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A Basal Alvarezsauroid Theropod from the Early Late Jurassic of Xinjiang, China

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The fossil record of Jurassic theropod dinosaurs closely related to birds remains poor. A new theropod from the earliest Late Jurassic of western China represents the earliest diverging member of the enigmatic theropod group Alvarezsauroida and confirms that this group is a basal member of Maniraptora, the clade containing birds and their closest theropod relatives. It extends the fossil record of Alvarezsauroida by 63 million years and provides evidence for maniraptorans earlier in the fossil record than *Archaeopteryx*. The new taxon confirms extreme morphological convergence between birds and derived alvarezsauroids and illuminates incipient stages of the highly modified alvarezsaurid forelimb.

The presence of the basal avialan (*I-3*) *Archaeopteryx* in the latest Late Jurassic (Tithonian) and the poor fossil representation of more basal maniraptoran taxa in contemporaneous or slightly older deposits indicate either a gap in the stratigraphic record or, more controversially, that birds are not related to theropods (4). Recent discoveries of Middle-Late Jurassic maniraptorans (5–7) from China are starting to fill in the temporal gap, but the ages of these new taxa are poorly resolved (8, 9), and they do not clarify basal maniraptoran diversification because very little character evidence separates them from birds (5, 7).

Here, we describe a three-dimensionally preserved, nearly complete skeleton of an alvarezsaurid theropod, *Haplocheirus sollers*, gen. et spec. nov. (10), from orange mudstone beds in the upper part of the Shishugou Formation in Wucaiwan area, Junggar Basin, Xinjiang, China. Radiometric dating constrains the age of this fossil to between 158.7 ± 0.3 and 161.2 ± 0.2 Ma (million years ago) (11), corresponding to the Oxfordian marine stage in the early Late Jurassic (12). The dates for *Haplocheirus* reduce the conflict between the fossil record and phylogenetic hypotheses that early maniraptoran diversification took place in the Jurassic. Alvarezsauroids are known from South America (13–15), Asia (16–19), North America (20, 21), and Europe (22, 23). The basal phylogenetic position and early temporal position of *Haplocheirus* imply that Alvarezsauroida originated in Asia rather than South America (14, 20). Derived members of the Alvarezsaur-

oidea were originally thought to be flightless basal avialans (18) because they share many morphological characteristics with birds, including a loosely sutured skull, a keeled sternum, fused wrist elements, and a posteriorly directed pubis. *Haplocheirus* preserves plesiomorphic morphological characteristics that confirm a basal position for Alvarezsauroida within Maniraptora (24), demonstrating that these features of derived alvarezsauroids represent dramatic convergences with birds.

IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) V15988 (Figs. 1 and 2 and figs. S4 to S9) is ~140 cm in total body length as preserved but is missing the end of the tail (estimated total length 190 to 230 cm; table S1). The bones of the braincase are coossified and the neurocentral sutures are visible, suggesting that the animal is likely a young adult or late-stage subadult.

The gracile, low skull (Fig. 2A and figs. S4 to S7) is well preserved in three dimensions. The narrow, elongate rostrum becomes taller and wider just anterior to the large, anterolaterally facing orbits. The dorsoventrally thin jugal is triradiate, unlike the rodlike jugal of more derived alvarezsauroids (17). In lateral view, the basisphenoid is oriented at 45° to horizontal, a condition present in some troodontids (25) and in alvarezsauroids (17). The basiptyergoid processes are long and project ventrolaterally, a morphology known only in primitive birds and alvarezsauroids among Theropoda (17).

