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Cranial osteology of *Haplocheirus sollers* Choiniere et al., 2010 (Theropoda: Alvarezsauroidea)

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AND XING XU⁴

ABSTRACT

The basalmost alvarezsauroid *Haplocheirus sollers* is known from a single specimen collected in Upper Jurassic (Oxfordian) beds of the Shishugou Formation in northwestern China. *Haplocheirus* provides important data about the plesiomorphic morphology of the theropod group Alvarezsauroidea, whose derived members possess numerous skeletal autapomorphies. We present here a detailed description of the cranial anatomy of *Haplocheirus*. These data are important for understanding cranial evolution in Alvarezsauroidea because other basal members of the clade lack cranial material entirely and because derived parvicursorine alvarezsauroids have cranial features shared exclusively with members of Avialae that have been interpreted as synapomorphies in some analyses. We discuss the implications of this anatomy for cranial evolution within Alvarezsauroidea and at the base of Maniraptora.

INTRODUCTION

Alvarezsauroidea is a clade of theropod dinosaurs whose derived members possess remarkably birdlike features, including a lightly built, kinetic skull, several vertebral modifications, a keeled sternum, a fused carpometacarpus, a fully retroverted pubis and ischium

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that do not contact at the body midline, and a gracile hind limb. Furthermore, derived alvarezsauroids possess highly specialized forelimbs consisting of a short, robust humerus with large muscle attachments, an ulna with an extensive olecranon process, and a single functional claw on the manus that is hypertrophied relative to the other digits (Bonaparte, 1991; Perle et al., 1993; Novas, 1996; Chiappe et al., 1998; Suzuki et al., 2002; Longrich and Currie, 2008; Xu et al., 2010; Xu et al., 2011). There is strong direct (as opposed to phylogenetic) evidence of a feathered body covering in one member of this group (Schweitzer et al., 1999).

The recognition of Alvarezsauroida as a monophyletic clade of maniraptoran theropods is relatively recent, with members of the group first being described in 1991 (Bonaparte). The most complete skeletal material of alvarezsauroids is from Late Cretaceous deposits in Mongolia, first described in 1993 (Perle et al., 1993; Perle et al., 1994; Chiappe et al., 1998). Recently, there has been an explosion of alvarezsauroid discoveries in Asia (Xu et al., 2010; Nesbitt et al., 2011; Xu et al., 2011; Hone et al., 2012; Xu et al., 2013), Europe (Naish and Dyke, 2004; Kessler et al., 2005), North America (Longrich and Currie, 2008), and South America (Martinelli and Vera, 2007; Agnolin et al., 2012).

Several birdlike features of derived alvarezsauroids initially led to phylogenetic hypotheses that placed these taxa either within, or sister to, the derived theropod group Avialae (Perle et al., 1993; Chiappe et al., 1998). This phylogenetic result was contentious (Chiappe et al., 1997), and subsequent discovery of more plesiomorphic forms from South America (Novas, 1996; 1997) led to a new hypothesis for Alvarezsauroida as a basal coelurosaurian lineage (Sereno, 2001; Novas and Pol, 2002). The position of the clade is still an unresolved issue in theropod systematics (Zhou, 1995; Chiappe, 1996; Chiappe et al., 1997; Sereno, 2001; Novas and Pol, 2002; Suzuki et al., 2002; Lee and Worthy, 2011; Spencer and Wilberg, 2013). One of the reasons for the phylogenetic uncertainty is the scarcity of fossil material recovered for basal alvarezsauroid taxa. Until recently, these were primarily known from isolated limb bones and scant vertebral material but no cranial material, whereas derived forms are known from more complete skeletons. Additionally, regardless of the position of Alvarezsauroida within Coelurosauria, until recently a 70 million year ghost lineage (Norell, 1993) was implied for the clade (Choiniere et al., 2010b), indicating the potential for a great deal of evolution away from plesiomorphic conditions.

The discovery of the new, basal alvarezsauroid *Haplocheirus sollers* from the lowest Upper Jurassic Shishugou Formation in Xinjiang, People's Republic of China (Choiniere et al., 2010b), provided a first look at the morphology of a plesiomorphic and stratigraphically old member of the clade. Importantly, the holotype (IVPP V14988) of *Haplocheirus* preserves a nearly complete, uncrushed skull. Cranial material was previously known only from a few derived parvicursorine alvarezsauroids, including: two skulls of *Shuvuuia* (Chiappe et al., 1998), partial cranial material of *Mononykus* (Perle et al., 1993; Perle et al., 1994), and a partial skull of *Ceratonykus* (Alifanov and Barsbold, 2009). Here we present the detailed description of the cranial anatomy of *Haplocheirus* and discuss the implications of this material for cranial evolution and feeding ecology in the earliest alvarezsaurs.

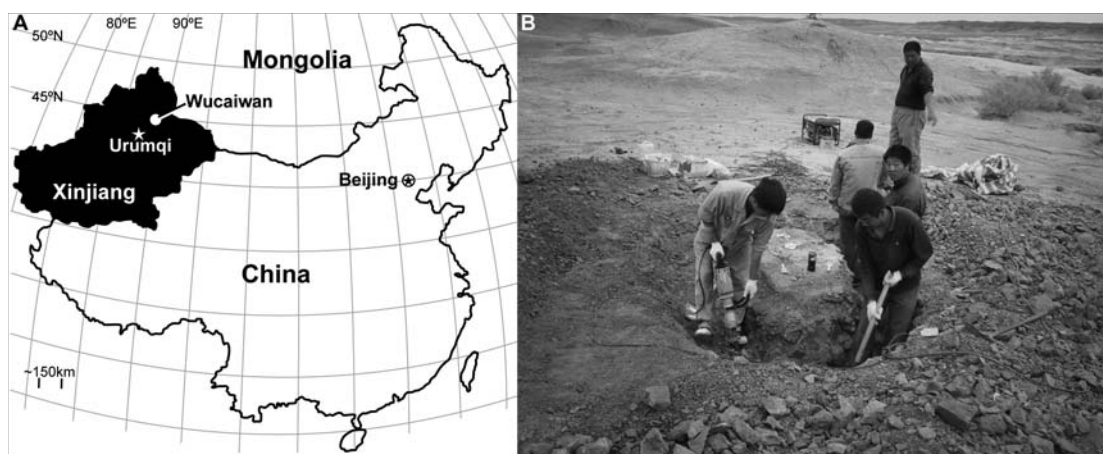


FIGURE 1. **A.** Map showing location of Shishugou Formation and Wucaiwan locality in Xinjiang, People's Republic of China. **B.** View of type locality of *Haplocheirus sollers* at Wucaiwan. View is looking toward the SW.

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Coelurosauria sensu Gauthier, 1986

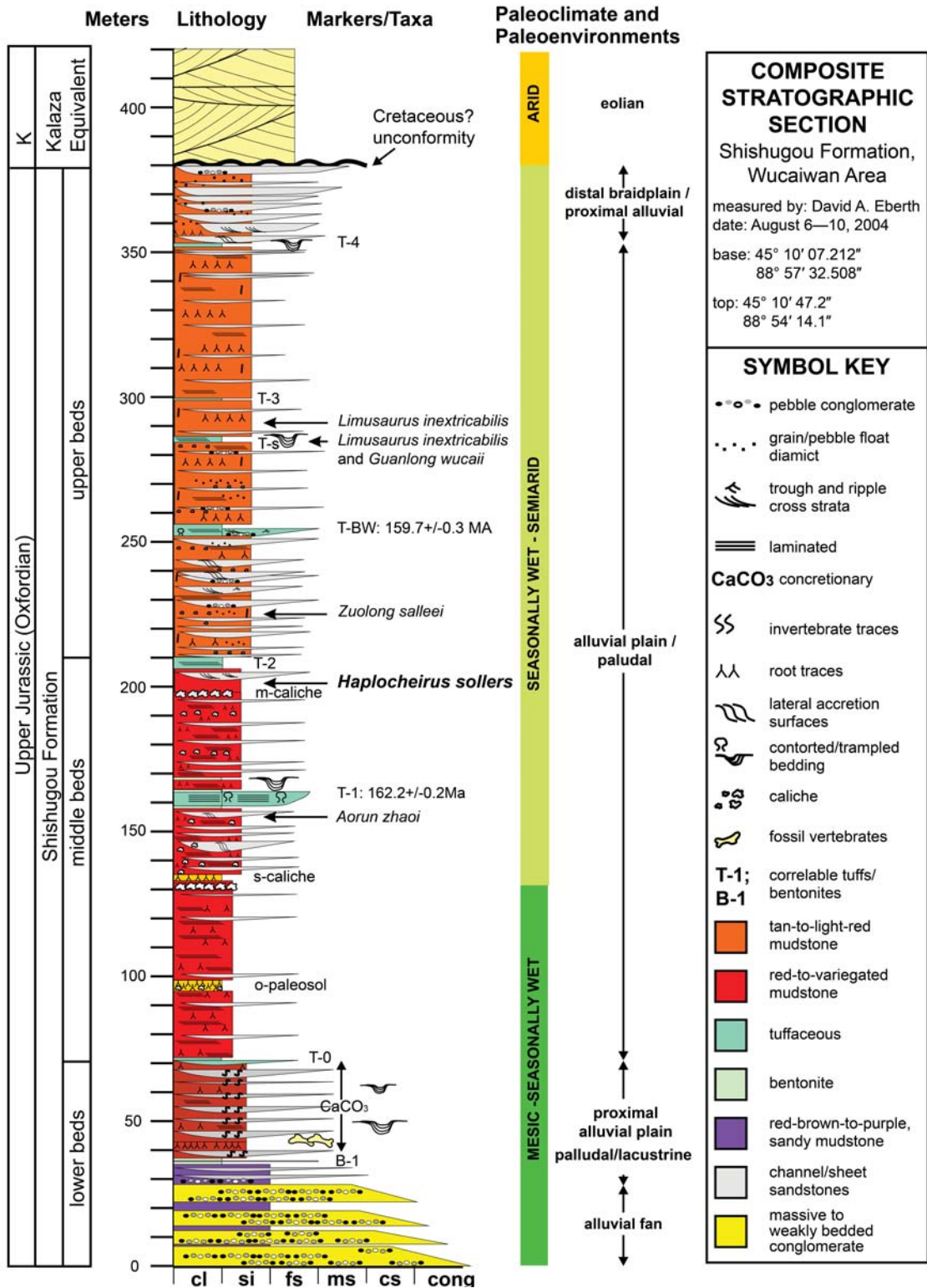
Alvarezsauroidea Bonaparte, 1991

Haplocheirus Choiniere et al., 2010

H. sollers Choiniere et al., 2010

HOLOTYPE: IVPP V14988, a nearly complete skeleton lacking the dorsal parts of the ilium and the caudal vertebrae distal to caudal 13. An articulated skeleton of a crocodyliform is preserved surrounding its cervical vertebrae.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION: "Middle beds" of the Shishugou Formation, Xinjiang, China (fig. 1). The section of the Shishugou Formation at Wucaiwan in which the specimen was found (fig. 2) is under- and overlain by radiometrically dated volcanic tuffs (Eberth et al., 2001). They bracket the age of the fossils to between 159.7 ± 0.3 and 162.2 ± 0.2 Ma (previously reported as between 158.7 ± 0.3 and 161.2 ± 0.2 mya [Clark et al., 2006], but recalibration of the Fish Canyon Sanidine [Kuiper et al., 2008]) adds 0.6% to our previous dates Clark et al., 2006), which corresponds to the Oxfordian stage (Gradstein et al., 2012). Unlike the recently described Shishugou theropods *Guanlong* (Xu et al., 2006) and *Limusaurus* (Xu et al., 2009), which were discovered in mud mires (Eberth et al., 2010), the holotype of *Haplocheirus* was discovered in a fine-grained red to brown mudstone, with no evidence of miring.



REVISED DIAGNOSIS: Differs from all other theropods in: ventral edge of the distal end of the paroccipital processes twisted posteriorly; metacarpal III one-half the length of metacarpal II. Differs from all other alvarezsauroids in the following derived cranial features: dorsally expanded distal end of the jugal process of the maxilla; heterodont dentary tooth row with enlarged tooth in the 4th alveolus; alveolar margin of anterior end of dentary dorsally convex; maxillary and dentary teeth with serrations on distal carinae. Additional research on the holotype skull indicates that a second mandibular fenestra, considered by Choiniere et al. (2010b) as an autapomorphy of *Haplocheirus*, is a preservational artifact.

DESCRIPTION

GENERAL OVERVIEW AND OPENINGS: The skull and mandible are nearly complete and uncrushed, although many of the skull bones are in very poor condition (figs. 3–12). The skull exhibits no mediolateral crushing and is only mildly distorted, the most significant aspect of which is the slight dorsoventral displacement of the posterior bones on the right half. The skull roof is poorly preserved, with numerous breaks and missing cortical bone in the nasals, frontals, and parietals. The right parietal, squamosal, frontal, and postorbital are absent. The anterior end of the right nasal is missing. Many of the maxillary teeth are missing on the left side, and the right maxillary and most of the dentary teeth are obscured by matrix.

The rostrum is long and low, as in ornithomimosaurs (Makovicky et al., 2004), *Shuvuuia* (Chiappe et al., 1998; Chiappe et al., 2002) and some troodontids (Makovicky and Norell, 2004). The orbital region and posterior ends of the skull are expanded from the narrow rostrum both mediolaterally and dorsoventrally. The antorbital fossa is large and anteroventrally pointed, extending almost to the anteriormost tip of the maxilla and dorsally onto the ventrolateral surface of the nasals. The internal margin of the antorbital fenestra is bordered dorsally by the maxilla and the lacrimal, but the dorsal margin of the antorbital fossa is rimmed by the nasal and the lacrimal. A small maxillary fenestra is anteriorly rounded and squared posteriorly, and it is separated from the antorbital fenestra by an anteroposteriorly narrow maxillary pila (interfenestral bar). It is offset posteriorly from the anterior margin of the antorbital fossa and is located approximately at midlevel in the antorbital fossa unlike the dorsally displaced maxillary fenestrae of many dromaeosaurids (Turner et al., 2012). A dorsoventrally tall, slitlike promaxillary foramen is located under the anterior margin of the antorbital fossa, and is hidden in lateral view by the lateral lamina of the nasal ramus of the maxilla at the anteroventral margin of the fossa. The orbits face anterolaterally. The maxilla would have participated in the posterior margin of the external naris, although it probably only contributed a small portion. The ovoid external naris is anteroposteriorly long and dorsoventrally low, and its long axis is oriented nearly horizontally. This suite of features of the external naris is common to the basal tyrannosauroids *Guanlong* (IVPP V14531, V14532) and *Proceratosaurus* (Rauhut et al., 2010), ornithomimosaurs (e.g., *Gallimimus* (IGM 100/1133), troodontids (e.g., *Sinovenator* [IVPP V12632] and *Byronosaurus* (Makovicky et

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FIGURE 2. Composite stratigraphic section of the Shishugou Formation at the Wucuiwan locality. Stratigraphic position of holotype of *Haplocheirus sollers* and other theropod genera from this formation indicated by arrows.

