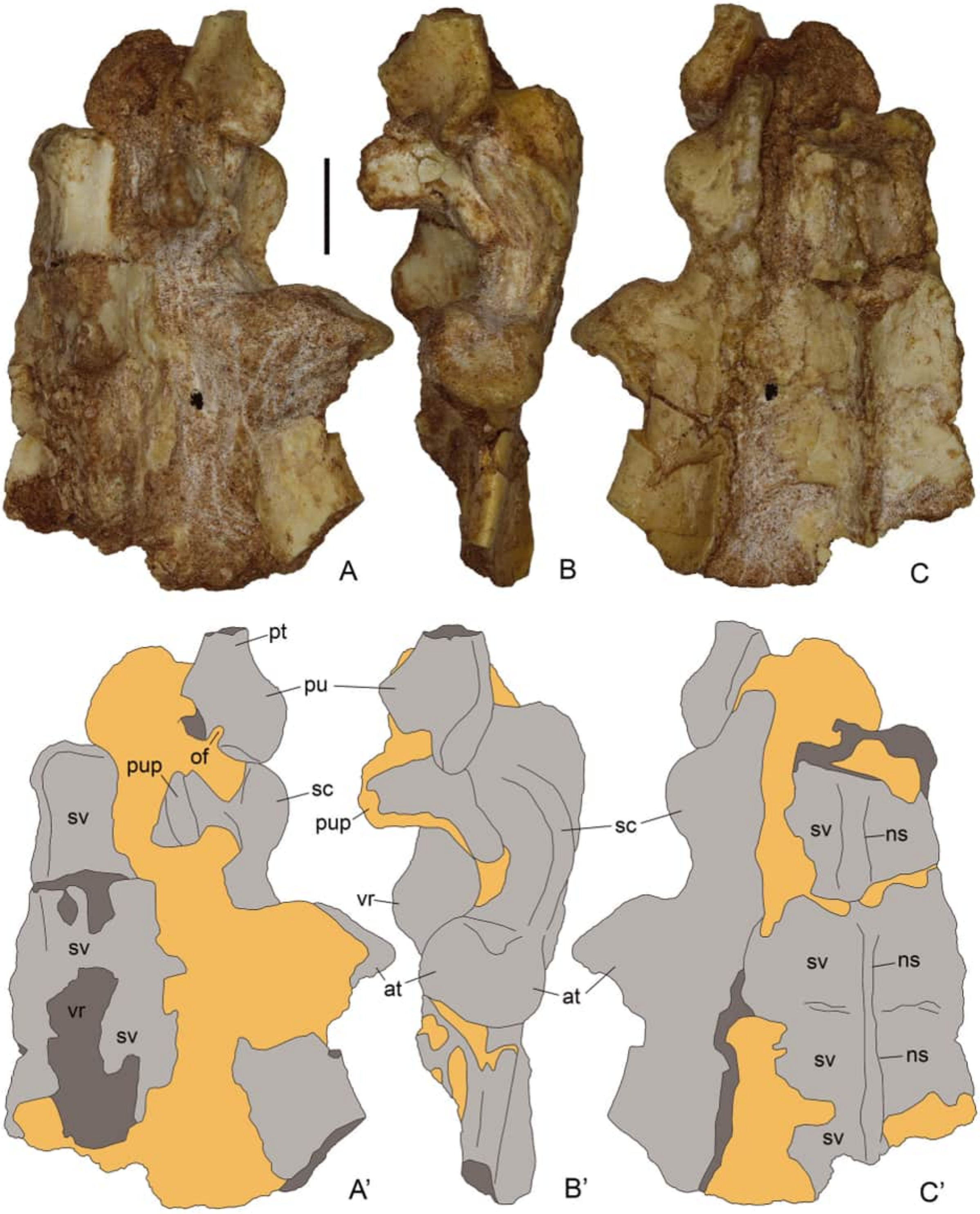

Fig. 2. *Manipulonyx reshetovi* gen. et sp. nov., PIN 3142/364, sacrum and pelvis. A. Ventral view. B. Left lateral view. C. Dorsal view. Photographs (A–C) and explanatory drawings (A'–C'). *Abbreviations:* at, antitrochanter; ns, neural spine; of, obturator foramen; pt, prepubic peduncle; pu, pubis; pup, pubic peduncle; sc, supracetabular crest; sv, sacral vertebra; vr, ventral ridge. Scale bar: 5 mm.

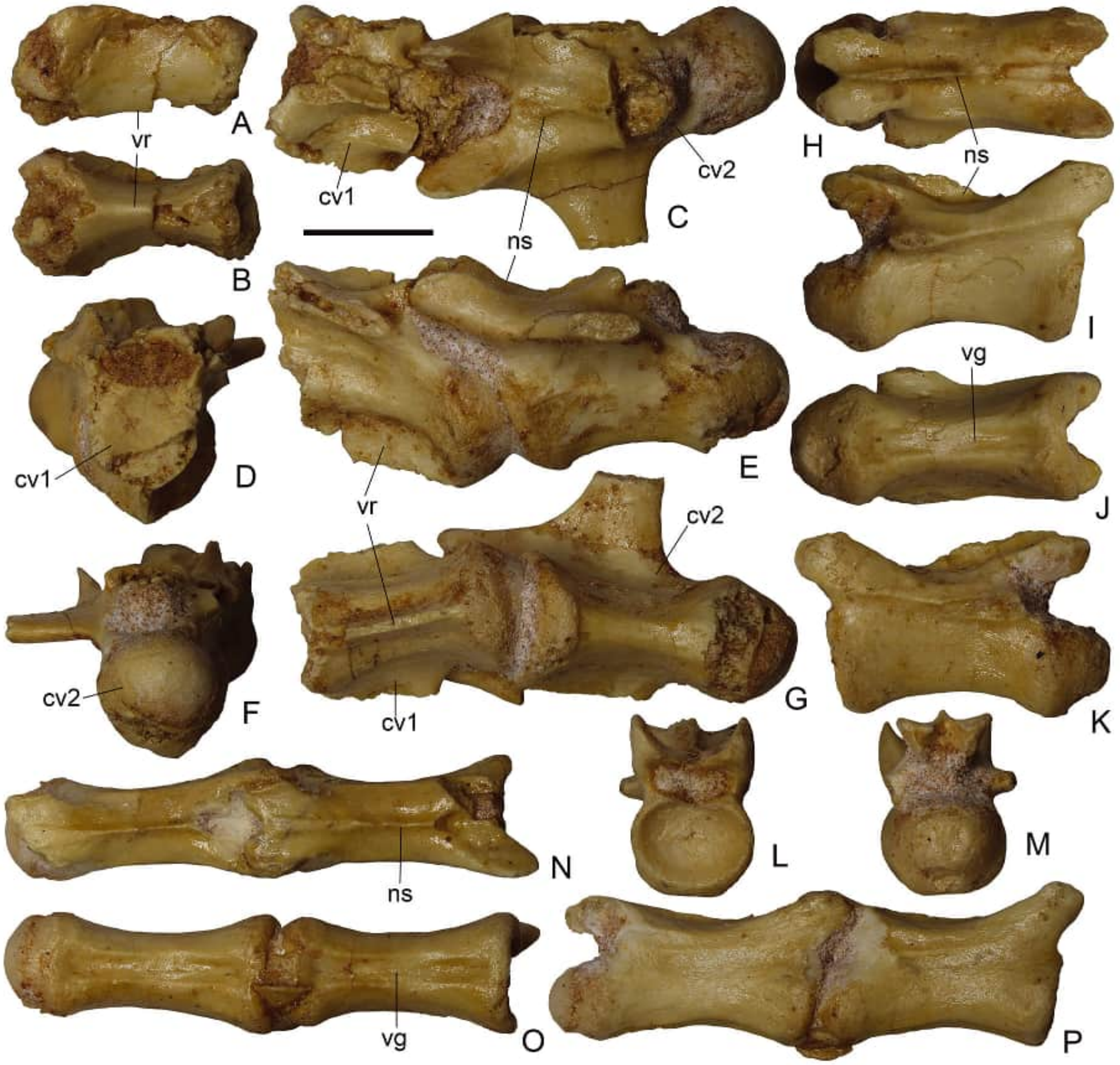

Fig. 3. *Manipulonyx reshetovi* gen. et sp. nov., PIN 3142/364, last (?) sacral and caudal vertebrae. A, B. Last (?) sacral vertebra centrum, in right lateral (A) and ventral (B) views. C–G. Articulated first and second caudal vertebrae, in dorsal (C), anterior (D), left lateral (E), posterior (F), and ventral (G) views. H–M. Middle caudal vertebra, in dorsal (H), right lateral (I), ventral (J), left lateral (K), anterior (L), and posterior (M) views. N–P. Two articulated posterior caudal vertebrae, in dorsal (N), ventral (O), and right lateral (P) views. Photographs. *Abbreviations:* cv1 and cv2, caudal vertebrae 1 and 2; ns, neural spine; vg, ventral groove; vr, ventral ridge. Scale bar: 5 mm.

A large oval bone on the flexor side of the carpometacarpus and distal to the radiale is termed here the palmar spike (Figs 5A, 6C, 7B, C, 10I–K). This bone might represent the sesamoid ossification of the second digit flexor muscle. The palmar spike has a flat side contacting the carpometacarpus and the ridged opposite side.