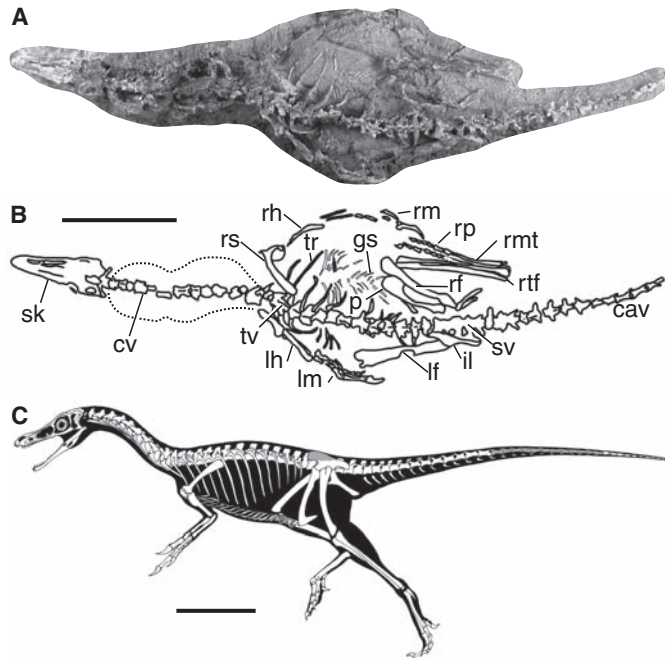
At least 30 small maxillary teeth are present in *Haplocheirus*, as in *Shuvuuia* (17), *Pelecanimimus* (26), therizinosauroids (27), and troodontids (28). Unlike the conical, un serrated teeth of *Mononykus* (28) and *Shuvuuia* (29), however, the maxillary teeth of *Haplocheirus* are

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Fig. 1. *Haplocheirus sollers* (IVPP V15988).

(A) Photograph of holotype in dorsal view. (B) Line drawing of holotype in dorsal view. Dashed line indicates crocodyli-form fossil underlying cervical vertebrae. (C) Reconstruction. Gray fill indicates portions of the skeleton that are not preserved. Abbreviations: cav, caudal vertebrae; cv, cervical vertebrae; gs, gastralia; il, left ilium; lf, left femur; lh, left humerus; lm, left manus; p, pubis; rf, right femur; rh, right humerus; rm, right manus; rmt, right metatarsus; rp, right pes; rs, right scapula; rtf, right tibia and fibula; sk, skull; sv, sacral vertebrae; tr, thoracic ribs; tv, thoracic vertebrae. Scale bar: 25 cm.



recurved and bear small serrations posteriorly (fig. S4). *Haplocheirus* shows marked heterodonty in both the maxilla and the dentary, with the maxillary teeth diminishing in size posteriorly (fig. S5) and the lower jaw bearing large, subconical, unserrated anterior teeth and smaller, recurved, serrated posterior teeth (fig. S4).

The cervical centra lack the strong opisthocoealous condition of *Shuvuuia* and *Mononykus* (29). The five sacral vertebrae all lack the ventral keel present in other alvarezsauroids (29). The centrum of sacral five is amphiplatyan, whereas in *Mononykus* and *Shuvuuia* (29) the last sacral centrum bears a convex posterior surface for articulation with the procoelous first caudal vertebra. Similar to other alvarezsauroids, the mid-caudal vertebrae have short and anterodorsally oriented prezygapophyses, whereas in most coelurosaurs the prezygapophyses of the mid-caudal vertebrae are long and horizontally oriented. A sternum was not found with the specimen.