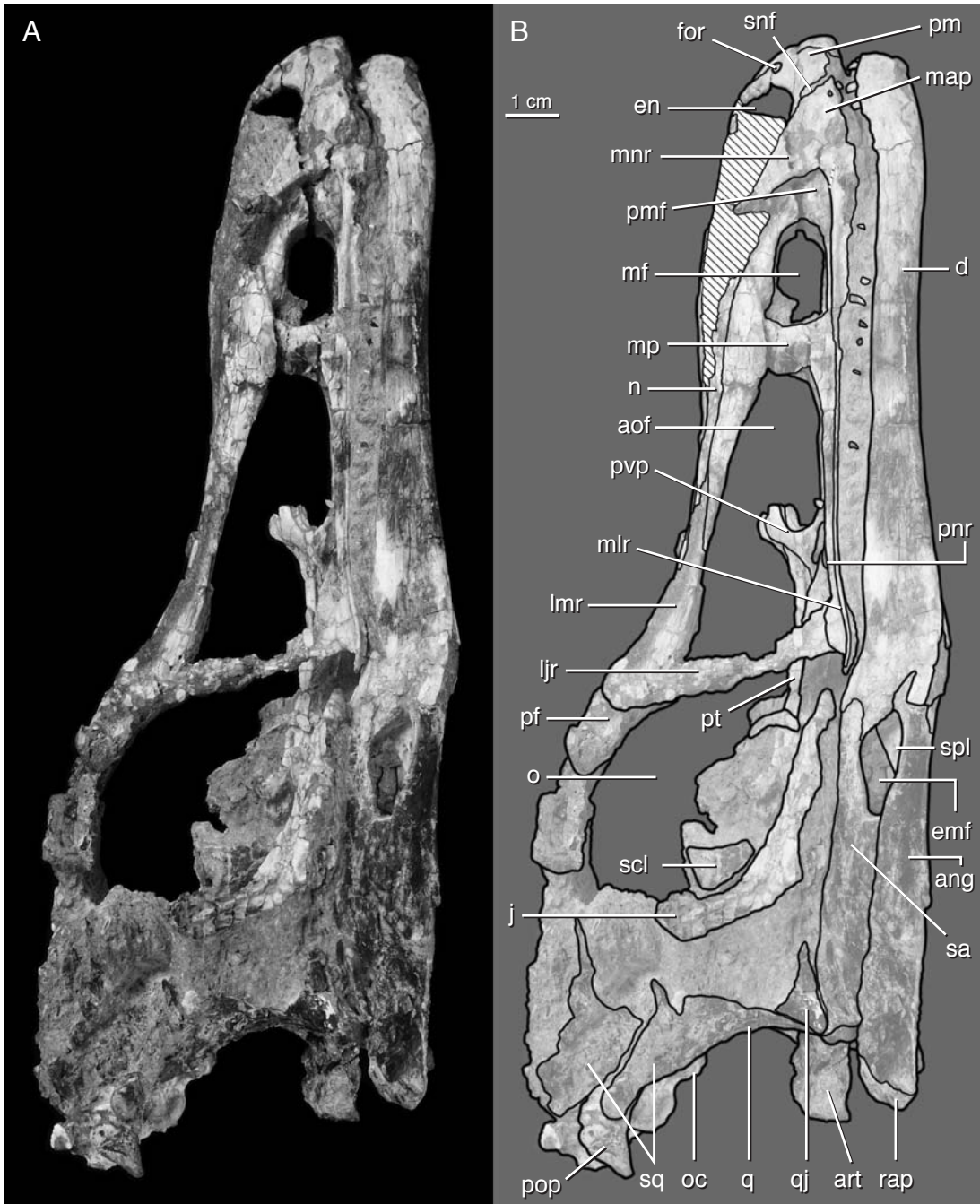


FIGURE 3. **A.** Skull and mandible of holotype of *Haplocheirus sollers* (IVPP V14988) in right lateral view. **B.** Line drawing of A. Abbreviations in appendix 1.

al., 2003)), and the parvicursorine alvarezsaurid *Shuvuuia* (Chiappe et al., 1998). The supra-temporal fenestrae form large emarginations on the posterior ends of the postorbital processes of the frontals and are separated medially by a very low, mediolaterally narrow sagittal ridge along the midline of the parietals, unlike the mediolaterally wide, dorsally smooth

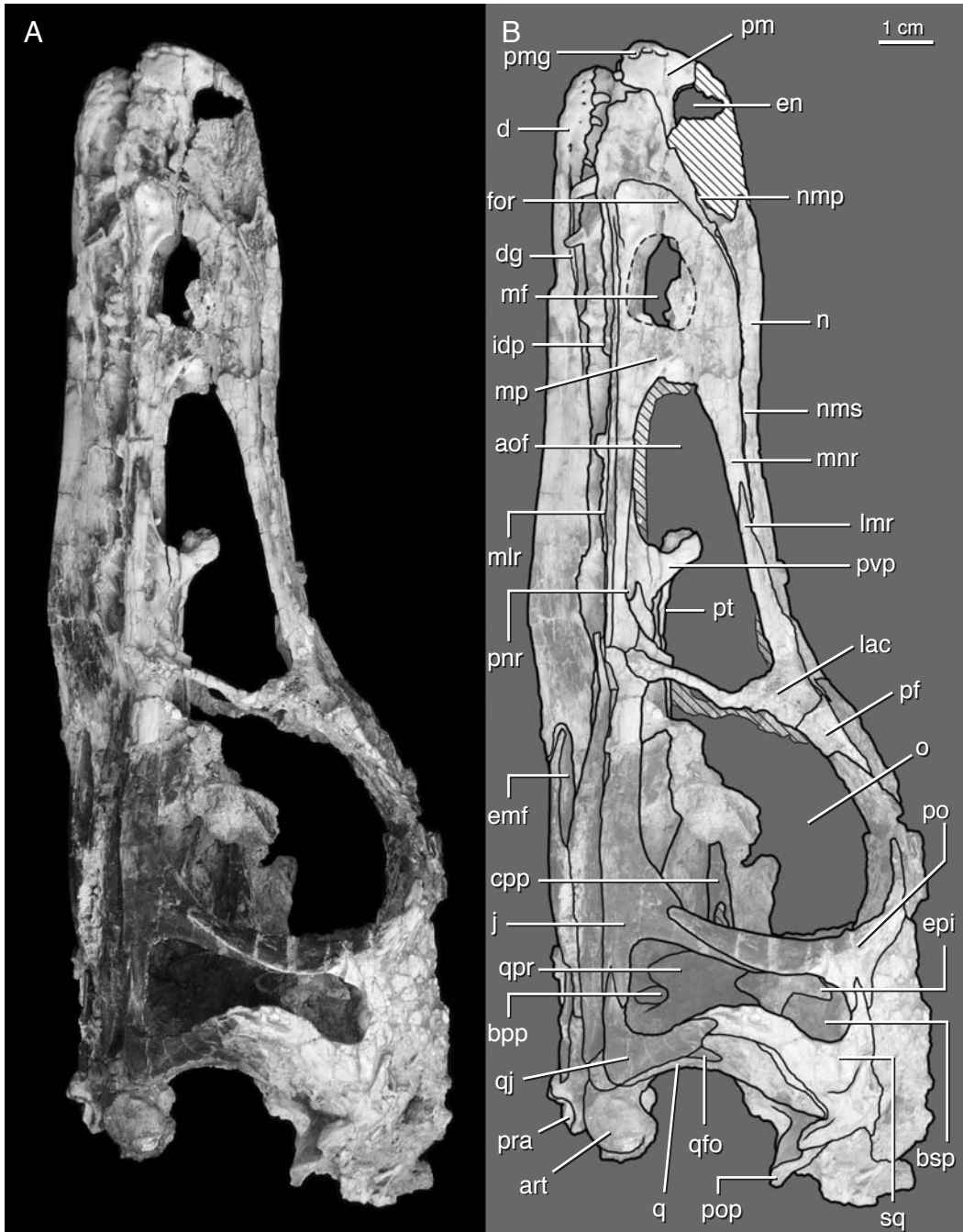


FIGURE 4. **A.** Skull and mandible of holotype of *Haplocheirus sollers* (IVPP V14988) in left lateral view. **B.** Line drawing of A. Abbreviations in appendix 1.

portions of the parietals that separate the supratemporal fenestrae in many basal theropods (Rauhut, 2003), ornithomimosaur (Makovicky et al., 2004), and *Shuvuuia* (IGM 100/977). The lateral margin of the supratemporal fenestra is straight and the medial margin is medially convex. The infratemporal fenestra is dorsoventrally high and anteroposteriorly short,

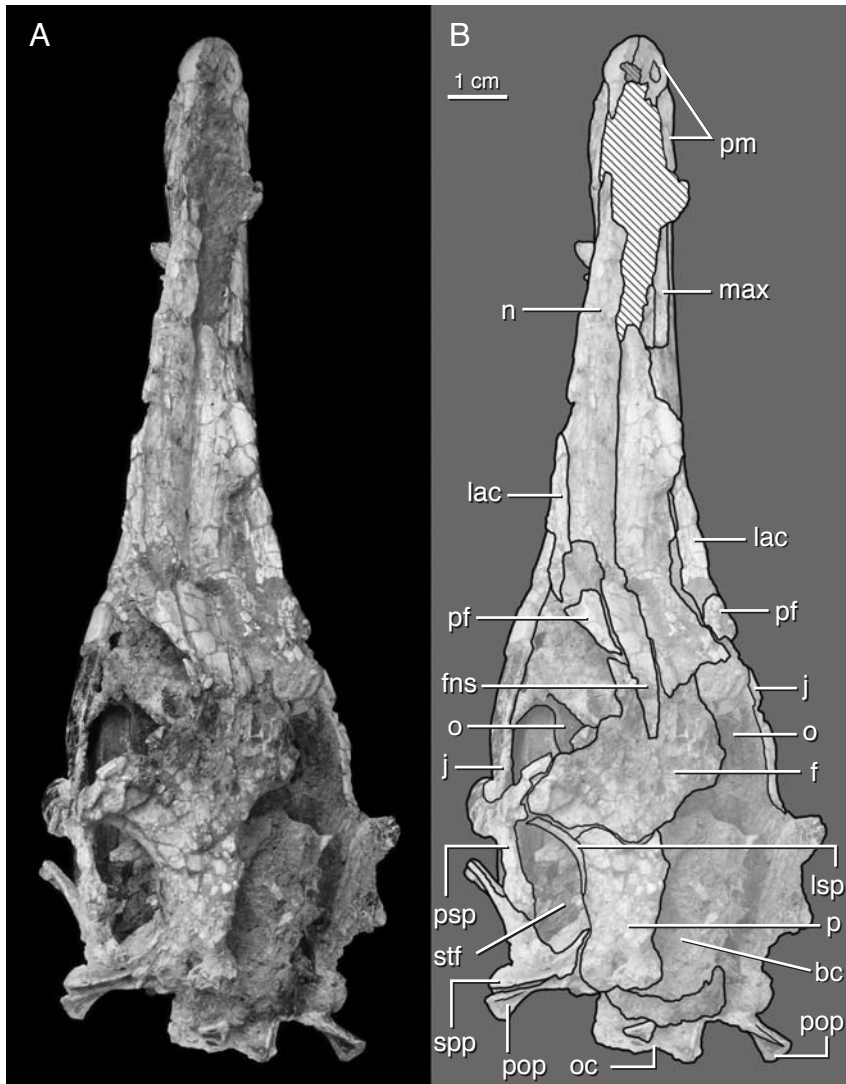


FIGURE 5. **A.** Skull and mandible of holotype of *Haplocheirus sollers* (IVPP V14988) in dorsal view. **B.** Line drawing of A. Abbreviations in appendix 1.

as in ornithomimosaur (e.g., *Garudimimus* [Kobayashi and Barsbold, 2005a]), and the therizinosaurid *Erlikosaurus* (Clark et al., 1994). It is mesially constricted by the quadratojugal and squamosal approaching the postorbital bar.

SKULL

PREMAXILLA: Both premaxillary bodies are well preserved, but their nasal and maxillary processes are distally broken (figs. 3–5, 8). The premaxillary body is square in lateral view, and only a small portion of it underlies the external naris, with the majority of the body located anterior to the anterior narial margin, as in *Ornitholestes* (AMNH FARB 619). In ventral view, the articulated premaxillae form a U-shaped junction. Sutural marks on the anterior surface of the

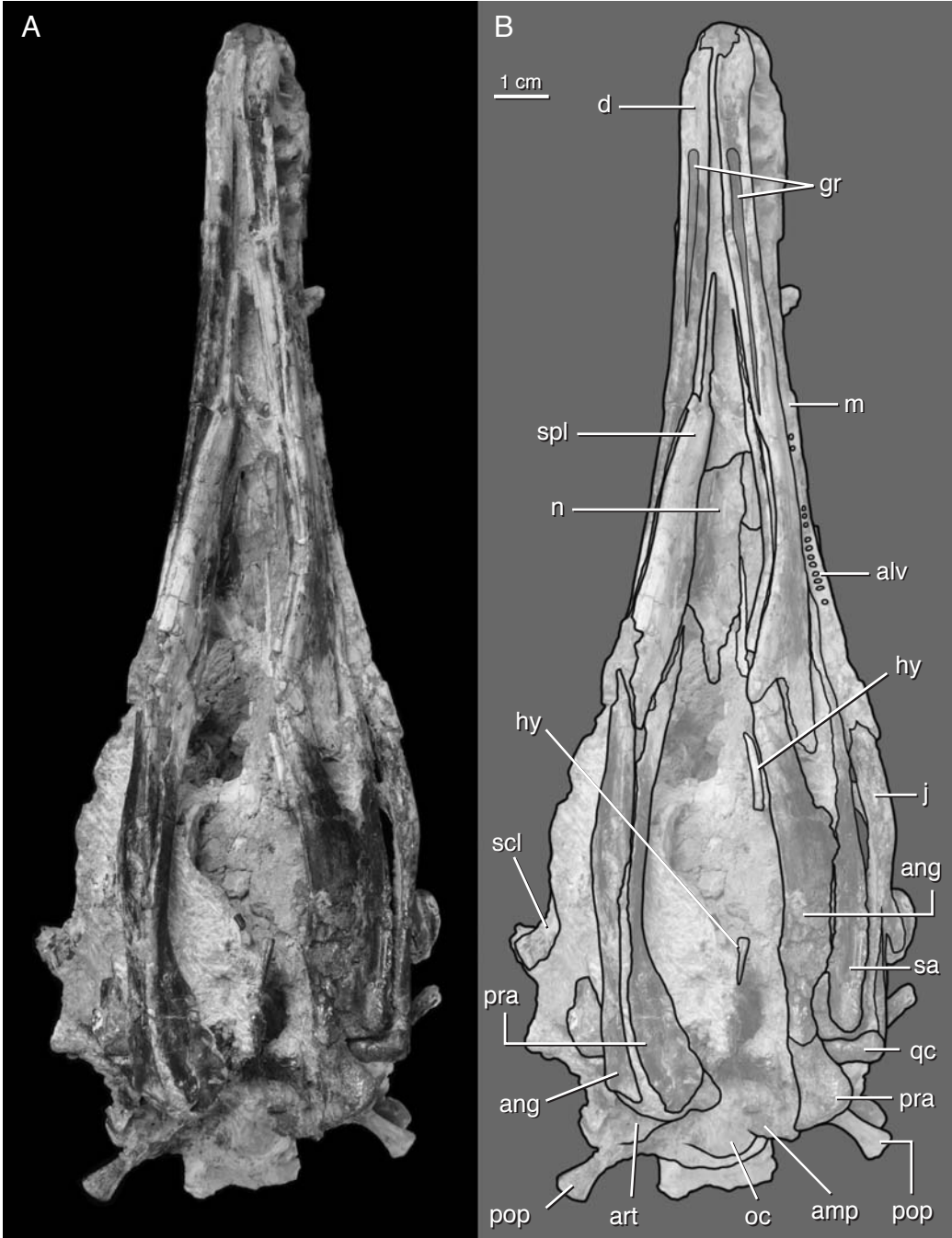


FIGURE 6. **A.** Skull and mandible of holotype of *Haplocheirus sollers* (IVPP V14988) in ventral view. **B.** Line drawing of A. Abbreviations in appendix 1.

nasal ramus of the maxilla show that the maxillary process of the premaxilla would not have contacted the nasals on the posteroventral border of the naris. This differs from the condition in almost all ornithomimosaur, in which the maxillary process extends posteriorly to contact the