The metacarpus consists of three metacarpals (2–4), which are completely fused. Both left and right metacarpi are completely preserved. The sutures between the metacarpals are closed but can be traced on the extensor side (Figs 5, 6A, 7A), as in *Mononykus* (Perle et al. 1994: fig. 13C). The carpometacarpus is dorsoventrally compressed, and the lateral metacarpals (3 and 4) are inclined ventrally relative to metacarpal 2. Metacarpal 2 is about twice as wide proximally as both metacarpals 3 and 4. It has a trochlear articular surface for proximal phalanx II-1, which

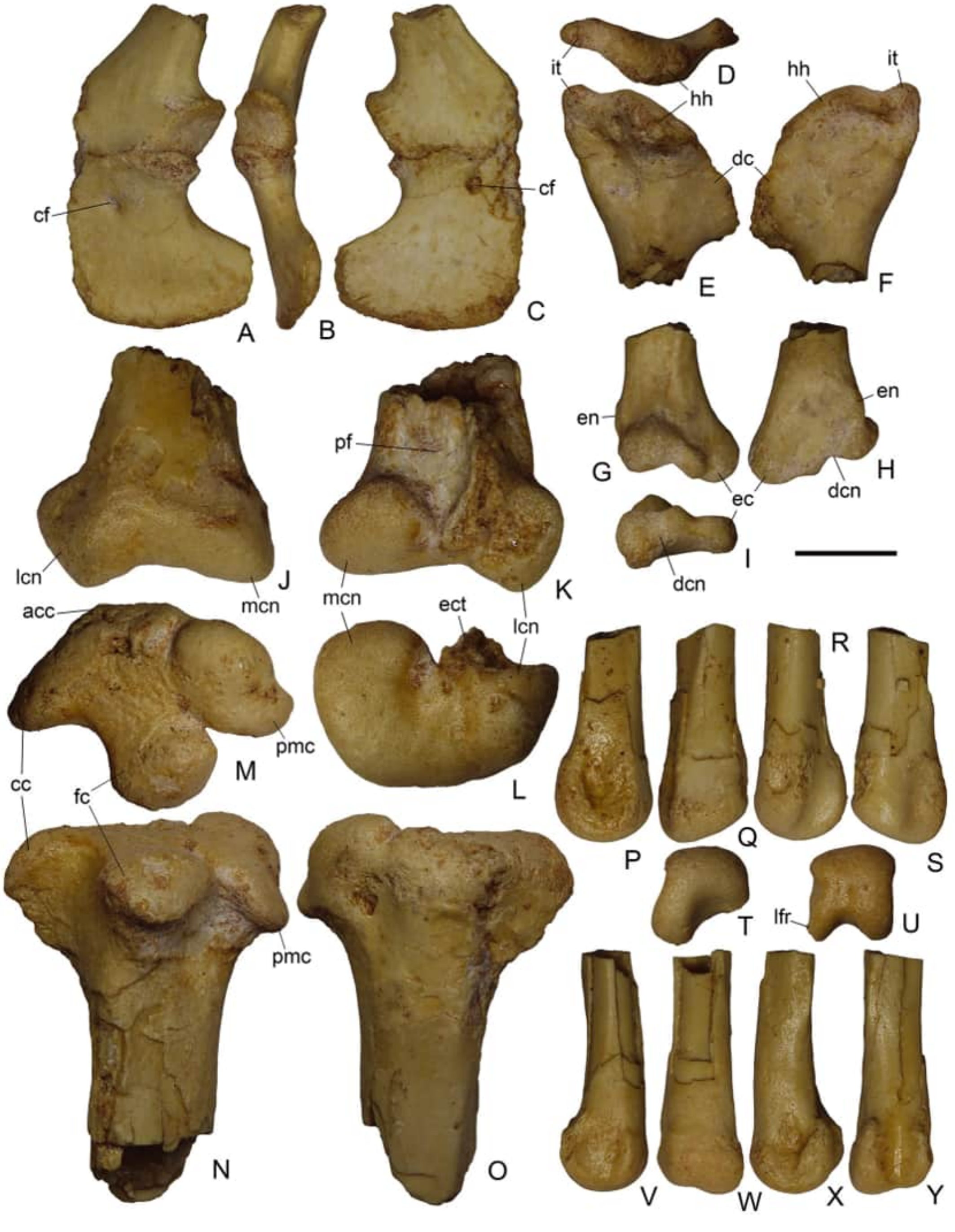

Fig. 4. *Manipulonyx reshetovi* gen. et sp. nov., PIN 3142/364, bones of appendicular skeleton. A–C. Left scapulocoracoid, in lateral (A), posterior (B), and medial (C) views. D–F. Left humerus proximal fragment, in proximal (D), anterior (E), and posterior (F) views. G–I. Right humerus distal fragment, in anterior (G), posterior (H), and distal (I) views. J–L. Left femur distal fragment, in anterior (J), posterior (K), and distal (L) views. M–O. Left tibia proximal fragment, in proximal (M), lateral (N), and medial (O) views. P–T. Right metatarsal 2 distal fragment, in lateral (P), extensor (Q), medial (R), flexor (S), and distal (T) views. U–Y. Right metatarsal 4 distal fragment, in distal (U), lateral (V), extensor (W), medial (X), and flexor (Y) views. Photographs. *Abbreviations:* acc, accessory cnemial crest; cc, cnemial crest; cf, coracoid foramen; dc, deltopectoral crest; dcn, distal condyle; ec, ectepicondyle; ect, ectocondylar tuber; en, entepicondyle; fc, fibular condyle; hh, humeral head; it, internal tuberosity; lcn, lateral condyle; lfr, lateral flexor ridge; mcn, medial condyle; pf, popliteal fossa; pmc, posteromedial condyle. Scale bar: 5 mm.

occupies most of the distal margin of the metacarpus. This articular surface is figure-of-eight shaped in distal view, with convex condyles widely separated by the intercondylar groove (Figs 6A, 7A, C, D). The lateral condyle is slightly larger dorsoventrally, while the medial condyle is slightly wider transversely. Both condyles are equally exposed on the flexor and extensor sides. In contrast with *Mononykus* (Perle et al. 1994: fig. 13B, C), there is no common articular surface within the intercondylar groove, which is exposed in extensor and flexor views. The articular surface for phalanx II-1 is flanked by two prominences, a larger medial (=medial tab) and a smaller lateral, which are covered on the right manus by cone-like spikes termed medial and lateral spikes, respectively (Figs 6A, B, D, 10A–H, 11). Both these prominences are within metacarpal 2. The medial spike is about three times as large as the lateral spike. On the proximal side of metacarpal 2 there are two articulation facets, a transversely elongate pulley-like medial proximal facet formed by the fused distal "semilunate" carpal articulating with the radiale and a round central proximal facet articulating with the ulnare. The latter facet is distinctly smaller than that in *Mononykus* (Perle et al. 1994: fig. 13D). The lateral part of the central proximal facet is formed by metacarpal 3. The metacarpal 3 is slightly wider distally than proximally. Almost the entire distal surface is occupied by a small ball-like articular surface for phalanx III-1. This surface is adjacent to a similarly sized articular surface on the distoventral side of metacarpal 4 for phalanx IV-1. On the proximal side of metacarpal 4, there is a small but deeply concave articular surface contacting the lateral side of the ulnare (on the left manus the ulnare is displaced from this facet; Fig. 7B, C).

Manual digit 2 is hypertrophied as in other alvarezsaurids and consists of two phalanges, which is typical for theropods. Both phalanges (II-1 and II-2) are completely preserved in articulation in the right manus (Figs 5, 6, 8, 9, 11). In the left manus, there are the distal condyle of the preungual phalanx (II-1) articulated with the complete ungual phalanx (II-2; not figured). The proximal articular surface of the preungual phalanx is asymmetrical, with the lateral cotyle about twice as large as the medial cotyle. The dorsolateral margin of the lateral cotyle is greatly extended proximally and laterally, forming the proximodorsal process. The extensor side is depressed proximally between the cotylae and convex in the middle, in contrast with *Mononykus*, where the extensor side of phalanx II-1 is deeply concave (Perle et al. 1994: fig. 14B). At the distal end of the extensor surface there is a very large and deep extensor fossa between the condylar ridges. The lateral and medial side of phalanx II-1 are concave. The distal condyle is distinctly narrower transversely than the proximal end of the phalanx. The flexor side of the phalanx is deeply grooved between the high medial and lateral ridges. The size disparity between these ridges is not so great as in *Mononykus* (Perle et al. 1994: fig. 14C). The higher ridge in *Mononykus* is termed the "proximomedial" ridge by Novas (1996: fig. 13C), although it is on the lateral side of the bone. A deeper transversely oriented flexor pit on the flexor side is adjacent to the distal condyle. The distal condyle is deeply ginglymoid, with the lateral and medial condyles separated by a wide groove. The distal condyles are nearly symmetrical, with the lateral condyle only slightly larger than the medial condyle. This contrasts with the condition in *Mononykus*, where the lateral distal condyle is distinctly larger (Perle et al. 1994: fig. 14A). The ligament pits are large, deep, and equally developed on both distal condyles (Fig. 8A, C).