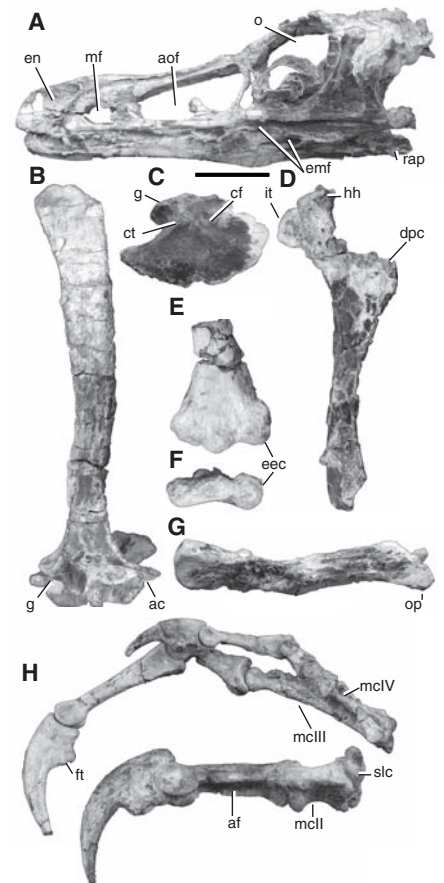
The ovate coracoid has a long posteroventral process and bears a well-developed biceps tubercle, which is lost in other alvarezsauroids. Similar to the basal alvarezsauroid *Patagonykus* (30), the hypertrophied rectangular internal tuberosity of the humerus is separated from the humeral head by a distinct notch, and the humeral ectepicondyle is large and hemispherical distally. The incomplete ulna bears a well-developed olecranon process, as do all alvarezsauroids. Proximally, the radius articulates with a lateral concavity on the ulna.

Unlike the avianlike carpometacarpus (29) of more derived alvarezsauroids, the distal carpals are unfused. Metacarpal II (the medial metacarpal) is 1.9 times the width of metacarpal III (Fig. 3), wider than in most maniraptorans but narrower

than in *Mononykus* and *Shuvuuia* (29). Metacarpal IV is only half the length of metacarpal III, a condition unknown in other theropod dinosaurs. The middle digit is the longest in the manus, unlike in *Shuvuuia*, where the second and third digits are both much shorter than the first digit (31). Manual phalanx II-1 bears a deep axial furrow, unlike in *Shuvuuia*, which are flat and lack flexor tubercles.

The pubis projects anteroventrally (figs. S8 and S9), which is the plesiomorphic condition for maniraptorans, in contrast with the vertical pubes of *Patagonykus* (30) and highly retroverted pubes of derived alvarezsauroids (29). The curved femur bears a plesiomorphic alariform lesser trochanter, consistent with the femoral morphology of *Alvarezsaurus* (14) and *Patagonykus* (30). The lateral distal condyle of the femur is conical (fig. S9) and projects further distally than the medial condyle, a morphology known only in some troodontids and alvarezsauroids (14). There is no development of an avianlike medial cnemial crest, as in *Mononykus* and *Shuvuuia* (26). The third metatarsal is fully exposed in anterior view and is a component of the ankle joint, as in the basal alvarezsauroids *Patagonykus* and *Alvarezsaurus* (13, 30).