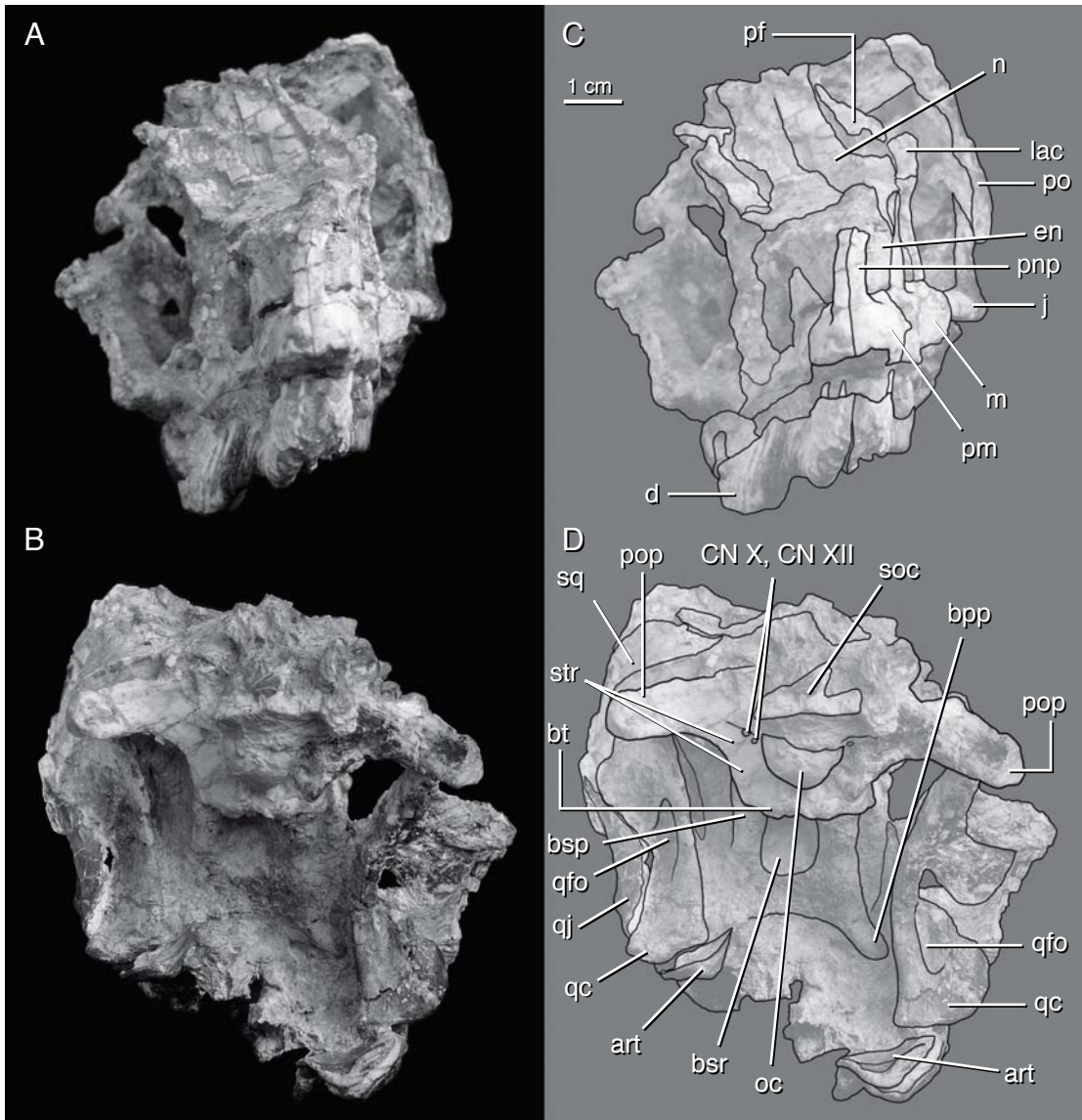


FIGURE 7. **A.** Skull and mandible of holotype of *Haplocheirus sollers* (IVPP V14988) in anterior view. **B.** Skull and mandible of holotype of *Haplocheirus sollers* (IVPP V14988) in posterior view. **C.** Line drawing of **A.** **D.** Line drawing of **B.** Abbreviations in appendix 1.

nasals, excluding the maxilla from participating in the external naris. Often, as in many dromaeosaurids, the maxillary ramus of the premaxilla extends between the nasomaxillary suture. The condition in *Shuvuuia* (IGM 100/977, 100/1001) cannot be determined because the maxillary processes are either missing or broken in both skulls. The nasal processes, which form the internarial bar, are broken close to their bases above the anterior end of the external naris. The morphology of their bases suggests that they were dorsoventrally flat, as in troodontids (Makovicky

and Norell, 2004), *Shuvuuia* (IGM 100/977), the basal tyrannosauroid *Dilong* (IVPP V14243) and in most ornithomimosaur (e.g., *Shenzhousaurus* (Ji et al., 2003).

The narial fossa is well developed, extending almost to the anterior end of the premaxilla and emarginating the ventrolateral edge of the ascending process. Similar conditions are present in *Shuvuuia* (IGM 100/977), ornithomimosaur (e.g., *Pelecanimimus* [LH 7777]), and in *Mei* (Xu and Norell, 2004). A groove begins on the anteroventral margin of the narial fossa and extends ventrolaterally (fig. 4), ending at the midheight of the premaxillary body and leaving an isolated triangular region of bone anteriorly. This anterior premaxillary groove was previously considered an autapomorphy of *Guanlong wucaii* (Xu et al., 2006) but is also present in the tyrannosauroids *Proceratosaurus* (Rauhut et al., 2010), *Zuolong* (Choiniere et al., 2010a), and *Eotyrannus lengi* (IWCMS 1997.550). There are numerous shallow foramina on the external surface and within the narial fossa on the body of the premaxilla and along the posterior margin of the nasal process, as in theropods generally. A subnarial foramen (fig. 3) lies at midheight on the posterior edge of the body, opening between the premaxilla and the maxilla, as in most theropods.

MAXILLA: The maxillae are well preserved and mostly complete (figs. 3,4), with the left maxilla missing only its anterior tip at its contact with the premaxilla. The two maxillae are narrowly separated and subparallel to each other along the rostrum in dorsal view, but diverge laterally just anterior to the lacrimal-jugal sutures to create a long, narrow snout with a medio-laterally expanded orbital region. In lateral view, the nasal ramus is posteriorly offset from the anterior end of the body, so that the maxilla has a short anterior process (fig. 3) (Rauhut, 2003). Within Alvarezsauroidea, a short anterior process is also present in *Shuvuuia* (IGM 100/977), and this feature has a sporadic distribution within Coelurosauria, being present in *Juravenator* (Chiappe and Göhlich, 2010), tyrannosauroids (Xu et al., 2006; Rauhut and Milner, 2008), *Ornitholestes* (AMNH FARB 619), and the troodontid *Mei* (Xu and Norell, 2004). An anterior process is more widespread in noncoelurosaurian theropods (e.g., *Monolophosaurus* (Zhao and Currie, 1993) and ceratosaurs [Rauhut, 2003]), but in these taxa the anterior process has a more pronounced, steplike morphology. The nasal ramus is composed of two laminae: a horizontal lateral lamina that is well developed only anteriorly, and a ventral lamina that forms the medial wall of the anterior end of the antorbital fossa and contacts the nasals dorsally and lacrimal posteriorly. The posterior two-thirds of the nasal ramus consists only of the ventral lamina, as in dromaeosaurids (Turner et al., 2007), and as a result the nasomaxillary suture is visible in lateral view. The angle of the nasal ramus changes at the posterior end of the lateral lamina (approximately dorsal to the midpoint of the maxillary fenestra), where the nasal ramus becomes subhorizontal, rather than posterodorsally inclined. The posterior end of the ventral lamina of the nasal ramus bifurcates posteriorly to articulate with the maxillary process of the lacrimal. The ends of the fork project posteriorly along the ventral and dorsal surfaces of the maxillary ramus of the lacrimal for approximately one centimeter as thin, tapering splints. A shallow groove with rounded ends embays the lateral surface of the ventral lamina of the nasal ramus, extending anteriorly from the lacrimal contact and lying ventral to the series of pneumatic fossae between the nasal and maxilla. It is likely that this groove is also a product of this

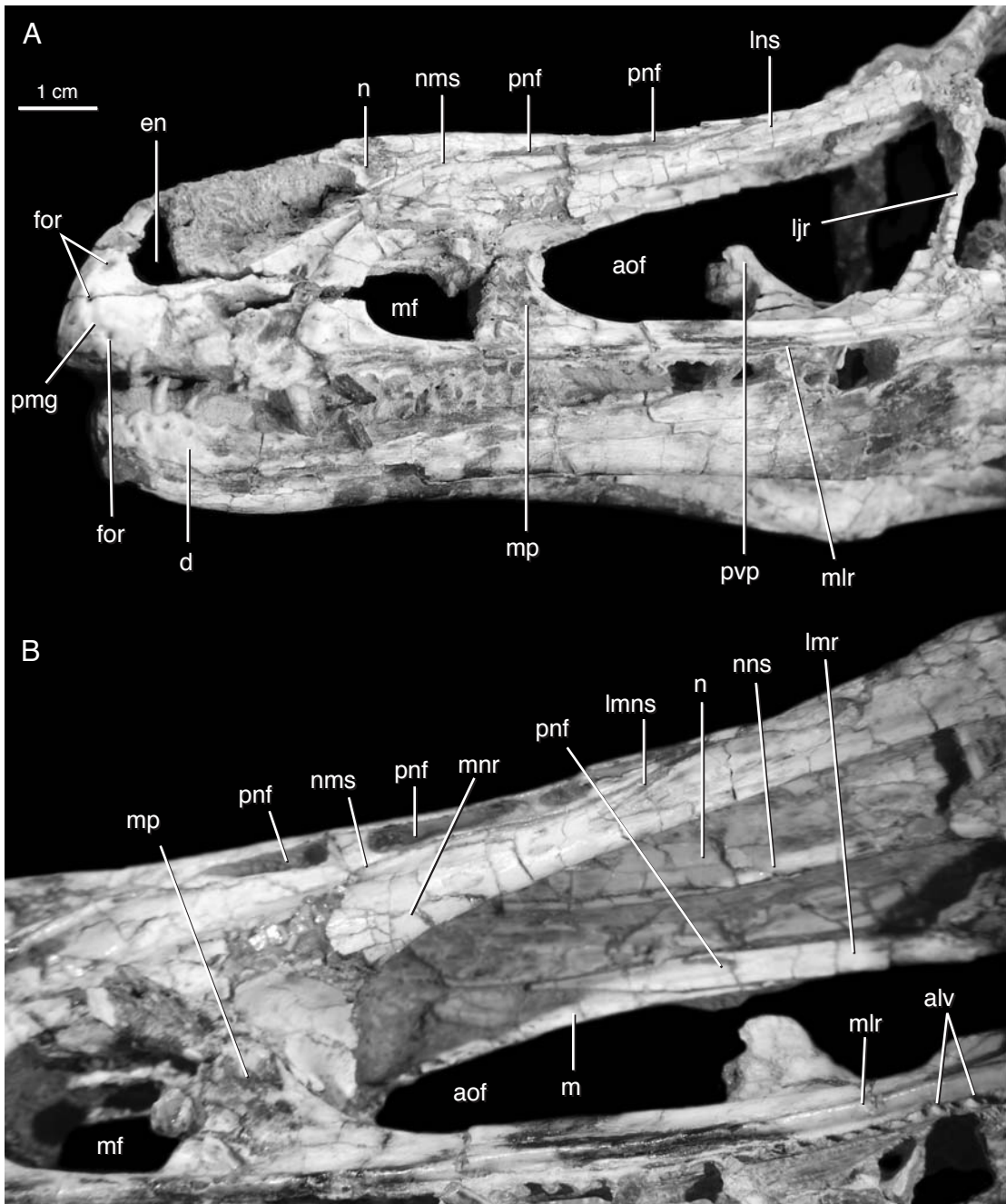


FIGURE 8. A. Rostrum and anterior mandible of holotype of *Haplocheirus sollers* (IVPP V14988) in left lateral view. B. Maxillary region of holotype of *Haplocheirus sollers* (IVPP V14988) in left ventrolateral view. Abbreviations in appendix 1.

pneumatization. The medial surface of the maxillary nasal ramus is embayed by two shallow, vertically arranged depressions along its anterior junction with the maxillary pila. The more dorsal of the two is continuous with the anteromedial recess on the maxillary ramus of the lacrimal. The ventral depression is located slightly anterior to the dorsal depression. Medial processes contact each other posterodorsal to the maxillary fenestra to form a short ventral floor for the nasal chamber.

The maxillary pila has a foramen centered on its posterior surface (the fenestra posterioris antri maxillaris) (Witmer, 1997b) that would have allowed communication between the maxillary fenestra and the antorbital fenestra (fig. 8). This foramen is present in the ornithomimosaurs *Gallimimus* (IGM 100/1133) and *Pelecanimimus* (LH 7777), the parvicursorine alvarezsauroid *Shuvuuia* (IGM 100/977) and in most troodontids (Makovicky and Norell, 2004). A foramen in this position is also present in tyrannosaurids (Witmer, 1997b; Brochu, 2003), but in these theropods it is developed as part of an inflated maxillary antrum. The lateral surface of the jugal ramus of the maxilla has a prominent horizontally oriented and laterally projecting lamina of bone extending from the anterior edge of the antorbital fossa to its posterior terminus that forms the ventral margin of the antorbital fossa. This lamina appears variably in theropods (Rauhut, 2003) and is present in two other small coelurosaurs from Wucaiwan, *Zuolong* (Choiniere et al., 2010a) and *Aorun* (Choiniere et al., 2014). On the anterior end of the lateral surface of the alveolar margin, immediately ventral to the lateral ridge, is a shallow sulcus (fig. 12B) containing several large, oval foramina. These are in the same position as the nutrient foramina of other theropods, but they are much larger than typical nutrient foramina and may represent further pneumatized pockets of the maxilla. The groove makes the tooth row very slightly medially inset from the lateral edge, an effect that is most pronounced in the middle of the tooth row.

On the medial surface of the jugal ramus, the palatal shelves converge at the anterior end of the antorbital fenestra, forming the secondary palate in conjunction with the premaxillae and likely the vomers, which are not preserved. Evidence of a vomerine contribution to the secondary palate is the slight separation of the maxillary palatal shelves that are preserved in life position (although this may be an artifact of postmortem distortion as these bones are not suturally connected). In most maniraptorans, the vomer overlies the contacting maxillary shelves. The posterior end of the jugal ramus of the maxilla expands dorsally where it meets the descending ramus of the lacrimal, a morphology that is autapomorphic for *Haplocheirus* within Alvarezsauroidea. This expansion excludes the jugal from participation in the internal margin of the antorbital fenestra. The lateral component of the alveolar margin is missing and the interdental plates on the medial surface can be seen in lateral view. Though small, they are unfused, approximately square, and similar to the general morphology of most theropod interdental plates (however, see discussion in Bever and Norell, 2009).

NASAL: The nasals are broken anteriorly, missing the premaxillary processes and the anterior termini of the maxillary processes (figs. 3–5). They are unfused and the midline contact between the adjoining nasals can be seen in both dorsal and ventral views. During preservation, the medial edges of the nasals were displaced slightly ventrally, so that the

internasal suture is depressed ventrally, below the lateral margins. In life position, the nasals probably would have formed a shallow, dorsally convex arc along the dorsal surface of the rostrum in transverse cross section. The nasals form the posterior, posterodorsal, and posteroventral margins of the external nares. Sutural marks on the anterior surface of the maxilla indicate that the maxillary process of the nasal failed to contact the maxillary process of the premaxilla along the ventral margin of the external naris. The dorsal surface of the nasal is smooth and expands slightly mediolaterally as it extends posteriorly. The dorsal surface of the anterior end of the left nasal bears three small, shallow foramina immediately posterior to the premaxillary contact (fig. 9A), typical of theropods generally. These foramina cannot be seen on the right side because the anterior end of the right nasal is not preserved. The ventrolateral surface of the nasal forms the dorsal margin of the antorbital fossa. It is undercut by three deep, anteroposteriorly long, ovoid pneumatic fossae. These are similar to those of *Sinraptor* (Currie and Zhao, 1993), but they are more extensively developed along the lateral margin of the nasal in *Haplocheirus* and are ovoid rather than subcircular. The ventromedial surface of the right nasal shows that these fossae do not penetrate the lateral wall of the nasal.

The nasomaxillary suture follows the ventral edge of these pneumatic fossae and lies entirely within the antorbital fossa. The posterior end of the nasal is poorly preserved, but its dorsal suture with the anterior end of the frontal appears to have been transversely oriented. It overlaps the dorsal surface of the anterior end of the frontal in a lap joint that is perpendicular to the long axis of the skull.