The ungual phalanx II-2 is strongly curved as in other alvarezsaurids (Figs 5, 6, 9, 11). The proximal articular surface is nearly symmetrical, with the lateral cotyle only slightly larger than the medial cotyle. Both cotylae are separated by a high ridge and well exposed in side views. The lateral grooves widen posteriorly and continue proximally within the laterally closed channels that open on the flexor side as ventral foramina. The ventral sulcus extends only for the proximal part of the claw, in contrast with *Mononykus* where it extends for the entire claw length (Perle et al. 1994: fig. 14D). The ventral sulcus widens proximally and is flanked at the proximal end by prominent tubercles.

The manual digits 3 and 4 are very small (Figs 5A, 6C, 11), as in the Tugriken Shireh parvicursorine (Suzuki et al. 2002). Phalanx III-1 is only slightly longer than phalanx III-2. Both phalanges have a ginglymoid distal end. The ungual phalanx III-3 is distinctly longer than phalanx III-1. It is slightly curved and transversely narrower than the preungual phalanx. Phalanges IV-1 and IV-2 are smaller but similar in morphology to the preungual phalanges of the third digit. The articulation between phalanges IV-1 and IV-2 is not clear and the ginglymoid joint is developed only at the distal end of phalanx IV-2. It is likely that the preungual phalanx and thus

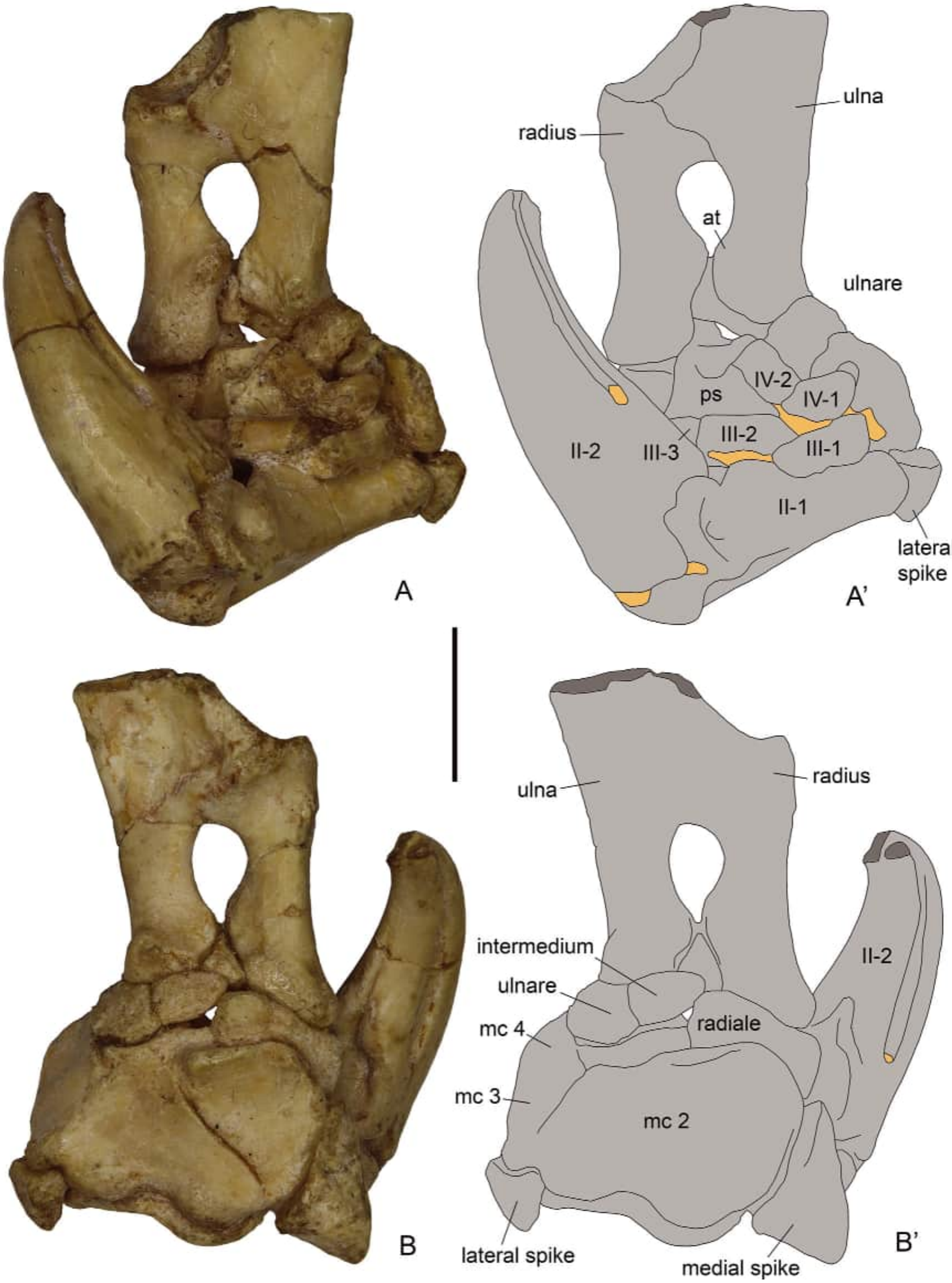

Fig. 5. *Manipulonyx reshetovi* gen. et sp. nov., PIN 3142/364, right manus. A. Flexor view of radius and ulna. B. Extensor view of radius, ulna, and carpal bones. Photographs (A, B) and explanatory drawings (A', B'). *Abbreviations:* II-1 and II-2, manual phalanges II-1 and II-2; III-1–III-3, manual phalanges III-1–III-3; IV-1 and IV-2, manual phalanges IV-1 and IV-2; at, aponeurosis tubercle; mc 2–4, metacarpals 2–4; ps, palmar spike. Scale bar: 5 mm.

manual digit 4 has three phalanges, in contrast with four phalanges in other theropods. Three phalanges were likely present in manual digit 4 in Tugriken Shireh parvicursorine with similarly unclear articulation between phalanges IV-1 and IV-2 (Suzuki et al. 2002: fig. 6C).

There are fragments of the right ilium and pubis associated with the anterior synsacrum fragment (Fig. 2). On the ilium, there are a large antitrochanter and a well-developed supracetabular crest (Fig. 2). The latter is arcuate and does not extend anteriorly beyond the pubic peduncle of the ilium. The small pubic peduncle is subtriangular in lateral view and has a knob-like articular surface (Fig. 2A, B). The pubis has the prepubic tubercle (Fig. 2A, B). The pubic shaft is mediolaterally compressed. There is the obturator foramen between the pubis and ischium (Fig. 2A, B).

The femur is known from two distal fragments from the left and right sides (Fig. 4J, L). The deep popliteal fossa is open distally and bounded laterally and medially by sharp ridges. The lateral condyle is conical and distally projecting. The ectocondylar tuber projects posteriorly beyond the medial condyle (Fig. 4L).

The tibia is represented by the left and right proximal fragments, which have a weak accessory cnemial crest (Fig. 4M–O). There are also fragments of metatarsals (Fig. 4P–Y) and pedal phalanges. There is a distinct lateral flexor ridge on metatarsal 4 (Fig. 4U).

DISCUSSION

Reduction of carpal elements in Theropoda. There are several reviews of the carpus evolution in Theropoda (Chure 2001; Botelho et al. 2014; Xu et al. 2014; Barta et al. 2018). The initial stage is represented by the basal theropod *Tawa*, which has eight separate disk-shaped carpals: three proximal (radiale, intermedium, and ulnare), a centrale, and four distal carpals (dc 1–4) (Burch 2013; Barta et al. 2018). *Tawa* also has an additional ossification in the distal carpal row, the pisiforme. In another basal theropod, *Herrerasaurus*, the intermedium and pisiforme are absent (Sereno 1994). In the coelophysoids *Coelophysis* and *Megapnosaurus* the intermedium and the centrale are variably present, and distal carpals 1 and 2 are fused (Raath 1969; Colbert 1989; Barta et al. 2018). In the coelophysoid *Dilophosaurus* there are three proximal carpals (Welles 1984; Barta et al. 2018). The carpal bones apparently were not ossified in *Ceratosaurus* (Gilmore 1920; Carrano and Choiniere 2016), and possibly in other neoceratosaurs. In the allosauroids *Allosaurus*, *Asfaltovenator*, and *Acrocanthosaurus* there are only two proximal carpals (radiale and intermedium) and one or two distal carpals (Currie and Carpenter 2000; Chure 2001; Rauhut and Pol 2019). In the megaraptors *Megaraptor* and *Australovenator* there are only two carpals, a disk-shaped radiale and an enlarged distal carpal 1 (White et al. 2012; Novas et al. 2016). In Coelurosauria, according to the review based on embryological and paleontological data (Botelho et al. 2014), the ulnare was subsequently lost and the intermedium was fused with the radiale.

