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SHORT COMMUNICATION

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A chicken-sized crane precursor from the early Oligocene of France

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Abstract A skeleton of a chicken-sized crane precursor is described from the Lower Oligocene of the Lubéron in Southern France. *Parvigrus pohli* gen. et sp. nov. is the most substantial Paleogene fossil record of the Grues (Aramidae [limpkin] + Gruidae [cranes]), and among its oldest representatives. The fossil species is classified in the new taxon Parvigruidae, which is shown to be the sister group of extant Grues. It is the first fossil record of a stem lineage representative of the Grues and, among others, differs from modern Grues in its smaller size, shorter beak, and rail-like limb proportions. Size increase in the stem lineage of the Gruidae may be related to the spread of grasslands during the Oligocene and Miocene. Occurrence of stem lineage Grues in the Lower Oligocene of Europe is in concordance with the fact that there is no evidence for the presence of crown group members of modern avian "families" in pre-Oligocene fossil deposits.

Introduction

Cranes (Aves, Gruidae) today include 15 species of large, long-legged birds that occur in open grass and wetland areas of all continents except South America and Antarctica (Archibald and Meine 1996). Modern cranes have their greatest diversity in Asia and are classified into the sister taxa Balearicinae (two species of African crowned cranes) and Gruinae (all other extant species) (Krajewski 1989). Their closest living relative is the limpkin (Aramidae) (Livezey 1998; Fain and Houde 2004), which is a medium-sized bird of aquatic habitats in South, Central, and southern North America with a more rail-like external appearance but a very similar osteology to cranes.

Little is known about the early evolution of Aramidae and Gruidae, i.e. the Grues sensu Stresemann (1927–1934). Except for the Upper Eocene *Geranopsis hastingsiae*, which is based on a coracoid, all Paleogene taxa referred to the Gruidae are known from distal ends of the tibiotarsus only (Cracraft 1973), and their identification is thus far from being certain (Olson 1985; Mayr 2005). Neogene fossil cranes, on the other hand, already closely resemble their modern relatives (e.g., Feduccia and Voorhies 1992). Aramidae also have a poor Paleogene fossil record, with the earliest species being based on isolated bones from the Lower Oligocene of North America (Cracraft 1973; Olson 1985). So far, no fossil Grues outside the crown group (the clade including the stem species of the modern taxa and all its descendants) have been reported.

Here I describe a complete skeleton of a stem lineage representative of the Grues from the Lower Oligocene (about 30 million years ago) of France, which is among the best preserved avian remains from this fossil locality and the most substantial Paleogene fossil record of the Grues.

Systematic paleontology

– Aves Linnaeus 1758
– Gruoidea (sensu Wetmore 1960)
– Grues (sensu Stresemann 1927–1934)
– Parvigruidae fam. nov.

Type genus: Parvigrus gen. nov.

Diagnosis: Medium-sized birds with rail-like limb bone length proportions, which are characterized by: (1) beak shorter than cranium; (2) mandible with hook-like processus retroarticularis as in *Balearica*; (3) coracoid with lateral section of crista articularis sternalis hardly protruding in sternal direction; (4) sternum elongated and narrow, being narrowest in its midsection; (5) many tendons along hindlimb ossified; (6) proximal end of first phalanx of fourth toe with marked medially protruding projection.

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Parvigrus gen. nov.

Type species: *Parvigrus pohli* sp. nov.
Diagnosis: As for family.
Etymology: From *parvus* (Lat.): small and *Grus*, the type genus of modern Gruidae.

–Parvigrus pohli sp. nov.

Holotype: WDC-CCF 02, skeleton on a slab (Figs. 1–3), deposited in the Wyoming Dinosaur Center, Thermopolis, USA.

Type locality and horizon: Pichovet, Vachères, Southern France; Lower Oligocene (Mourer-Chauviré 1996).

Diagnosis: As for family. *Parvigrus pohli* sp. nov. is smaller than all other known species of the Grues.

Measurements (maximum length in mm): Skull, 71.9; upper beak (from nasofrontal hinge to tip), 30.5; humerus: 66.9 (left), 69.2 (right); ulna, 64.7 (left), 65.1 (right); carpometacarpus, 40.4 (left), 39.5 (right); femur, 62.8 (right); tibiotarsus, 97.7 (left), 99.2 (right); tarsometatarsus, 71.1 (left), 71.9 (right).

Etymology: The species is named after Burkhard Pohl who enabled acquisition of the fossil for the Wyoming Dinosaur Center.

Description and comparison (terminology after Baumel and Witmer 1993)

The skeleton is largely dissociated and the sternum turned at an angle of 180°. The left wing and the right femur, left humerus, and right wing were originally situated on the left margin of the slab, near the furcula, and were put in their present position by the preparator of the specimen (F. Escuillié, personal communication, see Fig. S1). Thus, ulna and hand of the left wing are now associated with the right humerus, and those of the right wing with the left humerus (Fig. 1). The proximal end of the left humerus, and only this element, was fabricated by the preparator.