LACRIMAL: The right lacrimal is fractured but nearly complete (figs. 3, 4). The left lacrimal is missing the lateral margin of the angle, but the ventrally directed jugal ramus is mostly complete and the maxillary ramus is well preserved. The jugal ramus extends the full height of the anterior border of the orbit, forming its anterior margin and the posterior boundary of the antorbital fenestra. The presence of a foramen for the nasolacrimal duct leading through the jugal ramus cannot be confirmed because of the poor preservation of both sides. As in most maniraptorans and in ornithomimosaurids, the jugal ramus is only slightly expanded anteroposteriorly as it extends ventrally. At the angle of the lacrimal, there is no evidence for a lacrimal foramen, as in *Shuvuuia* (IGM 100/977, 100/99) and most other theropods, but this may be an artifact of preservation.

The maxillary ramus of the lacrimal is very long and tapers anteriorly as in *Shuvuuia* (IGM 100/977) and in maniraptorans generally (e.g., *Byronosaurus* [Makovicky et al., 2003]). It articulates anteriorly with the forked posterior end of the nasal ramus of the maxilla and dorsally with the nasal along the posterior dorsal margin of the antorbital fossa. An embayment of the lateral surface of the maxillary ramus forms the posterodorsal corner of the antorbital fossa. The anterior end of the maxillary ramus of the right lacrimal extends along the medial surface of the rostrum, medial to the ventral lamina of the nasal process of the maxilla, and it extends anteriorly on the medial surface almost to the maxillary pila. The medial surface of the anterior end has a pocketlike ovoid foramen that extends posteriorly and slightly laterally from an origin on the anterior tip. As in *Shuvuuia*, there is no well-developed lacrimal posterodorsal

process (Chiappe et al., 1998). *Haplocheirus* lacks the small “lacrimal horn” that projects posterolaterally in *Shuvuuia* (IGM 100/977) and many other theropods.

PREFRONTAL: The left side of the skull preserves the prefrontal articulating with the posterior edge of the lacrimal angle (fig. 4), but the right lacrimal is badly damaged and is represented only by a small area of broken bone adhering to the lacrimal angle (fig. 5). Because the left lacrimal angle is poorly preserved, it is unclear whether the prefrontal was a completely separate ossification from the lacrimal or whether it was tightly sutured to the posterior margin of the lacrimal angle, as in *Ornitholestes* (AMNH FARB 619). Unlike the hypertrophied prefrontals of ornithomimosaurs (e.g., *Gallimimus* [IGM 100/1133]) and *Shuvuuia* (IGM 100/977), which are diamond shaped in dorsal view, the prefrontal of *Haplocheirus* is shaped like a narrow triangle in dorsal view with its long axis oriented sagittally and the base oriented mediolaterally. A similar morphology is observed in the therizinosauroid *Erlikosaurus* (Clark et al., 1994). The prefrontal is mediolaterally widest at the lacrimal contact, and in dorsal view, it tapers to a posteriorly directed point. Also when viewed dorsally, the straight medial margin forms an extensive contact with the lateral edge of the frontal. The posterior end forms a portion of the anterodorsal orbital rim. There is a small fossa on the ventrolateral margin of the posterior end. The ventral surface has a slender ventral process that runs along the medial edge of the lacrimal, but the ventralmost terminus of this process is broken, so its full extent cannot be determined. The anterolateral surface has a distinct, anteriorly concave notch for articulation with the lacrimal angle, a feature also present in *Ornitholestes* (AMNH FARB 619) but is not developed in either ornithomimosaurs or *Shuvuuia* (IGM 100/977, 100/99). The anterior end is broken, but it appears to have separated the posterior end of the lacrimal from the frontal margin. In ornithomimosaurs (e.g., *Gallimimus* [IGM 100/1133] and *Shuvuuia* [IGM 100/977]), the prefrontal separates the posterior half of the lacrimal from the frontal (Serenó, 2001).

SCLEROTIC OSSICLES: Well-preserved sclerotic rings are present in both orbits (figs. 3, 10; note breakage to specimen prior to final photography). The right sclerotic ring preserves the intact dorsal half, but it has been dislocated to the midline of the skull inside the orbit overlying the cultriform process and the pterygoid. The left sclerotic ring is mostly complete, but the dorsal half has been displaced ventrally and overlaps the ventral half. The sclerotic ring is composed of approximately 20 imbricating sclerotic ossicles. The ossicles are oval and medially flexed, so the outer surface of the ring is concave and the inner (eyeball side) of the ring is convex. The inner diameter of the ring is 33 mm, and the outer diameter is 39 mm. The inner diameter of the ring is approximately 76% of the diameter of the orbital fenestra.

POSTORBITAL: The left postorbital is complete and preserved in articulation with the surrounding frontal, laterosphenoid, squamosal, and jugal (figs. 4, 10). The right postorbital is not preserved. The frontal ramus is missing its anteriormost tip. In lateral view, the frontal ramus forms a dorsally convex arc that makes up the majority of the posterior border of the orbit. It arches well above the level of the squamosal process, as is typical for maniraptorans, and is mediolaterally restricted to a thin bar of bone along the anterolateral edge of the frontal, unlike the mediolaterally wide frontal ramus of basal coelurosaurs like *Zuolong* (Choiniere et al., 2010a). Although it is broken, the anterior end of the frontal ramus probably did not contact

the lacrimal (thus excluding the frontal from participation in the orbit) because these bones would have been separated by the prefrontal. The medial surface of the frontal ramus contacts the laterosphenoid at the level of the posterior end of the orbit. The contact surface for the laterosphenoid is medially concave and smaller in relative diameter than it is in more basal tetanuran theropods like *Allosaurus* (Madsen, 1976). The dorsal surface extends dorsal to the level of the suture with the frontal, which may mark the anterolateral border of the supratemporal fossa. This observation is tentative because of extensive breakage in this area and lack of preservation of the right postorbital.

The squamosal process is anteroposteriorly short, dorsoventrally low, and arches dorsally. The sutural boundary between it and the squamosal is unclear because of breakage, but there is possible fusion at the contact. The jugal ramus forms the anterodorsal half of the postorbital bar. It is triangular in cross section.

JUGAL: The left jugal (figs. 4, 8, 10) is complete and well preserved. The right jugal is missing its anterior end. The anterior jugal ends bluntly at the posteroventral corner of the antorbital fossa and lacks an anterior spur that extends below the antorbital fenestra, a feature of many other maniraptorans (e.g., *Erlikosaurus* [Clark et al., 1994], *Tsaagan* [Norell et al., 2006]). The jugal participates only in the posteroventralmost corner of the antorbital fossa, and is slightly emarginated on the anterolateral tip to form the posteroventral corner of the antorbital fossa. There is no jugal foramen at this corner as in some theropods (Madsen, 1976; Currie and Zhao, 1993; Zhao and Currie, 1993; Sereno et al., 1996; Rauhut, 2003). The suborbital portion of the jugal is strongly laterally convex and dorsoventrally low, as in *Shuvuuia* (IGM 100/977, 100/99), *Erlikosaurus* (Clark et al., 1994), and birds (Baumel and Witmer, 1993). The maximal lateral extent of the jugal is at a level immediately anterior to the postorbital process. The jugals of *Juravenator* (Chiappe and Göhlich, 2010) and ornithomimosaurs are also dorsoventrally low, but the lateral surface is generally flat in these taxa (e.g., *Pelecanimimus* [LH 7777]). The jugal expands dorsoventrally below the postorbital process to form a large triangular plate. The postorbital process extends two-thirds of the way up the anterior margin of the infratemporal fenestra and forms approximately half the postorbital bar before articulating with the overlapping postorbital.

The quadratojugal process is anteroposteriorly short and forked at the posterior end for reception of the jugal ramus of the quadratojugal. This morphology, typical of coelurosaurs, is unlike the condition in *Shuvuuia* (IGM 100/977, 100/99), whose quadratojugal and jugal are fused and indistinguishable from one another. The dorsal and ventral processes of the fork are subequal in length and the articular facet for the jugal process of the quadratojugal forms an anteriorly tapering trough centered between these processes. Two small pits are present on the ventral surface of the jugal lateral to the ectopterygoid contact. These pits do not appear to open into pneumatic foramina although they are clogged with matrix and their full depth cannot be determined.

QUADRATOJUGAL: The left quadratojugal is well preserved (fig. 4, 10), but the right quadratojugal is missing. It is a hook-shaped bone with a short, anteriorly tapering jugal process and a tall squamosal process. The angle between the squamosal process and the jugal process

is acute. The anteriorly expanded dorsal end of squamosal process trends anterodorsally, and together with the quadratojugal process of the squamosal this constricts the infratemporal fenestra at midheight. The squamosal process overlaps the quadratojugal process of the squamosal laterally at the same level where it expands anteriorly to constrict the infratemporal fenestra. Medially, the squamosal process contacts the lateral margin of the quadrate shaft. In posterior view, the posterior edge of the squamosal process wraps around the posterolateral edge of the quadrate. The jugal process is short relative to many other theropods. In most nonavian theropods (e.g., *Ornitholestes* [AMNH FARB 619], *Guanlong* [IVPP V14531]), the jugal process reaches anteriorly to at least the posterior margin of the postorbital process of the jugal. In *Haplocheirus*, the jugal process ends at approximately the midpoint of the infratemporal fenestra, well posterior to the postorbital process.

FRONTAL: The frontals (fig. 5) are poorly preserved and the lateral edge of the right frontal above the orbit is missing. The frontals are not coossified, and the suture between them appears to have been simple, without complex interdigitation. The dorsal surface of the frontal is smooth. Together, the frontals are hourglass shaped, with deeply concave orbital excavations on the lateral margins. The anterior end of the frontal terminates bluntly at the nasals in dorsal view, forming a transversely oriented suture, but in ventral view, a long, anteriorly tapering process of each frontal underlies the posterior ends of the nasals. The medial surfaces of these processes are poorly preserved, but they do not appear to have contacted each other along the midline of the skull. The ventral surface of each anterior process bears a low, anteroposteriorly oriented ridge. On the anterior end of the lateral surface, the frontal has a long, straight contact with the prefrontal. The poorly preserved orbital margin posterior to the prefrontal does not show any prominent rugosities or ornamentation.

Posterior to the lateral emargination for the orbits, the postorbital process is laterally extensive and anteroposteriorly short. The supratemporal fossa is well developed on the posterior edge of the postorbital process, forming a posterodorsally facing recessed area on almost the entire posterolateral margin. The anterior edge of this supratemporal emargination is anteriorly convex, not sinusoidal as it is in some paravians (Turner et al., 2007). The posterior sutural boundary with the parietal is indistinct due to extensive breakage in this area. The cristae cranii are well developed on the ventral surface of the frontal, forming laterally concave, ventrally extending ridges. They are narrowly separated medially and diverge strongly from each other anteriorly and posteriorly.

PARIETAL: Only the left half of the parietal is present (figs. 4, 5), but it is broken into small pieces that remain close to their original positions, so little can be described of its morphology. In ornithomimosaurs (Makovicky et al., 2004), therizinosaurids, and alvarezsaurids (Chiappe et al., 1998) and other maniraptorans (e.g., dromaeosaurids [Norell and Makovicky, 2004]), the parietals are fused. This was likely the case in *Haplocheirus* based on its phylogenetic position and based on the overall morphology of the preserved area. The dorsal surface appears to have been smooth and probably formed a shallowly convex plate between the supratemporal fenestrae, widely separating them along the skull midline. There is no sign of a sagittal crest or any other parietal ornamentation along the skull midline.

SQUAMOSAL: The left squamosal is complete but shattered and the right squamosal consists of only small fragments (figs. 3–5, 10, 12). Unlike the reduced, triradiate squamosal of *Shuvuuia* (Chiappe et al., 1998), the squamosal of *Haplocheirus* is tetraradiate, with a postorbital process projected anteriorly, a quadratojugal process directed ventrally, a medial process that contacts the parietal and the laterosphenoid, and a paroccipital process extending over the quadrate head and contacting the dorsal margin of the paroccipital process of the exoccipital-opisthotic. The squamosal bounds the supratemporal fossa laterally and posteriorly. The postorbital process is short and the suture between it and the squamosal process of the postorbital is indistinct in lateral view. Some of the obscurity is due to shattering in this area, but it is possible that this contact was fused. The quadratojugal process forms a sinuous posterior contact with the lateral margin of the quadrate. It is angled 45° anteroventrally from the near vertical quadrate shaft, tapers distally and contacts the squamosal process of the quadratojugal ventrally. The paroccipital process is pendant, overhanging the posterior margin of the quadrate head in lateral view, but does not project laterally as a tab as it does in dromaeosaurids. The quadrate cotyle of the squamosal opens laterally, exposing the head of the quadrate in lateral view, although some of the posterior portion of the quadrate head is covered laterally by the lateral expansion of the squamosal process. The posterior edge of the paroccipital process of the squamosal forms an extensive, horizontally oriented, flat contact with the dorsal margin of the paroccipital process itself. A low ridge of bone extends along the posterior boundary of the paroccipital process of the squamosal, defining this suture. The medial process that forms the posterior rim of the supratemporal fenestra is poorly preserved. A ventral extension of this process approaches the laterosphenoid along the medioventral wall of the supratemporal fossa; however, contact between the two elements cannot be confirmed. The dorsomedial aspect of the medial process is eroded away. It contacted the parietal at the posteromedial corner of the supratemporal fenestra. The dorsal surface of the body does not appear to have been emarginated by the supratemporal fossa.

QUADRATE: Both quadrates are preserved in their original articulations and positions. The shaft of the quadrate is anteriorly convex in lateral view and the mandibular condyles are situated directly ventral to the quadrate head. The quadrate head is simple and distinct from the quadrate shaft, forming a dorsally convex structure that projects posterodorsally. There is no evidence of a second, medial quadrate head, as in derived avialans (Baumel and Witmer, 1993), *Shuvuuia* (Chiappe et al., 1998), and oviraptorosaurs (Maryanska and Osmólska, 1997; Balanoff et al., 2009). In posterior view, there is a thin, dorsoventrally oriented ridge of bone along the medial edge of the quadrate shaft, forming a pillarlike structure. Lateral to this pillar, the ventral half of the posterior surface of the quadrate has a deep fossa extending medially from its lateral contact with the quadratojugal. This fossa is continuous with the small quadrate foramen that is present as a vertical slitlike opening between the quadrate and quadratojugal. The lateral side of the dorsal half of the posterior surface of the quadrate forms a large, laterally projecting flange above the quadrate foramen that has a sinuous contact with the squamosal in lateral view. The dorsal margin of this flange is convex.

The pterygoid ramus of the quadrate is anteriorly convex. The ventral margin has a notch close to the quadrate body, and as preserved, the basipterygoid process of the basisphenoid passes through this notch, although this is likely not life position.

The mandibular condyles of the quadrate are asymmetric. The hemicylindrical lateral condyle is mediolaterally wide and anteroposteriorly short. Mesially, it is poorly separated from the medial condyle. Laterally, the edge has an anteriorly projecting, mediolaterally flattened flange that articulates with the medial surface of the quadratojugal. The medial quadrate condyle has a subcircular outline in ventral view and is more robust than the lateral condyle, but the distal surface is too closely appressed to the mandibular glenoid fossa to make more detailed observations.

There are several points of similarity between the morphology of the quadrate in *Haplocheirus* and that of *Shuvuuia* (Chiappe et al., 1998; Chiappe et al., 2002). The lateral flange of the dorsal half of the quadrate in posterior view is similar in both taxa, being subequal in mediolateral width to the quadrate at the level of the mandibular condyles and in having a convex dorsal margin. In both taxa, the quadrate head is distinct from this lateral flange, whereas in coelurosaurs generally the head is confluent with this flange (e.g., *Zuolong* [Choiniere et al., 2010a]). Moreover, the deep, tall lateral excavation for the quadrate foramen is similar in both *Haplocheirus* and *Shuvuuia*, although in the former this excavation is mostly filled by the medial expansion of the quadratojugal and in the latter the quadratojugal is lost. Because the complete morphology of the quadrate head is not fully visible externally in *Haplocheirus*, it is possible that CT scans of the skull may reveal other similarities between it and *Shuvuuia*, for example an incipient medial contact with the braincase.