Although reduction of carpal bones in the theropod lineage leading to birds seems obvious, there are exceptions to the pattern described by Botelho et al. (2014). There is a separate intermedium (sometimes misidentified as ulnare) in the tyrannosauroid *Guanlong* (Sullivan et al. 2010), compsognathids *Huaxiagnathus* (Hwang et al. 2004) and *Compsognathus* (Peyer 2006), ornithomimid *Struthiomimus* (Osborn 1917; Nicholls and Russell 1985), and caenagnathid *Hagryphus* (Zanno and Sampson 2005). The bone between distal carpal 2 and pisiforme identified as intermedium in the ornithomimosaur *Harpymimus* (Kobayashi and Barsbold 2005: fig. 6.7B–D) is likely the distal carpal 3. In the tyrannosaurid *Gorgosaurus* there are three proximal and two distal carpals (Lambe 1917). Therizinosauroidea in the diagram by Botelho et al. (2014) are represented by *Falcarius*, whose carpus is known from isolated bones rather than articulated specimens (Zanno 2006). The carpus in *Falcarius* is interpreted as having one proximal carpal (fused radiale and intermedium), distal carpals 1 and 2, and possibly distal carpal 3. There are three separate proximal carpals (radiale, intermedium, and ulnare) in the articulated specimen of therizinosauroid *Alxasaurus* (Russell and Dong 1994; Sullivan et al. 2010). The ulnare is absent in oviraptorosaurs *Khaan*, *Heyuannia huangi*, and *Oksoko*, but present in some other oviraptorosaurian taxa (Balanoff and Norell 2012; Qiu et al. 2019, 2024; Funston 2024).

Among the non-alvarezsaurid alvarezsauroids, the carpal bones are known for *Aorun* and *Haplocheirus* (Choiniere et al. 2010, 2014; Sullivan et al. 2010). The number of carpals is uncertain in *Haplocheirus*; it is

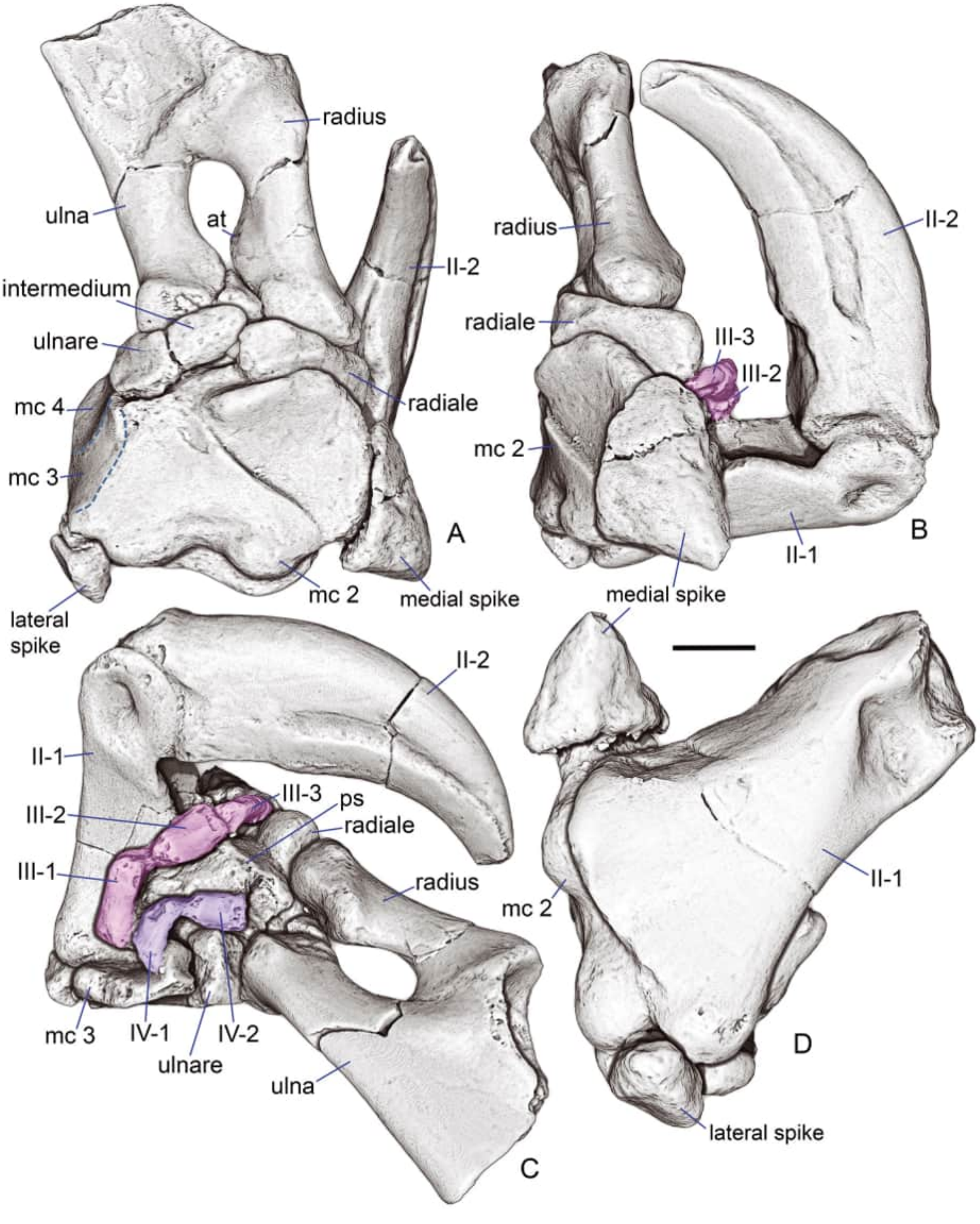

Fig. 6. *Manipulonyx reshetovi* gen. et sp. nov., PIN 3142/364, right manus. A. Extensor view of radius, ulna, and carpal bones. B. Medial view. C. Flexo-lateral view. D. Extensor view of phalanx II-1. Surface rendering based on X-ray computed tomography scans. *Abbreviations:* II-1 and II-2, manual phalanges II-1 and II-2; III-1–III-3, manual phalanges III-1–III-3; IV-1 and IV-2, manual phalanges IV-1 and IV-2; at, aponeurosis tubercle; mc 2–4, metacarpals 2–4; ps, palmar spike. The boundary between the metacarpals is shown by dotted line in A. The third and fourth fingers are highlighted with rose and violet, respectively. Scale bar: 2 mm.

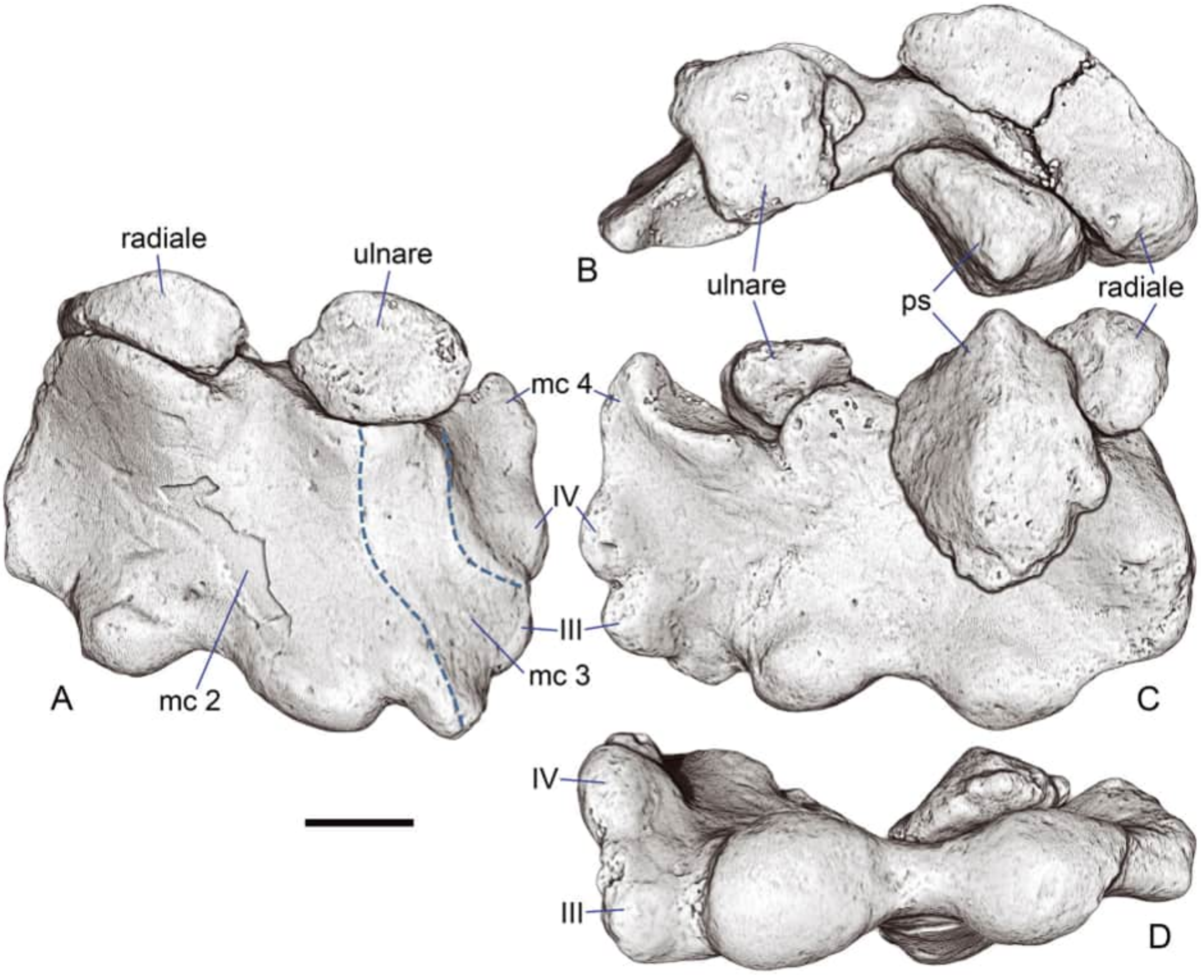

Fig. 7. *Manipulonyx reshetovi* gen. et sp. nov., PIN 3142/364, left carpus. A. Extensor view. B. Proximal view. C. Flexor view. D. Distal view. Surface rendering based on X-ray computed tomography scans. *Abbreviations:* mc 2–4, metacarpals 2–4; ps, palmar spike. Roman numerals III and IV denote articular condyles of metacarpals 3 and 4, respectively. The boundary between metacarpals is shown by a dotted line in A. Scale bar: 2 mm.