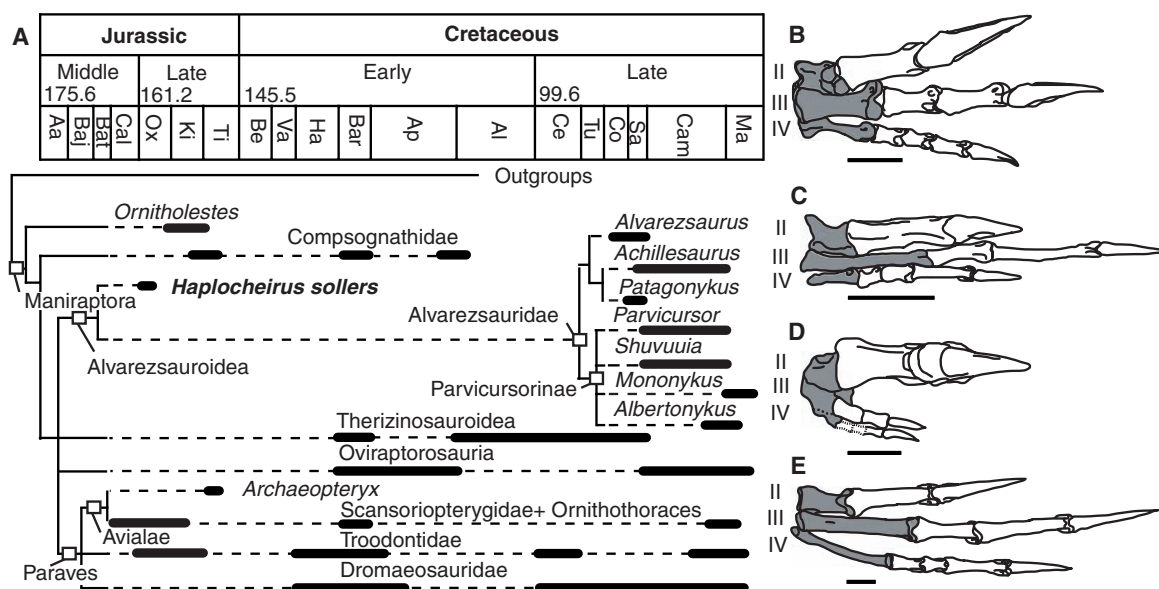
A phylogenetic analysis of 99 theropod taxa shows that *Haplocheirus* is the basalmost member of the Alvarezsauroida [Fig. 3 and fig. S1; see Supporting Online Material (SOM) for full details]. *Haplocheirus* possesses unambiguous synapomorphies that support the monophyly of the Alvarezsauroida, including long basiptyergoid processes, a vertically inclined basisphenoid,

**Fig. 2.** *Haplocheirus sollers* (IVPP V15988) skull and forelimb elements. (A) Skull in left lateral view. (B) Right scapula in lateral view. (C) Right coracoid in lateral view. (D) Right humerus in lateral view. (E) Left distal humerus in flexor view. (F) Left distal humerus in distal view. (G) Right ulna in medial view. (H) Left manus in lateral view, with digit II separated from manus. Abbreviations: ac, acromion process; af, axial furrow; aof, antorbital fenestra; cf, coracoid foramen; ct, coracoid tuberosity; dpc, deltopectoral crest; eec, ectepicondyle of humerus; emf, external mandibular fenestra; en, external naris; ft, flexor tubercle; g, glenoid; hh, humeral head; it, internal tuberosity; mclI to mclIV, metacarpals I to IV; mf, maxillary fenestra; o, orbit; op, olecranon process of the ulna; rap, retroarticular process; slc, semilunate carpal. Scale bar: 4 cm.

a hypertrophied internal tuberosity of the humerus proximally level with the humeral head, a large humeral ectepicondyle, a pronounced axial furrow on the flexor surface of manual phalanx II-1, and a conical lateral distal condyle of the femur.

Although a basal position of alvarezsauroids within Maniraptora has been proposed (24, 32–34), the global phylogenetic placement of this group within Theropoda has been untested by the recent description of new alvarezsauroid material from Canada (20), Argentina (15), and Mongolia (19). Early analyses placed alvarezsauroids as either sister to, or nested within, Avialae (28, 29). Alvarezsauroida has also been hypothesized as

Fig. 3. Phylogenetic relationships of *Haplocheirus sollers* and hand comparisons of selected theropods. **(A)** Simplified, temporally calibrated cladogram of the strict consensus of 69 most parsimonious trees produced in this analysis (see also fig. S1). Thick lines with rounded end caps indicate stratigraphic range of known taxa. Thin black lines with square ends indicate phylogenetic relationship. Dashed lines represent ghost lineages implied by the stratigraphic distribution of fossils with respect to the phylogenetic relationships shown here (note the exceptionally long ghost lineage for Alvarezsauroidea). Arabic numerals indicate ages in millions of years before present. Boxes represent named clades. **(B to E)** Reconstructed theropod mani scaled to digit two length. **(B)** *Allosaurus fragilis* after Madsen (40). **(C)** *Haplocheirus sollers* (IVPP V15988). **(D)** *Shuvuuia deserti* after Suzuki *et al.* (31). **(E)** *Deinonychus antirrhopus* after Ostrom (41). Metacarpal elements are shaded, dashed lines