PALATE

EPIPTERYGOID: An epipterygoid (fig. 10) is preserved in articulation on the anterodorsal surface of the pterygoid ramus of the left quadrate and is visible anterolaterally through the orbit and laterally through the infratemporal fenestra. It is mediolaterally narrow and forms a more extensive articulation with the dorsal and lateral margins of the pterygoid ramus of the quadrate than with the medial margin. It is tall, dorsally tapering, and curves posteriorly as it extends dorsally. The ventral end appears to form a forked contact with the pterygoid ramus of the quadrate, rather than a condylar/cotylar articulation as in oviraptorosaurs (Osmólska et al., 2004), but this may be due to breakage of bone at this contact. In lateral view, the dorsal end of the epipterygoid reaches the level of the ventral margin of the base of the squamosal process of the postorbital, but it appears that the osseous portion did not contact the laterosphenoid, as it does in *Gallimimus* (Makovicky et al., 2004) and some oviraptorosaurs (Osmólska et al., 2004). Although epipterygoids are only sporadically preserved in theropod skulls, the epipterygoid of *Haplocheirus* is generally similar to the morphology seen in other coelurosaurs, including *Tyrannosaurus* (Brochu, 2003), the ornithomimosaur *Gallimimus* (Makovicky et al., 2004), and the oviraptorosaurs *Incisivosaurus* (Balanoff et al., 2009), *Citipati* (Clark et al., 2001) and *Conchoraptor* (Osmólska et al., 2004).

PTERYGOID: The left pterygoid (figs. 3, 4, 9, 10) is intact and preserved in its original orientation. It can be seen laterally through the orbit and through the infratemporal fenestra, but the ventral surface is obscured by matrix. The right pterygoid is preserved, but is covered in matrix, and most of its articular region with the quadrate cannot be discerned. The pterygoid has a large articular surface for the quadrate, and the junction between this quadrate ramus and the palatine produce bears a pronounced, posteroventrolaterally oriented flange. The body of the pterygoid is

expanded near the articulation with the ectopterygoid. The palatine processes are thin, straplike elements. They taper slightly as they extend anteriorly, then expand again at their anterior tip where they contact the posterior end of the vomers and the vomeropterygoid process of the palatine. In lateral view, the palatine processes scribe a shallow, dorsally concave arc.

PALATINE: The palatines are complete and well preserved (fig. 10). The tetra-*radiate* palatine is located well anterior to the ectopterygoid as preserved, but its position may have shifted during preservation. On the medial edge, the contact between the palatine and the pterygoid is discontinuous in the midregion, resulting in a pronounced choana as in dromaeosaurids (Norell and Makovicky, 2004), ornithomimosaur (Rauhut, 2003), and the tyrannosaurid *Daspletosaurus* (Russell, 1970) (although not in *Tyrannosaurus* [Brochu, 2003]). The maxillary process is long and anteriorly tapering, and it extends along the mediodorsal edge of the posteromedial margin of the maxillary palatal process. The jugal process forms a complicated quadruple junction at the posteroventromedial margin of the antorbital fossa, contacting the medial surfaces of the maxilla, the maxillary ramus of the lacrimal, and the maxillary process of the jugal. The portion of the body between the maxillary process and the vomeropterygoid process is inclined dorsomedially, and the portion of the body between the jugal process and the pterygoid process is subhorizontally oriented.

A dorsolaterally projecting ridge extends anteriorly from the junction with the lacrimal, jugal, and maxilla and grades into the dorsolateral surface of the palatine body lateral and ventral to the anterior pterygoid process. The ridge divides the posterior end of the palatine into medial and lateral sections. Medial to this ridge, a deep fossa (fossa muscularis) (Witmer, 1997b) is present. Ventral and lateral to the anterior end of the ridge, an anteriorly opening, anteroposteriorly elongate pneumatic recess of the palatine (recessus pneumaticus palatinus) (Witmer, 1997b) is present. A similarly elongate fossa is present in *Pelecanimimus* (LH 7777) and *Gallimimus* (IGM 100/1133). In avialans like *Archaeopteryx* (Mayr et al., 2005), the palatine ridge is less pronounced and the anterior pneumatic fossa is enlarged and triangular relative to the condition in *Haplocheirus*, occupying the majority of the anterodorsal surface of the palatine. A pneumatic fossa is absent in most noncoelurosaurian theropods (Witmer, 1997b) including *Allosaurus* (Madsen, 1976), but one is present in *Sinraptor* (Currie and Zhao, 1993), where it is large, circular, and perforated by two foramina. Witmer (1997b) reports that a foramen is often developed in the position of the pneumatic recess in tyrannosaurids.

ECTOPTYERGID: The left ectopterygoid (not figured) is located posterior to the palatine and preserved in articulation with the jugal and pterygoid, but most of the ventral surface is obscured by matrix. The jugal process of the right ectopterygoid is preserved in articulation with the jugal, but the contact with the pterygoid is not preserved. Although similar to other theropods in being hook shaped, it is relatively small and slender when compared to the ectopterygoids of dromaeosaurs (Currie, 1995). No other alvarezsauroid preserves an ectopterygoid (Chiappe et al., 2002). The ectopterygoid body is inflated near its contact with the pterygoid, as in coelurosaurs generally (Rauhut, 2003), but the extent of this inflation cannot be determined. A matrix-filled foramen on the dorsal surface of the ectopterygoid may represent a dorsal recess, as in some dromaeosaurids (Ostrom, 1969; Currie, 1995), but it is possible it is a preservational artifact.

VOMER: A small fragment of the anterior end of the left vomer is preserved in contact with the medial edge of the anterior end of the maxillary palatal shelf.

BRAINCASE

EXOCCIPITAL-OPISTHOTIC: The condylar portions of the exoccipitals (figs. 7, 11) are tightly sutured to the occipital condyle, but the sutures can still be seen in posterior view. Each exoccipital contributes approximately one-quarter of the outer rim of the occipital condyle and forms the ventrolateral boundary of the foramen magnum, although they are separated along the ventral margin of this structure by the basioccipital. Lateral to the condylar portion of the exoccipitals, a pair of horizontally arranged foramina open posteriorly. The circular lateral foramen is smaller than the medial foramen. The medial foramen is divided interiorly by a very thin lamina into two distinct openings that represent separate branches of the hypoglossal nerve (CN XII). A horizontal strut (fig. 7) projects from the condylar portion of the exoccipital to merge smoothly with the posterior surface of the paroccipital process, forming a triangular roof over these foramina. This roof forms the dorsal boundary of a shallow subcondylar recess (Witmer, 1997a), a presumably pneumatic feature common in theropods and within Maniraptora (e.g., the basal therizinosauroid *Falcarius* [Smith et al., 2011]). A second bony strut emerges from the lateral margin of the exoccipital to form the ventral margin of the paroccipital processes and forms the lateral boundary of the recess. The suture between the exoccipital and the basioccipital is visible within the subcondylar recess. It is oriented 45° to the plane of the paroccipital processes.

The paroccipital process is mediolaterally long, dorsoventrally narrow, and slightly pendant. The degree of ventral deflection of the pendant paroccipital process is similar to that of *Erlikosaurus* (Clark et al., 1994), but less than that of *Incisivosaurus* (Balanoff et al., 2009) or other oviraptorosaurs (Clark et al., 2002). The ventral edge of the distal end of the process is twisted posteriorly, so that the ventral margin of the process is subhorizontal in distal view, but the dorsal margin retains its vertical orientation, a morphology autapomorphic for *Haplocheirus*. This differs from the morphology present in some dromaeosaurids where the dorsal edge of the distal end is twisted anteriorly (Norell and Makovicky, 2004). The ventral rim of the base of the paroccipital process is situated below the midpoint of the occipital condyle. It is not known whether the paroccipital process is hollow as in some maniraptorans. The anterior surface of the opisthotic has a deep excavation for the caudal tympanic recess. A shallow dorsal tympanic recess is present on the anterodorsal surface of the opisthotic.

BASIOCCIPITAL: The basioccipital (figs. 7, 11) forms the majority of the occipital condyle. The size of the foramen magnum is difficult to determine because of poor preservation and matrix infill, although it is clear that it is relatively smaller than in parvicursorine alvarezsaurids and avians where this opening is unusually large (Chiappe et al., 1998). The dorsal surface of the basioccipital is concave, emarginated by the foramen magnum of which it forms the median ventral margin. The basioccipital is mildly constricted anterior to its condylar portion, forming a very short “neck.” A poorly developed, shallow infracondylar fossa is developed on the ventral surface of the basioccipital neck. The lateral surfaces of the basal tubera are slightly eroded. Their medial margins are directly ventral to the lateral edge of the occipital condyle, and they are formed equally by the basioccipital and basisphenoid. The mediolaterally wide

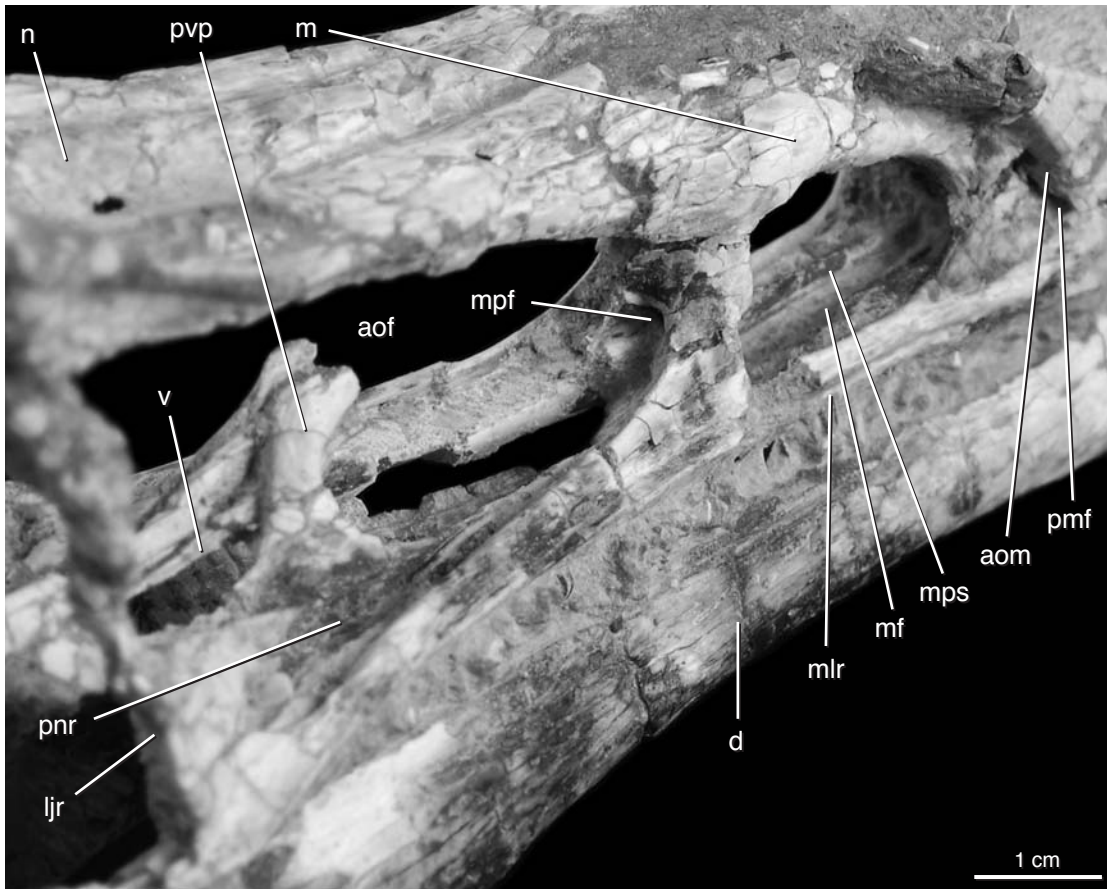


FIGURE 9. Maxillary and anterior palatal region of holotype of *Haplocheirus sollers* (IVPP V14988) in right dorsolateral view. Abbreviations in appendix 1.

basal tubera are narrowly separated along the skull midline. The shallow subcondylar recess is more deeply excavated on the basioccipital than on the exoccipital, extending as a deep pocket onto the posterodorsal surfaces of the basal tubera. Deep fossae are present at the ventromedial corners of the subcondylar recess, but they do not appear to fully penetrate the bone.

BASISPHENOID-PARASPHENOID: The basisphenoid (fig. 11) is anteroposteriorly long and inclined approximately 45° from horizontal as it is in *Shuvuuia* (IGM 100/99, 100/977) and in at least one small troodontid specimen (IGM 100/1128). In the spinosauroid *Baryonyx* (NHMUK R9951) and in some oviraptorosaurs (e.g., *Citipati* [Clark et al., 2002]), the basisphenoid is oriented nearly vertically, but more often it is horizontal in theropods. The basisphenoid forms the anterolateral portion of the basal tubera. The oval basisphenoid recess is deeply excavated and lacks the longitudinal midline ridge on its floor that is present in some maniraptorans. Due to the inclination of the basisphenoid, the basisphenoid recess is visible in posterior view. The left basiptyergoid process can be seen through the infratemporal fenestra passing ventral to the pterygoid ramus of the quadrate and abutting the mediadorsal surface

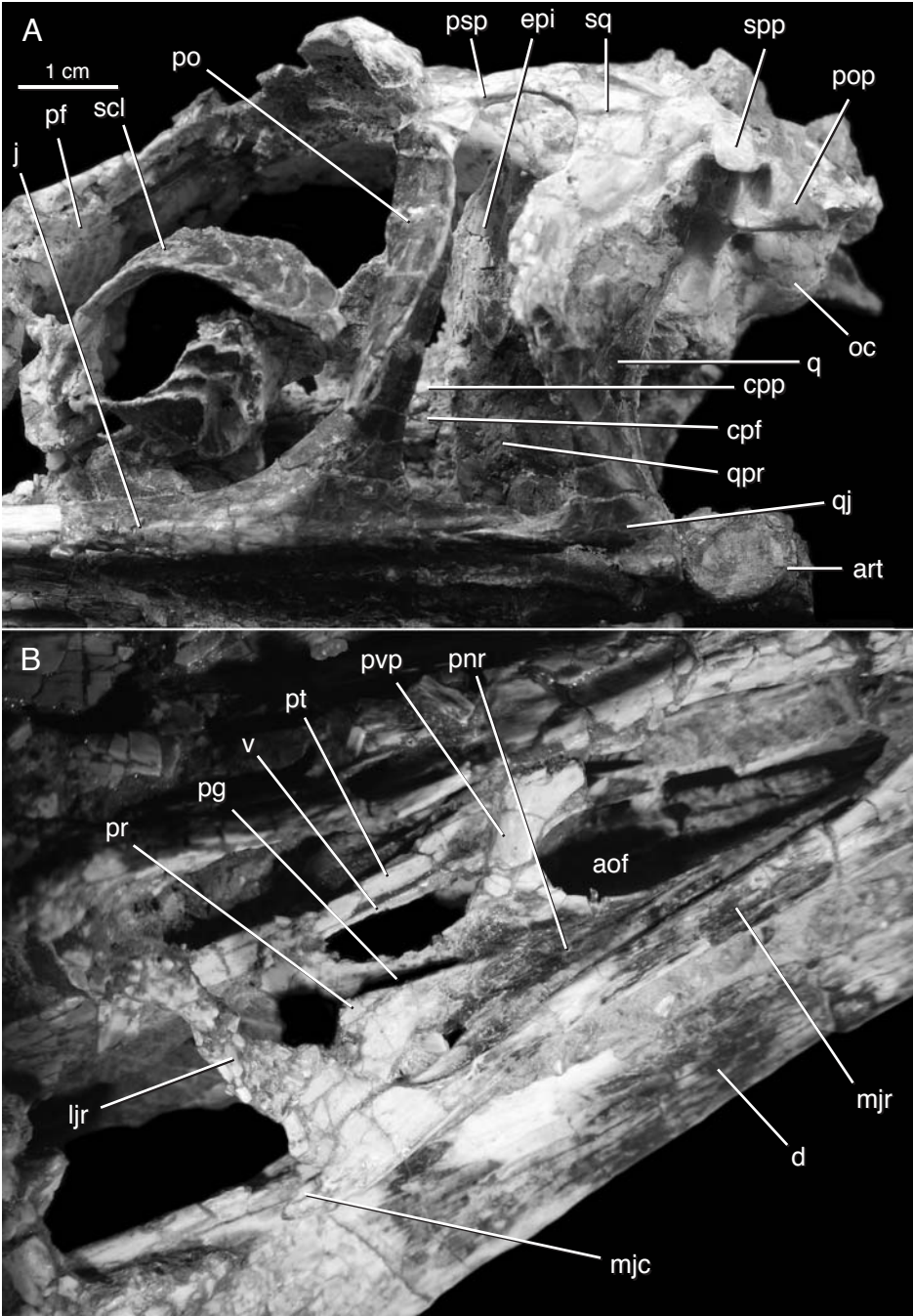


FIGURE 10. **A.** Posterior end of skull and mandible of holotype of *Haplocheirus sollers* (IVPP V14988) in left lateral view, showing original preservation of sclerotic ring (subsequently damaged). **B.** Palate of holotype of *Haplocheirus sollers* (IVPP V14988) in right dorsolateral view. Abbreviations in appendix 1.

of the surangular. It is long and distally tapering, projecting ventrolaterally as in *Shuvuuia* (Chiappe et al., 2002). The right basiptyergoid process is obscured by matrix in anterior view.