only said that distal carpals are unfused and only the semilunar carpal is illustrated (Choiniere et al. 2010: fig. 2H). In *Aorun* there are two carpal bones, identified as radiale and distal carpal 1 (Choiniere et al. 2014). According to the description in Choiniere et al. (2014), the radiale in *Aorun* and *Haplocheirus* is similar to that in many other theropods: it is disk-like, subcircular in proximal view and shallow proximodistally, with a convex distal surface articulating with a well-developed proximal trochlea on distal carpal 1.

The carpal bones were virtually unknown for Parvicursorinae previously, except for the generally accepted idea that the distal semilunate carpal was incorporated into the carpometacarpus (Perle et al. 1993, 1994; Chiappe et al. 2002). Perle et al. (1994) recognized three articular facets on the proximal end of the metacarpus in *Mononykus*: a medial facet formed by fused "semilunate" distal carpal with pulley-like proximal articular surface, a central facet formed by metacarpals 2 and 3, and a small lateral facet formed exclusively by metacarpal 4. The medial facet was incorrectly labelled "lateral proximal articular facet" in fig. 13D in Perle et al. (1994). According to Perle et al. (1994), the relationships between proximal facets of the carpometacarpus and the radius-ulna are not clear. Actually, these proximal facets do not match the distal facets of radius-ulna implying that they were separated by missing proximal

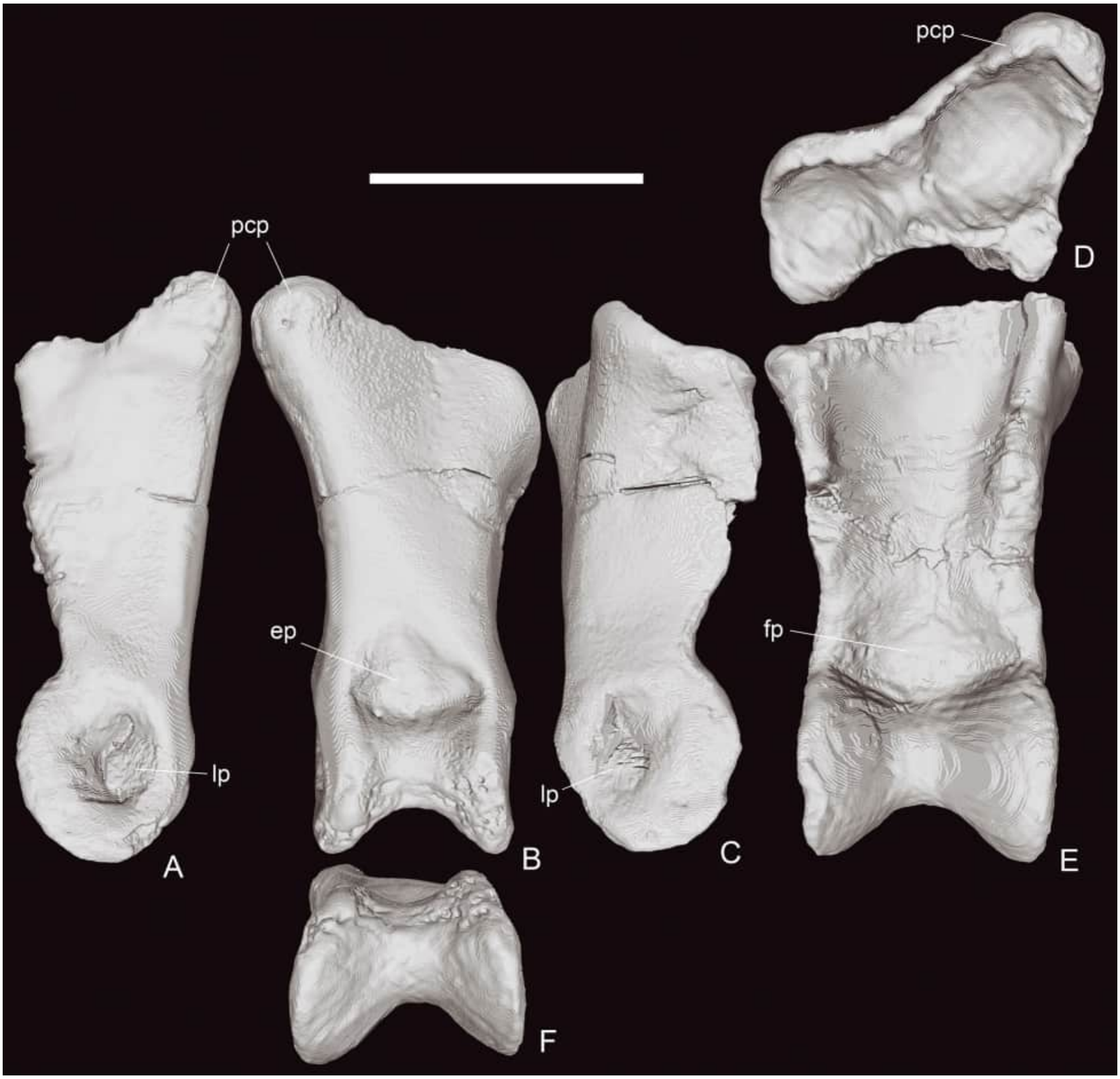

Fig. 8. *Manipulonyx reshetovi* gen. et sp. nov., PIN 3142/364, right manual phalanx II-1. Surface rendering based on X-ray computed tomography scans. A. Lateral view. B. Extensor view. C. Medial view. D. Proximal view. E. Flexor view. F. Distal view. *Abbreviations:* ep, extensor pit; fp, flexor pit; lp, ligament pit; pcp, proximocaudal process. Scale bar: 5 mm.

carpals. The space for these missing carpals is absent in an earlier reconstruction of the *Mononykus* forelimb (Perle et al. 1993: fig. 4) but was added on a later reconstruction (Novas 1996: fig. 8C).

A small carpal bone was identified as radiale on the left manus of *Linhenykus* (Xu et al. 2013: fig. 9A, B). This bone does not cover completely the medial proximal facet of the carpometacarpus and is therefore most likely incomplete. A possible ulnare was identified on the illustration of manus in *Jaculinykus* (Kubo et al. 2023: fig. 11A, C) but not described in the text. Since this bone is located distal to the radius, we doubt that it is an ulnare.

Interpretation of carpal elements in *Manipulonyx*. The putative homology of the three carpal bones in PIN 3142/364 can be tested using Remane's

Fig. 9. *Manipulonyx reshetovi* gen. et sp. nov., PIN 3142/364, right manual phalanx II-2. Surface rendering based on X-ray computed tomography scans. A. Lateral view. B. Flexor view. C. Medial view. D. Extensor view. E. Proximal view. *Abbreviations:* cg, collateral groove; vf, ventral foramen; vs, ventral sulcus. Scale bar: 2 mm.