The cranium (Fig. 2) is of similar proportions to that of other Grues but the beak is proportionally shorter than in even the shortest-billed modern taxon, *Balearica*, and of similar relative size to the beak of modern Psophiidae (trumpeters), the sister taxon of Grues (Livezey 1998; Mayr and Clarke 2003; Fain and Houde 2004). As in modern Grues but contrary to the Psophiidae, the nostrils are greatly elongated, measuring about 4/5 of the entire length of the beak which thus appears to have been rhynchokinetic. On the right side of the skull a small, poorly preserved processus supraorbitalis can be seen (Fig. 2). The fragmentary quadrate does not allow a meaningful description. The mandible resembles that of *Balearica*; as in the latter but contrary to Aramidae and Gruinae its caudal end exhibits a distinct, hook-like processus retroarticularis

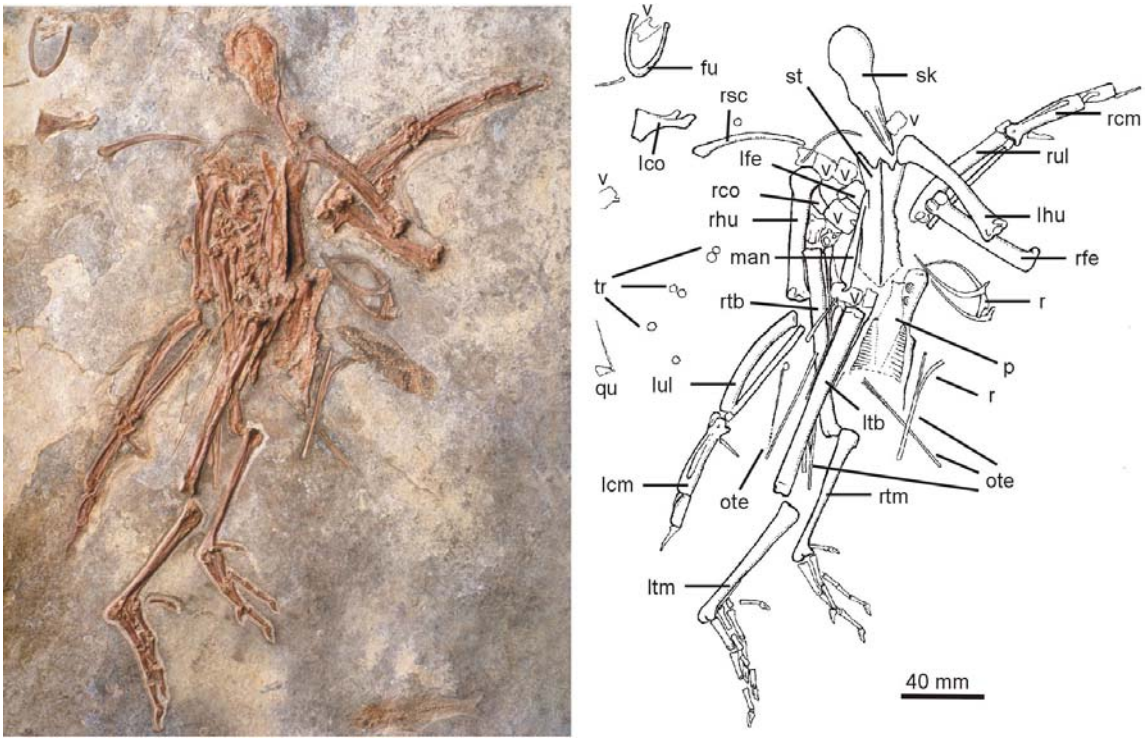

Fig. 1 *Parvigrus pohli* gen. et sp. nov., holotype (WDC-CCF 02) with interpretative drawing. Abbreviations: fu, furcula; lcm, left carpometacarpus; lco, left coracoid; lfe, left femur; lhu, left humerus; ltb, left tibiotarsus; ltm, left tarsometatarsus; lul, left ulna; man, mandible; ote, ossified tendons; p, pelvis; qu, right quadrate; r, rib; rcm, right carpometacarpus; rco, right coracoid; rfe, right femur; rhu, right humerus; rsc, right scapula; rtb, right tibiotarsus; rtm, right tarsometatarsus; rul, right ulna; sk, skull; st, sternum; tr, ossified tracheal rings; v, vertebra