The left lateral surface of the cultriform process of the parasphenoid can be seen inside the left orbit (figs. 4, 10). The cultriform process is long, low, and subhorizontally oriented. It tapers gradually as it extends anteriorly, unlike the proximally expanded and sharply anteriorly tapered cultriform process of troodontids, tyrannosaurids, and ornithomimosaurs (Chiappe et al., 1998; Currie and Dong, 2001; Chiappe et al., 2002; Makovicky et al., 2004; Makovicky and Norell, 2004; Kobayashi and Barsbold, 2005a). The ventral surface of the cultriform process is obscured by matrix. There is a large, oval, matrix-filled foramen or recess on the dorsolateral surface of the cultriform process. Dufeu (2002) maintains that this opening represents the tuba auditiva in *Shuvuuia*, but this awaits confirmation with CT scans in *Haplocheirus*.

LATEROSPHEOID: Only the capitate process of the left laterosphenoid (fig. 11) is well preserved. The capitate process is visible in dorsal view of the skull, extending mediolaterally along the anterior border of the supratemporal fenestra ventral to the frontal. It is mediolaterally long, and underlies the postorbital process of the frontal, contacting the medial surface of the postorbital laterally with a very slender projection of bone. The base of the capitate process is ventrally flat. The posteromedial portion of the laterosphenoid is poorly preserved where it contacts the parietal. Ventral to this contact the trigeminal nerve foramina (CN V) are obscured by matrix.

MANDIBLE

DENTARY: The dentary (figs. 3, 4, 6, 8–10, 12) is long, dorsoventrally low anteriorly and mildly dorsoventrally expanded posteriorly. The dentary symphyseal region is medially inturned slightly, making it U-shaped in ventral view. The dorsal surface of the anterior end expands from the alveolar margin to form a low, dorsally arcing eminence. A similar condition is present in the spinosaurid taxa *Baryonyx* (Charig and Milner, 1997) and *Suchomimus* (Serenó et al., 1998), and also in the primitive abelisaur *Masiakasaurus* (Carrano et al., 2002), although in the latter taxon the anterior dentary also shows a corresponding ventral expansion that is not present in *Haplocheirus*. This morphology contrasts with the dorsally convex anterior dentary of some ornithomimosaurs (e.g., *Garudimimus* [Kobayashi and Barsbold, 2005a]), which is a function of a ventral deflection at the anterior end of the dentary rather than a dorsal development of the dorsal margin. Large, widely separated mental foramina are present in positions ventral to each anterior dentary tooth on this expanded surface. Posterior to the anterior tip of the dentary the mental foramina descend progressively more posteriorly and ultimately join to form a deep, dorsolaterally located groove on the mid-to-posterior dentary. This groove deepens and moves dorsally as it extends posteriorly, ending posteriorly at a level just lateral to the tooth row on the dorsolateral margin of the dentary. Although the posterior ends of both dentaries are broken, the alveolar groove is continuous with a groove developed on the anterolateral surangular margin. This groove terminates at the posterior end of the mandibular fenestra, just anterior to the lateral surangular ridge. The groove is located more dorsally than the alveolar groove in troodontids (Makovicky and Norell, 2004), and is neither triangular nor dorsoventrally expanded as in that taxon.

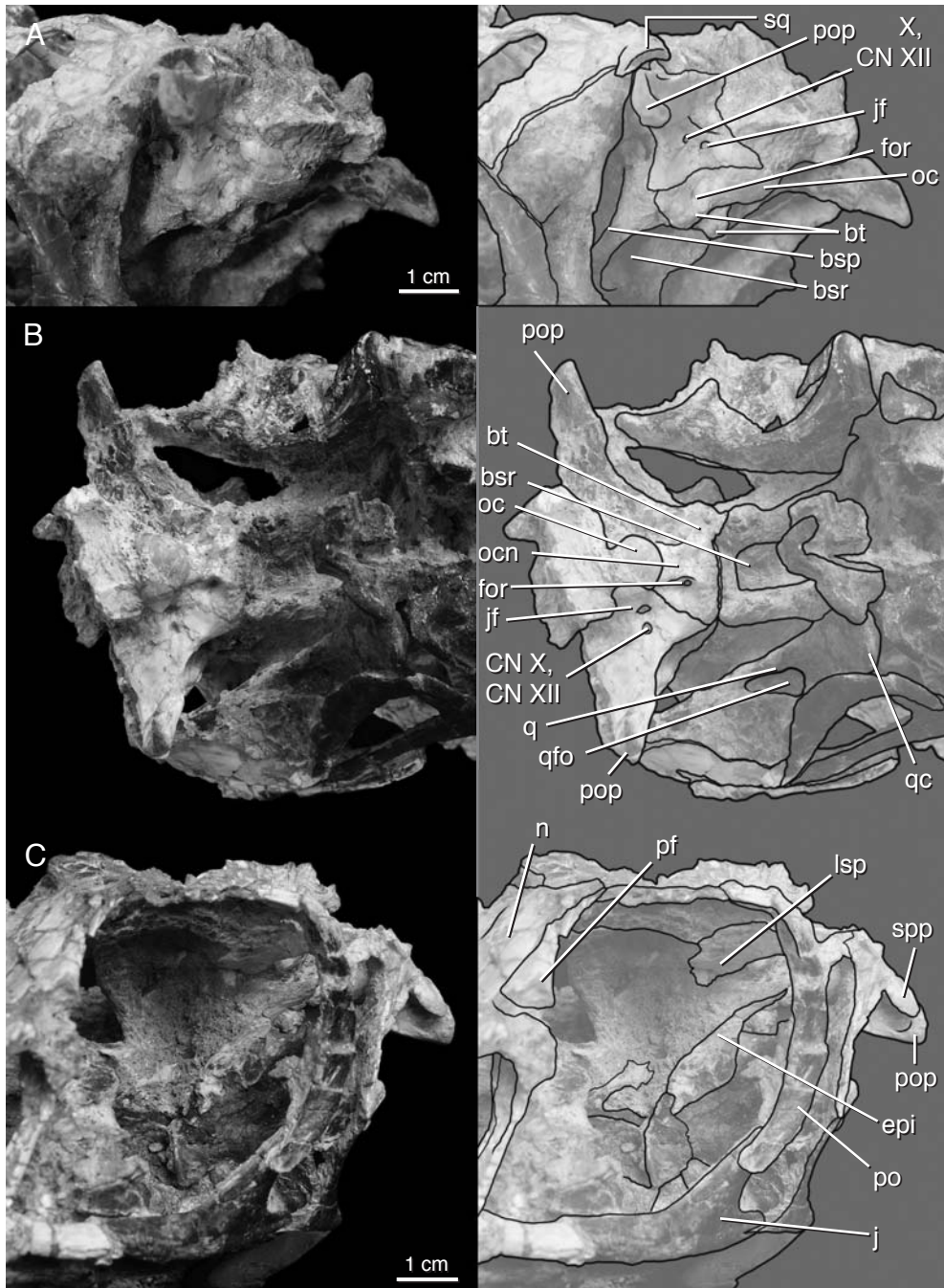


FIGURE 11. Braincase of holotype of *Haplocheirus sollers* (IVPP V14988). **A.** Left lateral view and interpretive line drawing. **B.** Ventral view and interpretive line drawing. **C.** Left anterodorsal view, through left orbit and interpretive line drawing. Abbreviations in appendix 1.

The dentary-surangular articulation is complex. Ventrally, a small, posteriorly projecting tab contacts the anterior edge of the angular, forming a short lap joint. The mesial portion of the posterior end of the dentary forms a horizontal, posteriorly projecting process that contacts a short, anteriorly projecting medial process of the surangular dorsal to the small mandibular fenestra. A small, posteriorly projecting, medially located process is present on the dentary of the basal ornithomimosaur *Harpyimimus*, but it does not contact the surangular (Kobayashi and Barsbold, 2005b). Dorsal to this process, the dorsal margin retreats anteriorly to contact the anterior process of the surangular at the anterior margin of what was described as a secondary mandibular fenestra (Choiniere et al., 2010b). A second external mandibular fenestra has never been reported in a theropod, and this morphology cannot be confirmed on the right side of the skull because of minor preservational distortion. In *Proceratosaurus* (NHMUK R4860), the posterior end of the dentary is similar to *Haplocheirus*, and the right mandible of *Proceratosaurus* also has what may be a second mandibular fenestra. On closer inspection, this fenestra in *Proceratosaurus* is the result of offset along the dentary-surangular articulation and coincident loss of bone from the posterior dentary. Continued study of *Haplocheirus* shows that what was reported as a second mandibular fenestra is actually missing pieces of bone on the lateral surface of the surangular, similar to the *Proceratosaurus* pseudoforamen. We therefore regard this previously described morphology as a preservational artifact for *Haplocheirus* and have removed it from the diagnosis.

SURANGULAR: Both the left and the right surangulars (figs. 3, 4, 6, 10, 12) are nearly complete and well preserved. The surangular is anteroposteriorly long and dorsoventrally low, forming the majority of the lateral surface of the posterior third of the mandible. The anterior process composes approximately half the overall length of the bone, and it is dorsoventrally much less than half the height of the mandible. It forms the dorsal border of the external mandibular fenestra. The dorsal edge of the lateral surface of the anterior process has a shallow groove that appears to be confluent with the mental alveolar groove on the dentary, a feature that is also present in *Proceratosaurus* (NHMUK R4860) and in *Ornitholestes* (AMNH FARB 619). Along the ventral margin of the anterior process, a small, anteriorly projecting spur contacts the mesial posterior process of the dentary to form the dorsal border of the mandibular fenestra. The labial surface of the spur is covered in very-fine (visible only under magnification) horizontally oriented striations. These striations indicate that this spur may have articulated with the medial surface of the dentary and further suggest that the dentary and surangular are anteroposteriorly displaced from each other contributing to the appearance of a “secondary” external mandibular fenestra.

The posterior half of the surangular has a well-developed lateral ridge (fig. 12) on the dorsal edge of the lateral surface. This ridge extends anteriorly from the anterior edge of the jaw articulation to the level of the posterior end of the mandibular fenestra. The posterior end of the ridge is more extensively developed laterally than the anterior end. A ridge in this position is also present in tyrannosauroids (Holtz, 2004), although it is weakly developed in *Proceratosaurus* (NHMUK R4860) and in *Guanlong* (IVPP V14532). Ventral to the posterior end of this ridge is a single small surangular foramen, located in a depressed fossa just anteroventral to the surangular contribution to the glenoid fossa.

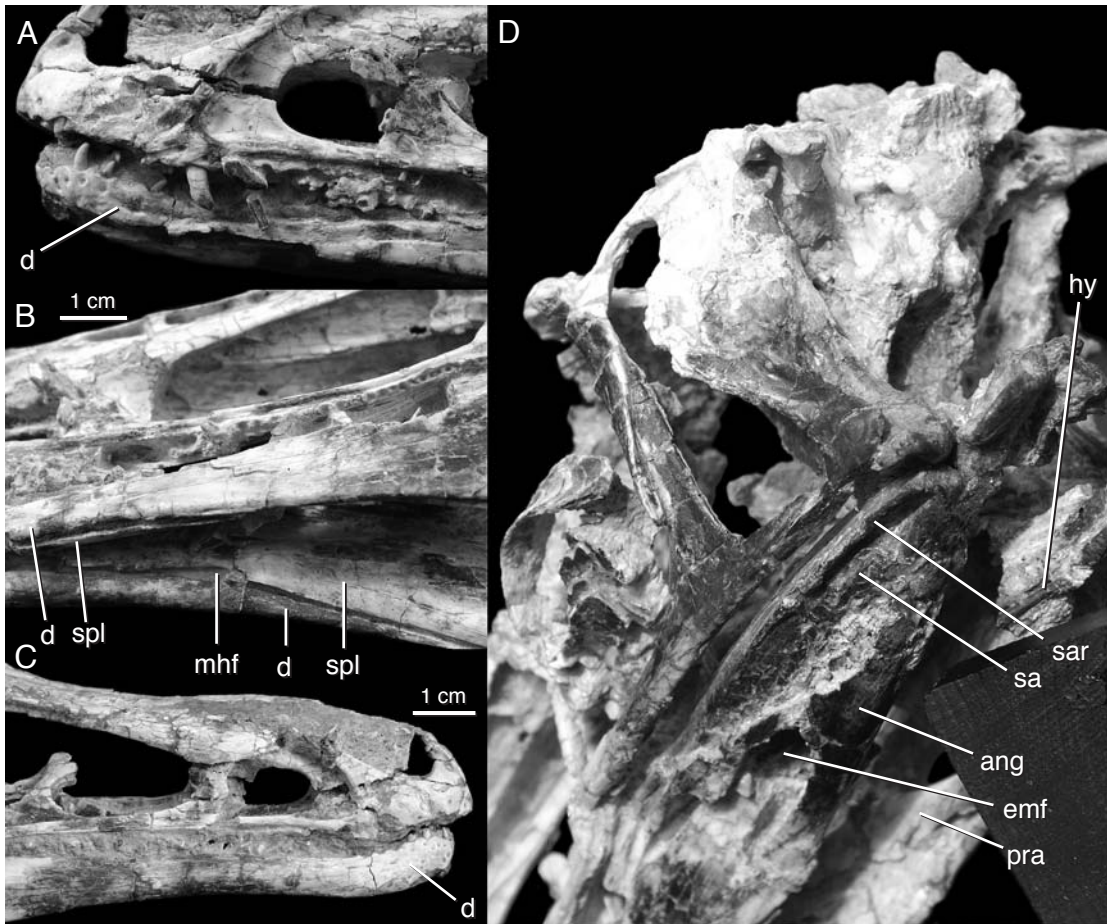


FIGURE 12. In situ dentition and mandibular articulation of holotype of *Haplocheirus sollers* (IVPP V14988). **A.** Anterior dentition of premaxilla, maxilla, and dentary in left lateral view. **B.** Posterior dentition of maxilla in left ventrolateral view. **C.** Anterior dentition of premaxilla, maxilla, and dentary in right lateral view. **D.** Mandibular articular region in left posteroventrolateral view. Abbreviations in appendix 1.

ANGULAR: Both angulars (figs. 3, 4, 6, 12) are complete and preserved in articulation with the corresponding surangulars dorsally and dentaries anteriorly. The angular is long, extending the entire length of the external mandibular fenestra and covering the splenial laterally. The dorsoventral height of the angular below the external mandibular fenestra is approximately the same as the height of the surangular above the fenestra. The surangular-angular suture is directed posteroventrally and meets the ventral edge of the mandible well anterior to the glenoid. The medial surface is medially concave, forming the labial border of the anteroposteriorly long internal mandibular fenestra. Ventrally, the angular forms an extensive medial contact with the prearticular.