(1952) three criteria of homology: positional, structural and transitional. According to the positional criterion, these bones are radiale, intermedium, and ulnare, because they are in the proximal carpal row and articulate with the radius (radiale) and the ulna (ulnare and intermedium). In addition, the radiale articulates with the part of the carpometacarpus apparently formed by the distal semilunate carpal. The structural criterion is of little use in this case, because the carpal bones of non-avian theropods are rarely preserved and even less often described in detail. The known carpal bones of non-avian theropods are quite variable in shape, but nothing closely resembling the described carpal bones of PIN 3142/364 has yet been discovered. The transitional criterion of homology supports the interpretation of the three carpal bones in PIN 3142/364 as radiale, intermedium, and ulnare. All these three proximal carpals are present in basal theropods (e.g., *Tawa*) and in the therizinosauroid *Alxasaurus* (Russell and Dong 1994; Sullivan et

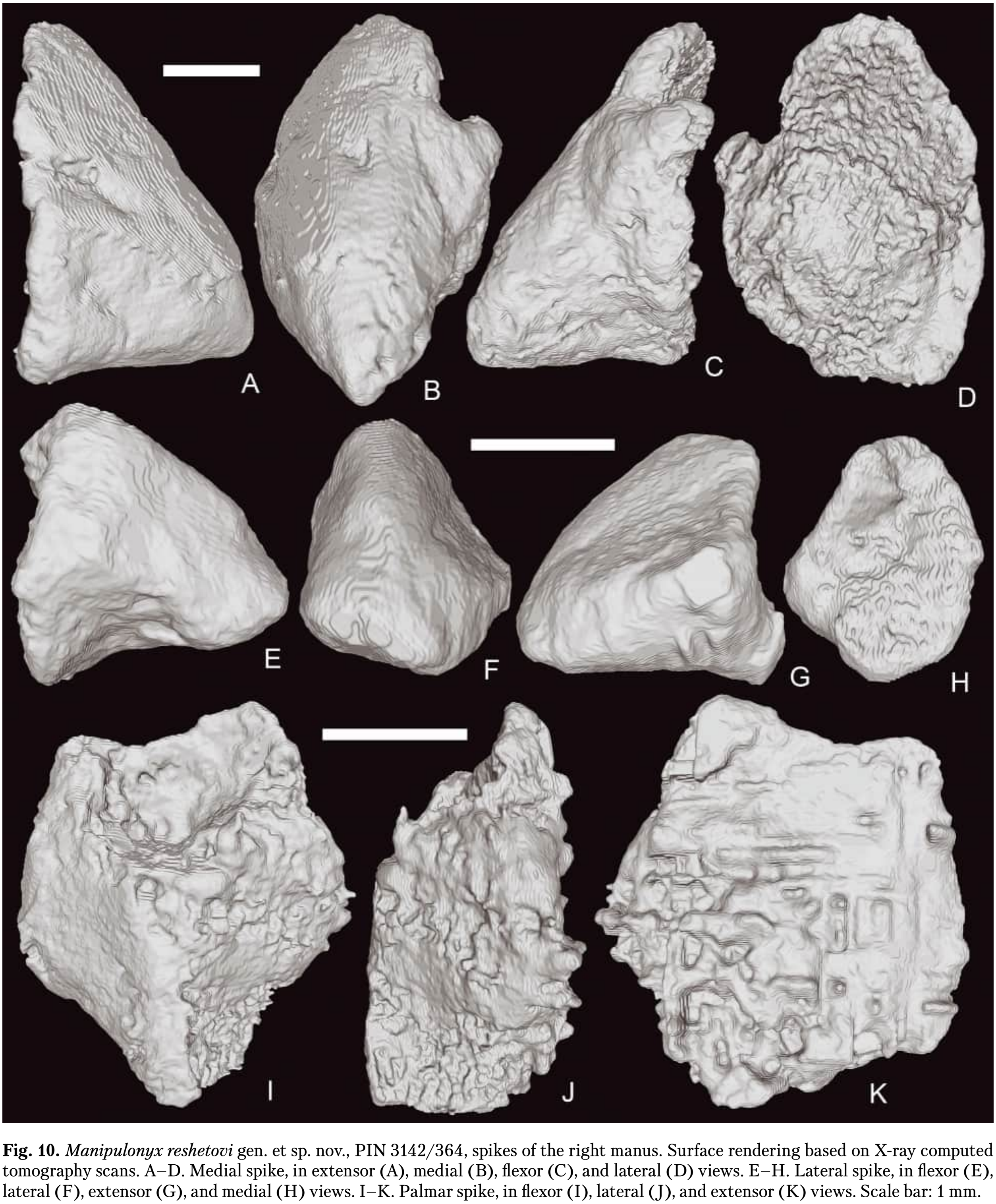

Fig. 10. *Manipulonyx reshetovi* gen. et sp. nov., PIN 3142/364, spikes of the right manus. Surface rendering based on X-ray computed tomography scans. A–D. Medial spike, in extensor (A), medial (B), flexor (C), and lateral (D) views. E–H. Lateral spike, in flexor (E), lateral (F), extensor (G), and medial (H) views. I–K. Palmar spike, in flexor (I), lateral (J), and extensor (K) views. Scale bar: 1 mm.

al. 2010). Therizinosaurians are basal maniraptorans (Zanno 2010) and thus phylogenetically close to alvarezsauroids. The current interpretation of the carpal bones in PIN 3142/364 contradicts the scheme of Botelho et al. (2014), according to which the intermedium is fused with the radiale in maniraptorans, but corresponds to the more ancestral pattern, where the intermedium tends to fuse with the ulnare (Barta et al. 2018).

Alifanov and Barsbold (2009: fig. 2q, r) described and figured two spikes in the manus of *Ceratonykus*, which are roughly similar in size and attached to the bone interpreted as the right(?) carpometacarpus. However, this bone does not look like a parvicursorine carpometacarpus. We are uncertain about the nature of these objects and their relations to the manual spikes in *Manipulonyx.* On the left carpometacarpus of *Ceratonykus* (Alifanov and Barsbold 2009: fig. 2o, p) the medial tab, where the medial spike attaches in PIN 3142/364, is not prominent, virtually absent. This may indicate the absence of a medial spike in *Ceratonykus.*

Averianov and Lopatin (2022) distinguished two different morphologies of the carpometacarpus in Parvicursorinae: 1) the side fingers (3 and 4) are articulated with the round distal articular surfaces of their metacarpals (metacarpal 3 and 4) placed along the lateral margin of the carpometacarpus (*Mononykus*, *Ondogurvel*, and the Tugriken Shireh parvicursorine); and 2) the round articular surface of metacarpal 3 is placed along the distal margin of the carpometacarpus, in line with the distal medial and lateral condyles of metacarpal 2 (*Dzharaonyx*). However, our study of the manus in *Manipulonyx* revealed that the condyle in the carpometacarpus of *Dzharaonyx*, which was mistaken for the condyle of the third digit, actually served to attach the lateral spike, and metacarpals 3 and 4 were not fused with metacarpal 2 in ZIN PH 2440/16 (Averianov and Sues 2017: fig. 3a–d). All three metacarpals are fused in ZIN PH 2443/16 (Averianov and Sues 2017: fig. 3e–h), but the condyles for fingers 3 and 4 are not preserved on that specimen. Thus, only the first described morphology is present in all known parvicursorines except *Linhenykus*, which has lost manual fingers 3 and 4.

Forelimb function and paleobiology of Parvicursorinae. According to the current hypothesis, parvicursorines were fossorial animals using their forelimbs for digging. This hypothesis was first proposed in the description of *Mononykus* (Perle et al. 1993, 1994). The authors of the cited papers found that its highly modified forelimb is similar to that of some fossorial tetrapods. These similarities include the large deltopectoral crest of the humerus, the huge olecranon of the ulna, the short and massive forelimb elements and carpometacarpus, and the robust claw of the single functional manual digit. These characters suggest extremely powerful movements of the forelimb. The authors noted, however, that the elongate gracile hindlimb of *Mononykus* was incongruous with a burrowing habitus, and the forelimbs were presumably used for some other function requiring powerful movement. Nevertheless, *Mononykus* was considered a fossorial animal by Ostrom (1994) and Zhou (1995). It was described as “a fleet-footed fossorial theropod” by Ostrom (1994). Both Ostrom (1994) and Zhou (1995) thought that the keeled sternum of *Mononykus* was convergent with that of fossorial insectivores and indicated its fossorial adaptation. McNeil (1998) noted that the keeled sternum of *Mononykus* was actually quite dissimilar to that structure in fossorial insectivores. In moles, the keel is located on a very elongated manubrium of the sternum, which is totally lacking in *Mononykus.*

According to McNeil (1998), among the six types of fossorial activity distinguished by Hildebrand (1985), only two are worth of consideration for *Mononykus*: the scratch-digging and the hook-and-pull digging. In mammalian scratch-diggers, the major musculoskeletal modifications provide increased strength in flexing the larger digits, flexing the wrist, extending the elbow, flexing the humerus on the scapula, and stabilizing the shoulder (Hildebrand 1985). The medial epicondyle of the humerus, which is an origin of digital and carpal flexors and the pronator, is very prominent, and the lateral epicondyle (an origin of extensors and the supinator) is moderately developed. McNeil (1998) noted that in *Mononykus* the development of the humeral epicondyles is the opposite: the lateral epicondyle (ectepicondyle) is very prominent, but the medial epicondyle (entepicondyle) is virtually absent. She also noted that the olecranon process in *Mononykus,* although greatly enlarged, completely lacks the medial curve that is usual in scratch-diggers. In addition, the pronation of the forelimb, required for scratch-digging, was not possible for *Mononykus* because of fusion of the radius and the ulna at the elbow joint. McNeil (1998) concluded that *Mononykus* was not a scratch-digger because of its