in (D) indicate inferred digital elements. Abbreviations: II to IV, manual digits II to IV; Aa, Aalenian; Baj, Bajocian; Bat, Bathonian; Cal, Callovian; Ox, Oxfordian; Ki, Kimmeridgian; Ti, Tithonian; Be, Berriasian; Va, Valanginian; Ha, Hauterivian; Bar, Barremian; Ap, Aptian; Al, Albanian; Ce, Cenomanian; Tu, Turonian; Co, Coniacian; Sa, Santonian; Cam, Campanian; Ma, Maastrichtian. Scale bar: 5 cm (B), 4 cm (C and E), 0.5 cm (D).

the sister taxon to Ornithomimosauria (33). Our phylogenetic analysis agrees with still other research (2, 24) in placing Alvarezsauroidea as a relatively basal maniraptoran group. Our most parsimonious trees do not support either avialan or ornithomimosaurian affinities for the Alvarezsauroidea, although the ornithomimosaur hypothesis is nearly as well supported. The shortest tree found when constraining the Alvarezsauroidea to be sister to or nested within Avialae is seven steps longer than the optimal tree. The minimum length of trees produced when constraining Alvarezsauroidea to be sister to or nested within Ornithomimosauria is one step longer than the optimal tree (see SOM for phylogenetic details).

The Middle to Late Jurassic (Bathonian-Kimmeridgian) age (8, 9) of newly described maniraptorans from China (6, 7) implies that the Alvarezsauroidea have a minimum ghost lineage (35) of ~63 million years (Fig. 3). The presence of *Haplocheirus* in the early Late Jurassic of China confirms the prediction made from this ghost lineage that alvarezsauroids were present at this time. To explore the effect of *Haplocheirus* on congruence between stratigraphic information and phylogenetic hypotheses for the Coelurosauria (36–39), we compared the gaps in the fossil record implied before and after inclusion of *Haplocheirus* (37, 39). The addition of the earliest Late Jurassic *Haplocheirus* improves the stratigraphic fit of the maniraptoran fossil record to the topologies recovered in our analysis by an average of 14%, from a mean fit of 0.41 to 0.48 (fig. S3).

Haplocheirus is the largest alvarezsauroid known from complete material (see SOM), and its

basal phylogenetic position suggests a pattern of miniaturization for the Alvarezsauroidea, relatively rare in dinosaurs but convergently evolved in Paraves (2). Derived alvarezsauroids have a simplified, homogeneous dentition convergent with that of some extant insectivorous mammals (20), but *Haplocheirus* has recurved, serrated teeth and caniniforms that suggest carnivory was the primitive condition for the clade. The presence in *Haplocheirus* of only slightly reduced second and third manual digits and curved unguals with flexor tubercles on these digits implies that the hand was fully functional and *Haplocheirus* retained some grasping ability, unlike the presumably limited function of the greatly reduced lateral manual elements of *Mononykus* and *Shuvuuia* (31). The mediolaterally narrow McIII (metacarpal three) and the greatly shortened and slender McIV suggest that the extensive digital reduction and fusion seen in derived alvarezsauroids was already under way by the earliest Late Jurassic, proceeded from lateral to medial on the manus and, surprisingly, initially involved reduction in length of only McIV.