SPLENIAL: The splenial (figs. 6, 12) is well preserved, but its medial surface is partly obscured by matrix. It is anteroposteriorly long and dorsoventrally low, with an anteroposteriorly extensive, thin anterior end that extends almost to the dentary symphysis. The mylohyoid

foramen is a very small notch opening anteroventrally, and is located on the anterior third of splenial. The posterior end of the splenial is straight, rather than forked, and it is angled posteroventrally. The splenial is not exposed in lateral view.

PREARTICULAR: The right prearticular (fig. 6) is complete and is exposed in medial view. It is dorsoventrally low and straplike, with the shallow curvature that is typical for small theropods and unlike the deep, U-shaped prearticulars of tyrannosauroids (Senter, 2007). The prearticular forms the ventral border of the internal mandibular fenestra, which is long and low. Posterior to the fenestra, the posterior one-fifth of the prearticular makes an anteroposteriorly extensive contact with the ventral surface of the articular.

ARTICULAR: Both articulars (figs. 6, 12) are nearly complete and preserved in their original positions. The right articular is best preserved. The articulation for the quadrate condyle is only as long as the condyle itself, allowing little anteroposterior movement at the jaw joint. The retroarticular process points strictly posteriorly and is mediolaterally wide with a shallow dorsal concavity for the attachment of *m. depressor mandibulae*. On the medial surface of the articular, medial and slightly ventral to the glenoid, a small process of the articular projects medioventrally. The dorsal surface of this process is deeply concave. In *Shuvuuia*, a very large medial process of the articular is present in a slightly more posterior location (Chiappe et al., 2002), but it appears likely these two features are homologous. In dromaeosaurids, a medial process of the articular is also present, but it originates from the medial surface of the posterior end of the retroarticular process (Currie, 1995).

DENTITION

PREMAXILLARY TEETH: The alveolar surface of the right premaxilla has not been fully prepared, but enough can be seen to infer that the roots of the four premaxillary teeth are of similar size and circular in cross section (figs. 12, 13). The anterior three teeth are closely spaced, and the spacing between the third and fourth alveoli is slightly larger. The left premaxilla preserves the two nearly complete posteriormost teeth. These teeth are unserrated, and the crown of the third tooth is conical and almost straight. There is no constriction between root and crown on any of the teeth where the root is visible. The fourth premaxillary tooth of *Haplocheirus* is only mildly recurved, and there is a suggestion of flattening on its posterior crown surface, but matrix partially obscures it.

MAXILLARY TEETH: Although only a few of the maxillary teeth are preserved (figs. 3, 4, 8, 9, 12, 13), the alveoli show that they were numerous, very small, and that the tooth row extends posteriorly to the level of the preorbital bar (clearly visible in fig. 12). Thirty alveoli can be seen in the left maxilla, and correcting for sections of the maxilla where alveoli are not preserved, we estimate that there were 35 maxillary teeth. Among theropods this number is approached only by *Pelecanimimus* (~30 maxillary teeth; Perez-Moreno et al., 1994), *Shuvuuia* (~30 maxillary teeth; IGM 100/0977; Chiappe et al., 1998) and some troodontids such as *Byronosaurus* (~30 maxillary teeth; Makovicky et al., 2003). The crowns increase in apicobasal height anteriorly, and the anterior teeth are subconical and the middle teeth are labiolingually flat. The posteriormost teeth are missing. The anteriormost teeth entirely lack serrations. Only the distal ends of the anterior maxillary teeth are recurved, as most of the tooth crown is straight. From

approximately the fifth tooth on, the middle teeth have serrations only on their distal carinae. In some of the middle teeth the serrations are developed along the entire distal carinae, but in others the serrations are developed only basally. Marked heterodonty as described above is uncommon in theropods, but is known in the troodontid taxon *Troodon* (Currie, 1987) and in *Ricardoestes* (Currie et al., 1990; Longrich, 2008), a putative troodontid (Hwang, 2005: examining *Paronychodon*). It is difficult to get a precise count of serration density, because nearly all the teeth have some minor crown damage, but it appears to be in the range of 5–7 serrations per millimeter, which is typical for coelurosaurs (Choiniere et al., 2010a) and unlike the more sparsely serrated teeth of some troodontids (e.g., *Saurornithoides* (Osborn, 1924; Norell et al., 2009)), and therizinosauroids (Clark et al., 2004). The serrations extend directly posteriorly. As in some troodontids (Norell et al., 2009), the serrations end well short of the tooth apices.

Left maxillary tooth 3 is preserved within its alveolus. The crown is subconical and only slightly recurved, as in *Pelecanimimus* (LH 7777). This tooth has strong apicobasally oriented striations, as in spinosaurids (Brusatte et al., 2007), although these striations are present only on one other maxillary tooth crown. Only one midmaxillary tooth is preserved (on the right side of the skull) in its alveolus. This tooth is markedly smaller than the anterior teeth, about half the height of tooth 3. It also differs in shape, being apicobasally short and mesiodistally wide. In lateral view, the mesial margin of the tooth crown abruptly changes angle at midheight, deflecting strongly apicodistally, as in some troodontids (Makovicky and Norell, 2004). Posterior to the eighth maxillary tooth position, the maxillary alveoli progressively decrease in size.

Interdental plates are well preserved between all the maxillary teeth and the broken pieces of osseous septae extend laterally from the lateral surface of the interdental plates between adjacent teeth. None of the preserved maxillary teeth show evidence of a constriction between the tooth crown and the root, as in *Archaeopteryx*, derived alvarezsauroids (Perle et al., 1993), ornithomimosaurs (e.g., *Pelecanimimus* (LH 7777)), and therizinosauroids (Clark et al., 2004).

DENTARY TEETH: The anterior seven dentary teeth are larger than more posterior dentary teeth, unserrated, subconical, mildly recurved, and widely spaced (figs. 3, 4, 12, 13). The entire dentary tooth row is not preserved on either side, but we estimate 30–40 dentary teeth for *Haplocheirus* based on the presence of alveolar foramina and alveolar notches in the dorsal dentary margin. The roots of these anterior teeth have circular cross sections. Only three middentary teeth are preserved on the left side, and they are similar in size to the anterior teeth but more mediolaterally compressed. These middentary teeth bear serrations on the distal carinae. The serrations average approximately 5 per mm. The size of the alveoli in the dentary decreases posteriorly, indicating that tooth size probably diminished in correspondence to the maxillary teeth.

DISCUSSION

We base our phylogenetic hypotheses and character distributions in the discussion below on the results of the large cladistic analysis of Coelurosauria by Choiniere et al. (2014: fig. 20A, and supplementary information therein). In that analysis (here reproduced in fig. 14), Alvarezsauroidae are monophyletic, with *Haplocheirus* as the basalmost member, the South American taxa *Patagonykus* and *Alvarezsaurus* forming a grade of intermediate alvarezsaurids, and with the most

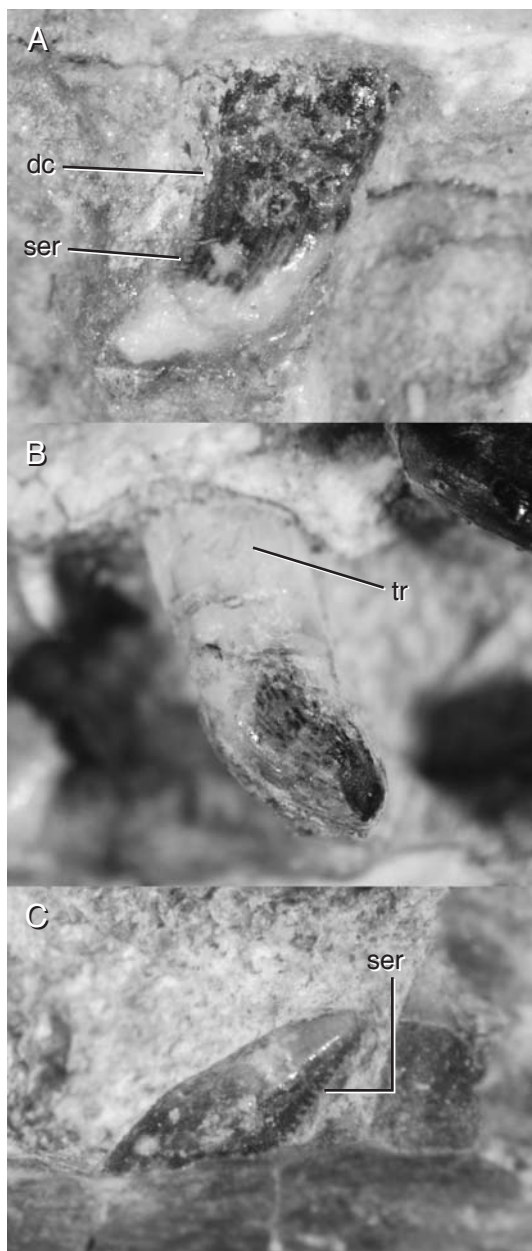
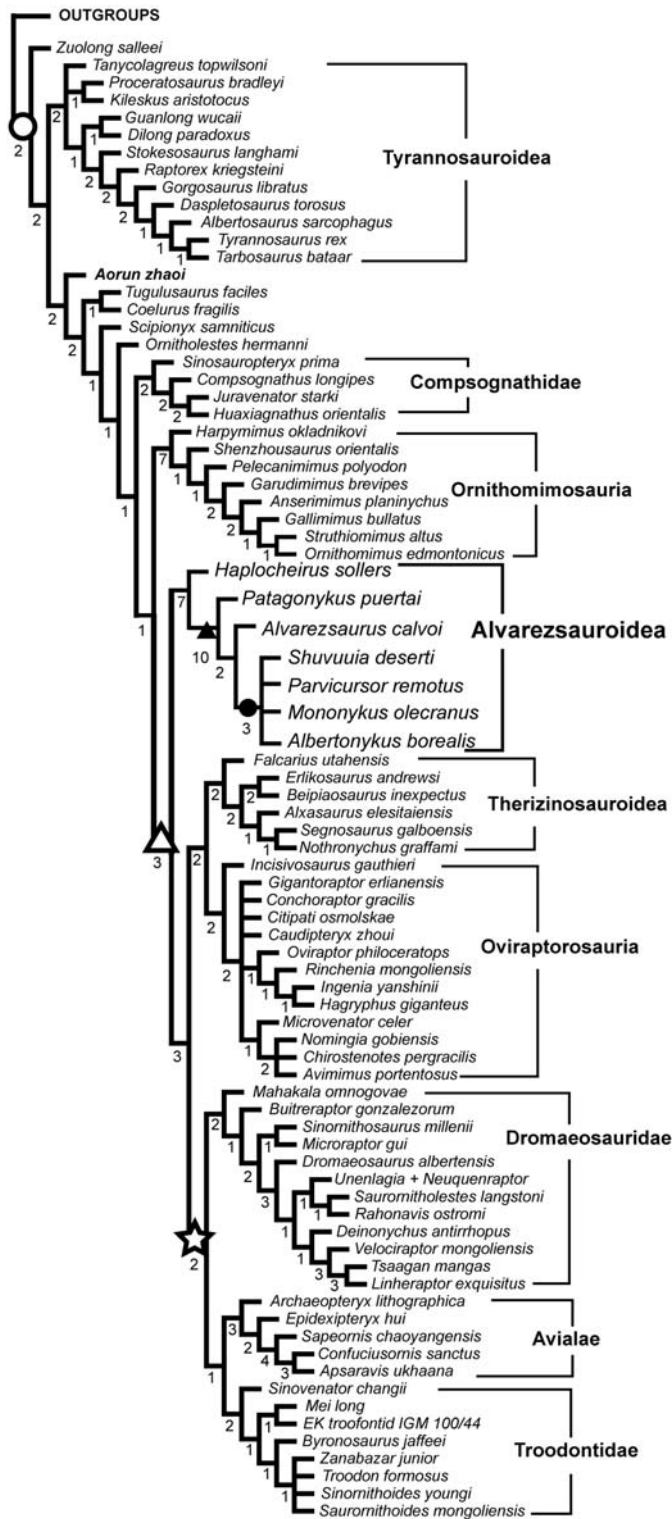


FIGURE 13. Enlarged views of dentition of holotype of *Haplocheirus sollers* (IVPP V14988). **A.** Right midmaxillary tooth (approximately position 8) in right lateral view. **B.** Left midmaxillary tooth (approximately position 5) in left lateral view. **C.** Left dentary tooth 6 in left lateral view. Abbreviations in appendix 1.

derived members of the clade forming a monophyletic but poorly resolved Parvicursorinae. The higher relationships recovered in that analysis show Alvarezsauroidea to be the basalmost taxon in Maniraptora, sister to ((*Therizinosauria* + *Oviraptorosauria*) + *Paraves*).

ANATOMICAL DISCUSSION: Fossil skull material for alvarezsauroids is partitioned between the most derived Upper Cretaceous taxa (*Parvicursorinae*) and the most basal, Upper Jurassic members of the clade (*Haplocheirus*), with no cranial remains from temporally or phylogenetically intermediate taxa such as *Patagonykus*. This preservational bias, coupled with the extreme structural modifications in the derived parvicursorine skull, makes recognizing intermediate conditions in the cranial anatomy of *Haplocheirus* difficult. It is therefore unsurprising that relatively few bones of the skull of *Haplocheirus* bear derived alvarezsauroid synapomorphies. Nevertheless, *Haplocheirus* preserves several features of cranial anatomy that are transitional between more basal maniraptoran conditions and those of parvicursorines, including a shift in orientation and morphology of the basisphenoid, reduction of the dentition, and reduction of the bones surrounding the infratemporal fenestra. We comment on these below.

The strongest cranial evidence for the alvarezsauroid affinities of *Haplocheirus* comes from the basisphenoid. The basisphenoid of parvicursorine alvarezsauroids is oriented approximately 45° to the horizontal axis of the skull, a very rare morphology in other theropods that is also seen in the unnamed Mongolian troodontid specimen IGM 100/1128. The basiptyergoid processes of parvicursorines are long and tapering (Chiappe et al., 2002), and due to the inclination of the basisphenoid, they project anteroventrally. Both of these features are present in *Haplochei-*



rus, in more or less the same degree as in parvicursorines, and therefore this characteristic basisphenoid anatomy forms an Alvarezsaurid cranial synapomorphy. Furthermore, *Haplocheirus* shows that this basic architecture of the braincase floor was already in place early in the evolution of Alvarezsauridae. Although reasons for this derived morphology are unclear, its presence in some small troodontids (e.g., IGM 100/1128) suggests that similar evolutionary pressures (constraints, adaptive scenarios, or otherwise) may have been acting in these lineages.

Parvicursorine alvarezsaurids have dentitions that differ markedly from the plesiomorphic coelurosaurian condition (Choiniere et al., 2010a) in the following ways: the number of maxillary and dentary teeth is greatly increased; both maxillary and dentary tooth crowns are homodont and set into an open groove (e.g., there are no inder-

FIGURE 14. Phylogenetic relationships of *Haplocheirus sollers* from Choiniere et al., 2014. Tree-shape parameters discussed in text. Tree is strict consensus of 80 MPTs, length = 3045, CI = 0.213, RI = 0.611. Open circle denotes Coelurosauria; open triangle denotes Maniraptora; open star denotes Paraves; closed triangle denotes Alvarezsauridae; closed circle denotes Parvicursorinae. Numbers below nodes are Bremer support values.

dental septae); the tooth crowns lack serrations on the carinae; the tooth crowns are only slightly recurved; and there is a constriction between the tooth crown and tooth root. Premaxillary teeth are unknown for parvicursorines, but from *Haplocheirus* it can be determined that early alvarezsauroids retained the four premaxillary teeth that are plesiomorphic for coelurosaurs generally (Rauhut, 2003; Choiniere et al., 2010a). Among other hyperdentate coelurosaur taxa, the troodontid *Byronosaurus* has four premaxillary teeth (Makovicky et al., 2003) and the ornithomimosaur *Pelecanimimus* bears seven (Perez-Moreno et al., 1994). *Haplocheirus* has at least 30 teeth in the maxilla (and likely many more) as well as in the dentary, and given similar tooth counts in *Falcarius* (Zanno, 2010) it now appears that a moderate increase in the number of teeth is plesiomorphic for Maniraptora. Within Alvarezsauroida, the tooth count in *Haplocheirus* is apparently greater than even *Shuvuuia* (in which the posterior end of the tooth row is poorly preserved) (Chiappe et al., 1998). This perhaps indicates that the number of maxillary teeth was reduced during alvarezsauroid evolution.