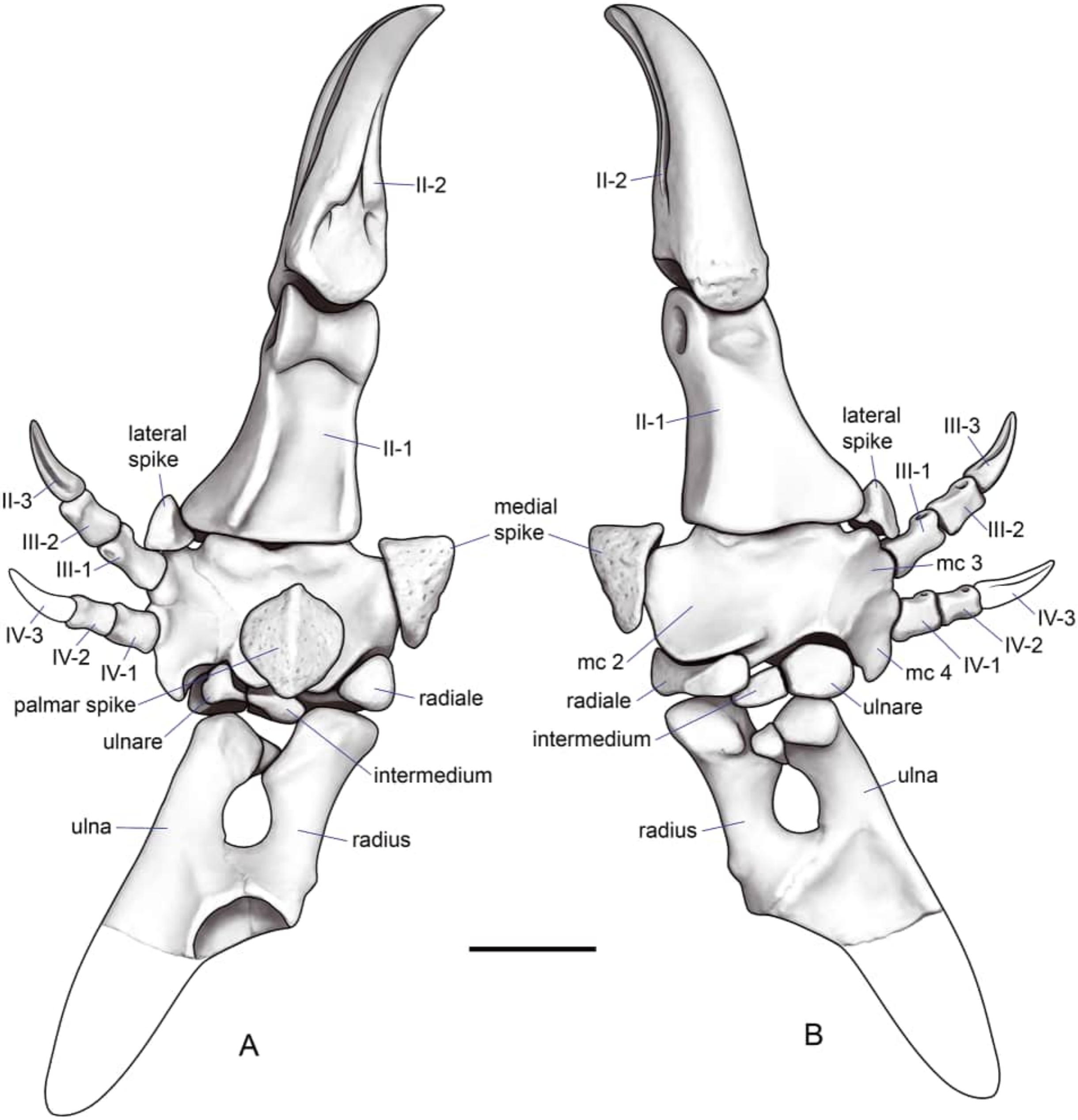

Fig. 11. *Manipulonyx reshetovi* gen. et sp. nov., PIN 3142/364, reconstruction of right forearm and manus in flexor (A) and extensor (B) views. *Abbreviations:* II-1 and II-2, manual phalanges II-1 and II-2; III-1–III-3, manual phalanges III-1–III-3; IV-1–IV-3, manual phalanges IV-1–IV-3; mc 2–4, metacarpals 2–4. Scale bar: 5 mm.

short forelimbs and medial orientation of the claws, coupled with the predominance of conspicuous extensor muscle attachments (rather than flexors).

The hook-and-pull method of digging is employed by anteaters (Taylor 1978; Hildebrand 1985). Anteaters insert the large claws of the second and third manual digits in a hole or crevice and then forcefully pull the forelimb toward the body. The claws can be flexed to a marked degree to grip against the palm, and there is strong pronation and supination

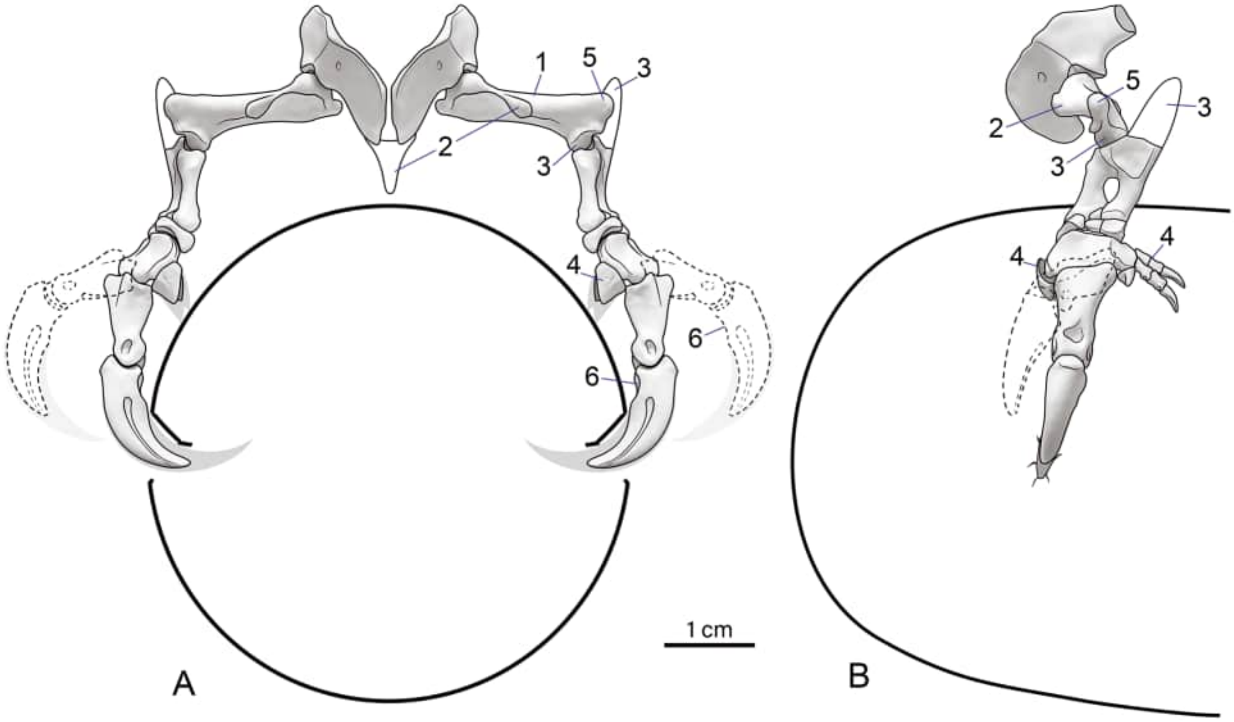

Fig. 12. Reconstruction of the position of forelimbs of *Manipulonyx reshetovi* gen. et sp. nov. during manipulation of a theropod egg (based on PIN 3142/364). A. Anterior view. B. Left lateral view. The theropod egg is about 6 cm in transverse diameter, which is within the common size range for oviraptorid eggs. The position of the manual digit II in maximum extension before puncturing the egg-shell is indicated by a dotted line. The keratinous sheaths of the carpal spikes and the ungual phalanx of manual digit II are shown in grey. Morphofunctional traits discussed in the paper: 1, lateral projection of humerus; 2, hypertrophied deltopectoral crest of humerus and keeled sternum; 3, single distal articular condyle of humerus and hypertrophied olecranon process of ulna; 4, carpal spikes and side manual digits; 5, humerus ectepicondyle; 6, lack of flexor tubercle on ungual phalanx of manual digit II.

of the forearm to deflect the claws from side to side. According to McNeil (1998), *Mononykus* lacks the features that facilitate digital flexion, such as the medial epicondyle and the flexor tubercle. The limited range of motion at individual joints in *Mononykus* effectively rules out pronation and supination. She concluded that *Mononykus* was not a hook-and-pull digger.

The functional study of the shortened forelimbs in *Mononykus* (Senter 2005, 2023) explored the range of motion of individual forelimb bones by manual manipulation of their casts. This method is based on the presumption that the articular surfaces at each joint between the bones represent the limits of their possible motion. It was concluded that the humerus of *Mononykus* had a wide range of motion that allowed the animal to tuck its arms in at the sides, in addition to allowing them to sprawl so as to orient the palm downward (Senter 2023).

Senter (2023) introduced the term skalodactyl (shovel finger) for a specialized finger with a prominent claw. He listed pangolins, anteaters, and some armadillos as extant skalodactylous animals, which use their forelimbs for hook-and-pull digging. He thought that Late Cretaceous alvarezsaurids were skalodactylous and used their forelimbs for a similar activity. However, there is a drastic difference in the forelimb structure between skalodactylous mammals and alvarezsaurids. In the discussed mammals, there is one large finger with a big claw accompanied by one or two side fingers of somewhat smaller size but also bearing a big claw. These two or three fingers effectively form the shovel blade useful for digging. In alvarezsaurids, the side fingers are greatly reduced in size or completely lost. Such a structure does not resemble a shovel in any way and cannot be used effectively for digging. Alvarezsaurids cannot be considered skalodactylous animals.