References and Notes

- We use the definition of Avialae from (2), the least inclusive clade containing *Archaeopteryx lithographica* and crown group birds, rather than the definition from (3), all taxa sharing a more recent common ancestor with *Archaeopteryx* than with *Troodon formosus*.
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Anciently Asexual Bdelloid Rotifers Escape Lethal Fungal Parasites by Drying Up and Blowing Away

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Asexuality has major theoretical advantages over sexual reproduction. An important evolutionary puzzle, therefore, is why exclusively asexual metazoan lineages rarely endure. The Red Queen hypothesis posits that asexuality is rapidly extinguished by relentlessly coevolving parasites and pathogens. If so, any long-lasting asexual lineage must have unusual alternative mechanisms to deal with these biotic enemies. Bdelloid rotifers are freshwater invertebrates that abandoned sexual reproduction millions of years ago. Here, we show that cultured populations of bdelloids can rid themselves of a deadly fungal parasite through complete desiccation (anhydrobiosis) and disperse by wind to establish new populations in its absence. In Red Queen models, spatiotemporal escape can decouple and protect asexuals from coevolving enemies. Thus, our results may help to explain the persistence of the anciently asexual Bdelloidea.

Sexual reproduction reduces the efficiency of gene transmission by up to 50%, disrupts favorable gene combinations, spreads disease, and is energetically expensive (1). Yet, paradoxically, sex is nearly ubiquitous: Obligate asexuality occurs in less than 1% of animal species (1, 2), and its scattered distribution at the tips of phylogenetic trees implies that abandoning sex condemns a clade to extinction before it can radiate sufficiently to achieve high taxonomic rank.

The class Bdelloidea (phylum Rotifera) is a famous exception. During three centuries of observation, more than 450 species of these tiny freshwater invertebrates have been described, but

neither males nor meiotic eggs have ever been recorded (3). Molecular evidence supports the inference that bdelloid rotifers have been obligately asexual for tens of millions of years (2–5).

Hypotheses for sexual reproduction suggest that it is maintained because it removes deleterious mutations, facilitates coevolution with parasites and pathogens, or both (2, 5–8). However, mutational hypotheses have been challenged empirically (1, 5, 6, 9), and mutational load may be less problematic than predicted, because the bdelloids have persisted despite accumulating mutations faster than related sexual clades (4). In contrast, the coevolution (Red Queen) hypothesis has received considerable empirical and theoretical support (1, 5–11).

Under Red Queen models, biotic interactions favor sex by relentlessly imposing fluctuating, time-lagged, frequency-dependent selection (6–10). However, asexuality can be maintained

in one special case: when vulnerable hosts can temporarily shed locally coadapted parasites and pathogens and disperse without them to uninfected habitats (11). Migration and clonal diversity at the population level can then substitute for recombination and genetic diversity at the individual level, allowing mobile hosts to avoid the costs of sex while continuing to “outrun” their enemies (11, 12). Dispersal further favors asexuality by reducing intergenerational transmission of infections (13).

Three unusual characteristics of bdelloid rotifers suggest that this scenario may apply to them (5, 11, 12). First, bdelloids can survive extended (up to 9 years) and repeated bouts of complete desiccation (anhydrobiosis) at any life stage (14, 15). Second, anhydrobiotic bdelloids have an extraordinary potential for wind dispersal as tiny (usually <300 μm) ovoid propagules (called “tuns”) (14–17), resulting in circumglobal distribution of some taxa (18). Third, bdelloids can thrive in almost any moist habitat, rapidly colonizing even the most ephemeral patches of moss or rainwater on every continent (14–18).

All identified parasites of bdelloid rotifers are oomycetes or hyphomycete fungi. Most belong to *Rotiferophthora*, a genus of obligate, lethal fungal endoparasites that are exclusive to bdelloids (19, 20). Infections spread when rotifers ingest spores (conidia), which lodge in their pharynx and produce assimilative hyphae. As the rotifer is killed and digested, hyphae puncture its integument and, at the air/water interface, produce conidiophores carrying hundreds of new conidia.

We investigated whether populations of the bdelloid rotifer *Habrotrocha ehusa* can escape the fungal parasite *Rotiferophthora angustispora* (19) in space and time, through anhydrobiosis and subsequent wind dispersal. We transferred rotifers from a monoclonal population singly to

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