Interestingly, *Haplocheirus* bears interdental septae, whereas septae are lost in *Shuvuuia* (Chiappe et al., 1998). Interdental septae are present in perinate specimens of the hyperdentate troodontid *Byronosaurus*, but they are markedly reduced in height relative to those of other maniraptorans (Bever and Norell, 2009). Interdental septae are clearly lost in both the basal-most ornithomimosaur *Nqwebasaurus* and between some but not all the alveoli in the hyperdentate basal ornithomimosaur *Pelecanimimus* (Perez-Moreno et al., 1994; Choiniere et al., 2012). These observations suggest that an increase in tooth number and loss of separate alveoli are separate evolutionary processes. However, *Haplocheirus* has heterodont dental morphology (as do basal oviraptorosaurs: Xu et al., 2002a; Balanoff et al., 2009; some troodontids: Currie, 1987; Longrich, 2008; and therizinosauroids: Zanno, 2010), whereas the aforementioned hyperdentate taxa are considerably more homodont. In developing *Alligator mississippiensis* specimens, interdental septae appear late in the ontogenetic sequence, and it is only after these septae are fully developed that the dentition becomes more heterodont (Westergaard and Ferguson, 1990). This suggests that if theropod dental ontogeny is similar to that of extant toothed archosaurs, then the loss of interdental septae and increased homodonty in these theropods may be due to paedomorphic retention of earlier developmental stages in adults, a phenomenon currently hypothesized to be largely responsible for the evolution of skull shape in the theropod to bird transition (Bhullar et al., 2012), or alternatively suggests that these taxa are represented by juvenile exemplars.

The distribution of derived tooth features in *Haplocheirus* is grossly similar to the pattern observed in basal members of the maniraptoran clades Therizinosauroida and Oviraptorosauria, where initial tooth modification begins with anterior dentition (Xu et al., 2002a; Zanno, 2010; Pu et al., 2013). This suggests a conserved maniraptoran tendency toward modification of premaxillary and anterior maxillary and dentary teeth rather than middle-to-posterior maxillary or dentary teeth, although anterior tooth modifications are apparently independently derived in Alvarezsauroida, Therizinosauroida, and Oviraptorosauria.

Specifically, the anterior teeth of *Haplocheirus* resemble the maxillary and dentary teeth of parvicursorines in lacking serrations and having only mild recurvature (Perle et al., 1993; Perle et al., 1994; Chiappe et al., 1998), whereas the middle and posterior maxillary and dentary teeth of

Haplocheirus retain serrations and recurvature (plesiomorphic for coelurosaurs) but resemble those of parvicursorines in having circular root cross sections and a reduced size. This suggests that changes in tooth morphology progressed either at two different rates or at different evolutionary intervals in the premaxilla and maxilla of alvarezsauroids, whereby the premaxillary tooth crown morphology changed either first or at a higher rate, and the maxillary tooth crown morphology changed at a slower rate and proceeded from posterior to anterior. This pattern seems to differ from that inferred in troodontids, where increases in tooth number and changes in tooth morphology appear nearly simultaneously (Hu et al., 2009), although both *Troodon* itself and the putative troodontid *Ricardoestes* show marked heterodonty (Currie, 1987; Longrich, 2008).

Some of the key features previously used in uniting parvicursorine alvarezsauroids with Avialae (reviewed in Chiappe et al., 2002), and now interpreted as homoplastically developed local synapomorphies of the group (Choiniere et al., 2010b), include the reduction in the bones surrounding the infratemporal fenestra, such as the fusion of the quadratojugal and jugal into a single rodlike structure, the loss of a contact between the ascending ramus of the quadratojugal and squamosal, and an incomplete postorbital bar where the jugal lacks an ascending postorbital process. The morphology of the posterior orbital and infratemporal region in *Haplocheirus* shows some features presaging this derived morphology.

The body of the jugal of *Haplocheirus* is reduced in dorsoventral height and is markedly more cylindrical than the platelike jugal of basal coelurosaurs (e.g., tyrannosauroids) and some maniraptorans (e.g., dromaeosaurids). This feature, however, seems to characterize at least some other basal maniraptorans (e.g., *Ornitholestes* [AMNH FARB 619]) and may be plesiomorphic for the group. The quadratojugal process of the jugal is posteriorly extensive, and the corresponding jugal process of the quadratojugal is short, suggesting that fusion between these two bones involved an early increase in jugal posterior length and decrease in quadratojugal length. However, neither the ascending process of the quadratojugal nor the postorbital process of the jugal show signs of reduction in *Haplocheirus*, indicating that early stages of the loss of this contact is nested deeper within Alvarezsauroidae. The loss of these contacts may occur in conjunction with further reduction in dental morphology and may indicate accompanying dietary shifts, although a number of other explanations are equally likely to result in this morphology, such as general lightening of the cranium or changes in skull function (e.g., prokinesis). More cranial remains from alvarezsauroids intermediate between *Haplocheirus* and parvicursorines are necessary to accurately time the loss of these features.

The homology of the prefrontal bone in parvicursorines has been contentious (Chiappe et al., 1998; Sereno, 1999; 2001; Suzuki et al., 2002). In the prefrontal region, the parvicursorine *Shuvuuia* has hypertrophied ossifications that make a large contribution to the anterodorsal orbital margin and the dorsal skull roof and meet ventrally at a position anterior to the orbits inside the skull forming a preorbital wall. Chiappe et al. (1998) suggested that these “prefrontal” elements might be homologous to the ectethmoid bones of Aves, which also form the anterodorsal corner of the orbit and meet along the skull midline. The prefrontal of *Haplocheirus* shows no signs of enlargement relative to the plesiomorphic coelurosaurian condition (e.g., *Ornitholestes* AMNH FARB 519), but it is positionally similar to the ossification in parvicursorines, and bears a descending process that extends along the medial surface of the lacrimal. This

suggests either that the feature present in parvicursorines in this area is a hypertrophied prefrontal, or that an ectethmoid element evolved later in the alvarezsauroid lineage. In either case, the condition in *Haplocheirus* shows that the ossification in parvicursorines is not homologous to that of birds (contra Chiappe et al., 1998) and that the hypertrophied prefrontals of ornithomimosaurs are not homologous to those of parvicursorines (contra Sereno, 2001).

Parvicursorine alvarezsaurids, along with avialans, some troodontids, and some oviraptorosaurs, have a quadrate with two dorsal contacts—one on the ventral surface of the squamosal and one on the prootic on the lateral wall of the braincase (Perle et al., 1993; Russell and Dong, 1994; Maryanska et al., 1997; Maryanska et al., 2002). The parvicursorine morphology is particularly similar to that of avialans because it contacts the prootic and squamosal (Chiappe et al., 1998) rather than the opisthotic and squamosal, as it does in oviraptorosaurs (Maryanska et al., 1997; Balanoff et al., 2009). The plesiomorphic, single-headed quadrate of *Haplocheirus* demonstrates that in alvarezsaurids, as in oviraptorosaurs and troodontids, this double-headed morphology is convergent with respect to avialans. If this quadrate morphology is related to streptostyly, as has been hypothesized (Chiappe et al., 1998), then the development of the accessory articulation of the quadrate may develop only in conjunction with increased mobility of other skull elements, including the loss of the postorbital bar and prokinesis of the frontonasal joint (Chiappe et al., 1998).

FEEDING ECOLOGY OF HAPLOCHEIRUS: Several lines of anatomical evidence suggest that *Haplocheirus* differs from most theropods in its ecology. The lightly built construction of the skull, with large antorbital and maxillary fenestrae, reduction of the lacrimal and postorbital bars, and reduction of the jugal, all suggest that the skull of *Haplocheirus* was incapable of withstanding strong bending forces from biting. The narrow snout and long, slender dentaries provide a low power-to-velocity ratio for the jaws of *Haplocheirus*, suggesting weak bite force but rapid jaw closure ability. The numerous small, weakly recurved teeth with reduced serrations are consistent with the ability to hold and pierce small prey. Together, these lines of evidence suggest that *Haplocheirus* was preferentially feeding on small vertebrates rather than on the larger dinosaurian fauna of the Shishugou Formation. *Haplocheirus* differs greatly in these ways from contemporary Shishugou theropods *Monolophosaurus* (Zhao and Currie, 1993; Brusatte et al., 2010), *Sinraptor* (Currie and Zhao, 1993), and *Zuolong* (Choiniere et al., 2010a), which all have more typical theropod configurations of the jaws that suggest stronger bite forces and larger prey items. The presence in the Shishugou of theropods with these “typical” jaw configurations coupled with theropod taxa bearing “atypical” configurations such as *Haplocheirus*, the longirostrine tyrannosauroid *Guanlong* (Xu et al., 2006) and the possibly herbivorous ceratosaur *Limusaurus* (Xu et al., 2009) shows that a range of theropod feeding ecologies were already present by the earliest Late Jurassic.

The orbit of *Haplocheirus* is strikingly large, and it preserves a large sclerotic ring composed of externally concave ossicles. Some recent work on activity patterns of dinosaurs employing scleral ring morphology (Schmitz and Motani, 2011) hypothesizes that several theropod taxa, including *Velociraptor mongoliensis*, were nocturnal. Based on a qualitative comparison with Schmitz and Motani’s (2011) data, the inner diameter of the scleral ring of *Haplocheirus* is approximately 15 mm larger than that of *Velociraptor* and the outer diameter of the scleral ring

is only approximately 9 mm larger, even though the skulls are of generally similar size. This indicates a much larger lens in *Haplocheirus* than in *Velociraptor* and, according to the data of Schmitz and Motani (2011), suggests the eye of *Haplocheirus* was optimized for scotopic ocular image formation and thus nocturnal habits. However, a similar analysis by Hall (2008) found equivocal evidence for nocturnality in most dinosaurs, and a recent critique of the Schmitz and Motani (2011) analysis by Hall et al. (2011) warrants caution for this interpretation.

ALVAREZSAUROID DISTRIBUTION AND HISTORICAL BIOGEOGRAPHY: *Haplocheirus* provides evidence for alvarezsauroids in the Late Jurassic, filling in one of the longest ghost lineages in the theropod fossil record (Choiniere et al., 2010b), yet Early Cretaceous alvarezsauroids remain elusive. Given the wealth of fossils of other derived coelurosaurs in Lower Cretaceous deposits in northeast China (Xu et al., 1999; Xu et al., 2002b; Xu and Norell, 2004), it is surprising that there have been no discoveries of alvarezsauroids in the Jehol Biota or the Daohugou beds.

Xu et al. (2013) recently provided a comprehensive review of alvarezsaur historical biogeography, but failed to mention that the presence of *Haplocheirus* in the Jurassic of China falsifies Novas' hypothesis of a Gondwanan origin for Alvarezsauroidea (Bonaparte, 1991; Novas, 1996). The diversity of basal alvarezsaurids in the Late Cretaceous of South America (Bonaparte, 1991; Novas, 1996; 1997; Martinelli and Vera, 2007; Agnolin et al., 2012; Makovicky et al., 2012) and their position as a grade basal to Parvicursorinae is possibly compatible with a Gondwanan origin for these more derived members of the clade. However, this hypothesis would require subsequent dispersal through land bridges to explain the presence of Parvicursorines in Asia (Perle et al., 1993; Chiappe et al., 1998; Xu et al., 2010; Xu et al., 2011), Europe (Naish and Dyke, 2004), and North America (Hutchinson and Chiappe, 1998; Longrich and Currie, 2008) during the Late Cretaceous. Given that alvarezsauroids are relatively rare components of theropod faunas (Makovicky et al., 2012), and the possibility of a panglobal distribution for coelurosaurian higher taxa prior to the split between Gondwana and Laurasia (Benson et al., 2010; Benson et al., 2012; Choiniere et al., 2012), it is possible that basal alvarezsaurs were widely distributed in the Mesozoic and that either local extinctions or preservational bias explains our current understanding of their distribution. Recovery of new alvarezsaur material from the Early Cretaceous, particularly from Gondwana, coupled with a better understanding of the phylogenetic relationships of poorly known forms like *Kol* (Turner et al., 2009) and *Heptasteornis* (Naish and Dyke, 2004), will undoubtedly clarify their biogeographic history (Xu et al., 2013).

CONCLUSION

The discovery of *Haplocheirus* provides direct evidence of alvarezsauroids in the Late Jurassic, confirming predictions from ghost lineages. Our knowledge of cranial material for *Haplocheirus* is particularly important because alvarezsauroid skulls are previously known only for a few specimens of derived taxa. The cranium of *Haplocheirus* preserves several plesiomorphic features, including a medium-sized prefrontal and an unfused jugal and quadratojugal, which show that some of the cranial traits shared between derived alvarezsauroids and avialans are homoplasies. Other characteristics of *Haplocheirus*, such as the orientation of the braincase,

indicate that the initial stages of the evolution of derived alvarezsauroid characteristics were already underway by the Late Jurassic. The discovery of additional alvarezsauroid material, particularly cranial material from Lower Cretaceous deposits, would help clarify the timing of other key changes in the alvarezsauroid skull.

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APPENDIX 1

ABBREVIATIONS

INSTITUTIONAL

AMNH FARB	American Museum of Natural History, Fossil Amphibians, Reptiles, and Birds
IGM	Institute of Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, People's Republic of China
IWCMS	Dinosaur Isle Visitor Center, Isle of Wight County Museums Service, Sandown, United Kingdom
LH	Museo de Cuenca, Cuenca, Spain, housed at Universidad Autónoma de Madrid, Madrid, Spain
NHMUK	Natural History Museum, London, United Kingdom

ANATOMICAL

alv	alveolus
amp	medial process of articular
ang	angular
aof	antorbital fenestra
aom	anterior margin of antorbital fossa
art	articular
bc	braincase
bpp	basipterygoid process of basisphenoid
bsp	basisphenoid
bsr	basisphenoid recess
bt	basal tubera
CN X	vagus foramen
CN XII	hypoglossal foramen
cpf	fossa in cultriform process of parasphenoid
cpp	cultriform process of parasphenoid

d	dentary
dc	distal carina
dg	dentary groove
emf	external mandibular fenestra
en	external naris
epi	epipterygoid
f	frontal
fns	frontonasal suture
for	foramen
gr	groove
hy	hyoid
idp	interdental plates
j	jugal
jf	jugular foramen
lac	lacrimal
ljr	jugal ramus of lacrimal
lmns	lacrimo-maxillary-nasal suture
lmr	maxillary ramus of lacrimal
lns	lacrimo-nasal suture
lsp	laterosphenoid
m	maxilla
map	maxilla anterior process
max	maxilla
mf	maxillary foramen
mhf	mylohyoid foramen
mjc	jugal contact of maxilla
mjr	jugal ramus of maxilla
mlr	lateral maxillary ridge
mnr	nasal ramus of maxilla
mp	maxillary pila
mpf	foramen in maxillary pila
mps	palatal shelf of maxilla
n	nasal
nmp	maxillary process of nasal
nms	nasomaxillary suture
nns	internasal suture
o	orbit
oc	occipital condyle
ocn	neck of occipital condyle
p	parietal
pf	prefrontal
pg	pterygoid groove
pm	premaxilla
pmf	promaxillary foramen
pmg	premaxillary groove
pnf	pneumatic foramen
pnp	nasal process of premaxilla
pnr	pneumatic recess

po	postorbital
pop	paroccipital process
pr	pterygoid ridge
pra	prearticular
psp	squamosal process of postorbital
pt	pterygoid
pvp	vomeropterygoid process of palatine
q	quadrate
qc	quadrate mandibular condyle
qfo	quadrate foramen
qj	quadratojugal
qpr	pterygoid ramus of quadrate
rap	retroarticular process
sa	surangular
sar	surangular ridge
scl	sclerotic ossicle(s)
ser	serrations
soc	supraoccipital
snf	subnarial foramen
spl	splenial
spp	paroccipital process of squamosal
sq	squamosal
stf	supratemporal fenestra
str	strut
tr	tooth root
v	vomer

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