The assumption that parvicursorines were fossorial animals seems implausible. Because of the great disparity between the length of the forelimbs and hind limbs in parvicursorines, their forelimbs were clearly unable to reach the ground from a standing position (McNeil 1998). The idea about the fossorial mode of life in parvicursorines is inconsistent with their elongated hindlimbs adapted for fast running. The fossorial hypothesis does not explain the evolutionary trends in parvicursorines for miniaturization and forelimb reduction. What evolutionary advantages would diggers gain by being short-armed? It is much more convenient to dig with long forelimbs than with short ones.

The idea that parvicursorines used their hypertrophied manual claw to break eggs and were egg-eating animals was first proposed by Lü et al. (2018) in the description of a *Qiupanykus* skeleton associated with oviraptorid egg shell fragments from the Maastrichtian Qiupa Formation of Henan Province, China. This association of a parvicursorine skeleton with theropod egg-shell fragments was first announced in the Society of Vertebrate Paleontology meeting abstract (Kundrát et al. 2017). The skeleton of *Manipulonyx* was also associated with egg-shell fragments according to its original label. Agnolin et al. (2012) described a fragmentary skeleton of a non-parvicursorine alvarezsaurid *Bonapartenykus* associated with two partially preserved eggs and several clusters of broken egg-shells from the Campanian–Maastrichtian Allen Formation of Argentina. According to Kundrát et al. (2017), these eggs were laid by *Bonapartenykus*. This interpretation was questioned by Lü et al. (2018), who thought that the eggs possibly belonged to an oviraptorosaurid theropod. We consider it equally probable that *Bonapartenykus* was eating these eggs, rather than laying them.

The hypothesis that parvicursorines were egg-eating animals and used their short powerful forelimbs with a hypertrophied manual claw to manipulate eggs is supported by a suite of morphofunctional traits that are outlined below (see also Fig. 12).

1) Lateral projection of humerus. The scapulocoracoid glenoid faces posterolaterally in *Manipulonyx*, other parvicursorines (Perle et al. 1994; Lee et al. 2019), and *Bonapartenykus* (Agnolin et al. 2012). In contrast, in *Alvarezsaurus* and non-alvarezsaurid alvarezsauroids the glenoid faces posteriorly (Bonaparte 1991; Xu et al. 2018). This would result in a more lateral projection of the humerus in parvicursorines. This allows both forelimbs to grasp the egg.

2) Hypertrophied deltopectoral crest of humerus and keeled sternum. The deltopectoral crest of humerus is hypertrophied in *Manipulonyx* and other parvicursorines. The sternum is unknown for *Manipulonyx*, but other parvicursorines have a keeled sternum (Perle et al. 1994; Chiappe et al. 2002; Alifanov and Barsbold 2009; Xu et al. 2013). In non-avian theropods, *m. pectoralis* may originate from several different shoulder girdle elements, including the sternum (Jasinoski et al. 2006; Burch 2017). In birds, this muscle originates from the sternum keel (Ostrom 1976). *M. pectoralis* inserts on the medial surface of the deltopectoral crest of humerus (Burch 2017). Thus, it is reasonable to assume that development of the sternum keel and the enlarged deltopectoral crest of humerus in parvicursorines indicate a powerful *m. pectoralis* in these animals. The function of this muscle is flexion (= "adduction") and abduction (= "protraction") of the humerus (Jasinoski et al. 2006). According to McNeil (1998), contraction of *m. pectoralis* in *Mononykus* would result in anteromedial adduction of the humerus. With the egg held in the forelimbs, these movements would squeeze the egg, preventing it from falling (Fig. 12).

3) Elbow joint and olecranon process. In *Manipulonyx* and other parvicursorines (Perle et al. 1994; Chiappe et al. 2002; Averianov and Sues 2022), the distal condyle of humerus is restricted to a small convex oval-shaped articular surface near the posterior margin of the distal side. The proximally fused ulna and radius has a joined oval-shaped concave articular surface that fits tightly into the distal articular surface of the humerus. This construction of the elbow joint in parvicursorines results in the orientation of the forearm perpendicular to its orientation in other non-avian theropods having two distal (ulnar and radial) condyles of the humerus. Such a configuration of the elbow joint in parvicursorines restricts movements of the forearm to flexion-extension in the transverse plane. The olecranon process is hypertrophied in parvicursorines (Perle et al. 1994; McNeil 1998; Longrich and Currie 2009). In *Manipulonyx*, the olecranon process is partially preserved, but it was undoubtedly as large as that of other parvicursorines (Fig. 11). The olecranon process is the place of insertion of *m. triceps brachii* whose function is extension of the forearm (McNeil 1998; Jasinoski et al. 2006). We hypothesize that rapid contraction of the powerful *m. triceps brachii* resulted in sharp extension of the elbow joint, causing an egg held be-

tween the forelimbs to be released and smashed on the ground. A fairly strong movement was needed to free the manual claw, which could become stuck in the egg-shell.

4) Carpal spikes and side manual digits. Carpal spikes have so far been discovered only in *Manipulonyx* (this report), but the prominent medial tab on the carpometacarpus of other parvicursorines (Perle et al. 1994; Xu et al. 2013; Averianov and Sues 2017; Averianov and Lopatin 2022) suggest that they also had at least the medial spike. We hypothesize that the medial and lateral spikes, as well as the rudimentary side fingers, were used to anchor the hand to the slippery surface of the egg, which was necessary to effectively pierce the shell (Fig. 12). During such anchoring, the shell could be fixed or slightly punctured by the sharp keratinous sheath covering the spikes.

5) Humerus ectepicondyle. The hypertrophied ectepicondyle of the humerus is present in *Manipulonyx*, other parvicursorines (Perle et al. 1994; Chiappe et al. 2002), and *Patagonykus* (Novas 1996, 1997). No other theropods possess such a structure (McNeil 1998). The ectepicondyle is the place of origin of *m. anconeus*, which acts to extend the elbow (McNeil 1998; Burch 2014; Smith 2021). According to McNeil (1998), the prominence of the ectepicondyle in the humerus of *Mononykus* suggests that the primary action of the forearm is related to powerful extension (rather than flexion) in that taxon. This observation contradicts the fossorial hypothesis, because digging requires powerful flexion and development of the medial epicondyle (entepicondyle) of the humerus, which is hypertrophied in specialized diggers (Taylor 1978; Hildebrand 1985; McNeil 1998; Rose 1999). However, powerful extension is required to free a manual claw stuck in an eggshell, as hypothesized in point 4.

6) Flexor tubercle of manual ungual phalanx. The lack of a flexor tubercle on the hypertrophied manual ungual phalanx of *Mononykus* was considered the most curious and striking feature of that taxon (McNeil 1998). The flexor tubercle is also absent in *Manipulonyx* and other parvicursorines (Perle et al. 1994; Longrich and Currie 2009; Xu et al. 2013; Averianov and Sues 2017, 2022). The flexor tubercle serves as attachment areas for the muscles that flex the ungual and is present in all other theropods. More powerful flexion of the ungual phalanx can be achieved either by increasing the size of the flexor tubercle or by placing it in a more distal position (Nicholls and Russell 1985). The lack of a flexor tubercle is inconsistent with the fossorial mode of life because all diggers have the developed flexor tubercle needed for powerful claw flexion during digging (Hildebrand 1985). The only function that requires a strong manual claw but would be impeded by the flexor tubercle is perforation of the egg-shell, when the entire finger fits tightly against the surface of the shell, leaving no space for the flexor tubercle (Fig. 12).

The above-discussed and other morphofunctional traits of Parvicursorinae allow us to assume that these animals were nocturnal hunters of dinosaur eggs and that they specialized in feeding on eggs. These animals had binocular vision and specialized hearing acuity, which indicates their nocturnal lifestyle (Choiniere et al. 2021). Apparently, they hunted when other dinosaurs were less active. They would find a clutch of eggs, grab one egg with their specialized forelimbs and quickly run away. The adaptation to fast running in their hind limbs definitely indicates the presence of parental care in the dinosaurs whose eggs they stole. Having reached a secluded place, parvicursorines loosened their forelimbs, the egg fell and broke on the ground. In cases where they were unlucky and were caught by angry parents, they died along with the stolen egg. This explains the associated finds of parvicursorine skeletons with dinosaur egg-shell fragments.

Qin et al. (2021) hypothesized that alvarezsauroid miniaturization was coincident with the emergence of ants and termites and indicates a shift to the myrmecophagous ecological niche. However, this hypothesis does not explain why it was necessary to decrease in size in order to feed on social insects (Averianov et al. 2023). In modern fauna, social insects are eaten by animals of various sizes. No line of specialized myrmecophages shows a tendency toward miniaturization. However, this tendency becomes understandable if we assume that the shift was to the egg-eating (ovivorous) ecological niche. To effectively grasp the egg with forelimbs, parvicursorines had to be close to the size of the egg. Our hypothesis of ovivorous parvicursorines can be tested by independent data: the discovery of dinosaur egg-shell fragments with characteristic punctures.

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