Fig. 2 *Parvigrus pohli* gen. et sp. nov., holotype (WDC-CCF 02), selected skeletal elements. **a** Skull. **b** Mandible and sternum in comparison to the sternum of **c** *Aramus guarauna* Aramidae) and **d** *Balearica regulorum* (Gruidae). **e** Furcula. **f** Right scapula. **g** Left coracoid in comparison to the left coracoid of **h** *A. guarauna* and **i** *B. regulorum*. Abbreviations: inc, incision in margo caudalis of sternum; lfe, left femur; mco, margo costalis of sternum; na, narial opening; ret, hook-like processus retroarticularis (also indicated by circle); sup, processus supraorbitalis; sym, pars symphysialis of mandible; v, vertebra. Arrows in **h** indicate the sternally protruding lateral section of the crista articularis sternalis of the coracoid of modern Grues. Scale bars equal 10 mm

(Fig. 2, "hamulus retroarticularis" of Livezey 1998: 2107). Fenestrae mandibulae seem to be absent.

Osteological details of the poorly preserved vertebrae cannot be recognized, nor can it be discerned whether a notarium was present as in other Gruoidea (the clade including Psophiidae, Aramidae, and Gruidae).

The furcula (Fig. 2) resembles that of *Aramus* and *Balearica* in its shape, whereas it is more V-shaped and fused with the apex carinae of the sternum in the Gruinae. The extremitas sternalis is wider than the scapi claviculae and bears no apophysis furculae. Contrary to the Gruidae, the extremitas omalis is blunt and lacks a processus acromialis, which probably is the primitive condition also found in Aramidae, Rallidae (rails), and Psophiidae.

The coracoid (Fig. 2) is smaller than that of the Upper Eocene *Geranopsis hastingsiae* (32.3 vs. 39.4 mm) and differs from this species and extant Gruidae in that the crista articularis sternalis is less concave and its lateral section not as strongly protruding in sternal direction (Fig. 2h). The processus procoracoideus is somewhat wider than in modern Grues; contrary to the Aramidae it is not continuous with a marked crest along the medial side of the bone.

The scapula (Fig. 2) is of similar proportions to that of modern Grues, the acromion is very short. Contrary to modern Grues, however, the extremitas cranialis does not exhibit a large pneumatic foramen on its medial surface.

The sternum (Fig. 2) exhibits the characteristic derived shape of the corresponding bone of the Grues in that the corpus sterni is very elongated and narrow, without deep incisions in its caudal margin. It is proportionally narrower in its midsection than the sternum of the Gruidae, and thus more similar to the corpus sterni of the Aramidae (in which the caudal end is however not as wide). In *Parvigrus* the left side of the caudal margin exhibits an irregular shape, which probably is due to breakage; on the right side, however, there is a small incision that appears to reflect the original condition of the bone (Fig. 2). By contrast, the caudal margin of the sternum of modern Grues lacks incisions. The margo costalis is long, five processus costales can be counted but their actual number may be higher as in modern Grues. Most notably for a skeleton on a slab, the ventral portion of the carina sterni is preserved in its original position. Most of the dorsal portion is broken, but according to the inclination of the completely preserved caudalmost section, the carina appears to have been low as in modern Psophiidae. Contrary to the Gruinae, the sulcus carinae does not form a marked excavation for the tracheal loops. A spina externa is absent, the processus craniolaterales cannot be discerned.

The humerus (Fig. 3) is proportionally shorter than the corresponding bone of modern Grues. The crista deltopectoralis is low and elongated as in modern Grues, but the crista bicipitalis is less developed. The distal end of

Fig. 3 *Parvigrus pohli* gen. et sp. nov., holotype (WDC-CCF 02), selected skeletal elements. **a** Left humerus, proximal end of right ulna, and right femur (note that the proximal end of the humerus was fabricated by the preparator of the specimen). **b** Distal end of left wing. **c** Pelvis. **d** Left foot. **e** Distal left tibiotarsus, proximal right tarsometatarsus, and left tarsometatarsus. Abbreviations: api, ala praecetabularis ilii; lcm, left carpometacarpus; lhu, left humerus; ltb, left tibiotarsus; ltm, left tarsometatarsus; ote, ossified tendons; p, pelvis; pdm, phalanx proximalis digiti majoris; prt, medially projecting proximal end of first phalanx of fourth toe; rfe, right femur; rhu, right humerus; rra, right radius; rtm, right tarsometatarsus; rul, right ulna; syn, synsacrum. Scale bars equal 10 mm

the bone closely resembles the distal humerus of living Grues.

As in extant Aramidae, the ulna measures only about 2/3 the size of the tibiotarsus, whereas it is slightly shorter or about as long as the tibiotarsus in the Gruidae. The ulna is further shorter than the humerus, whereas it is longer than the latter in modern Grues. The proximal ulna is virtually identical to that of *Aramus*, the distal end also seems to be similar but few details are discernible in the fossil.

The carpometacarpus (Fig. 3) does not differ from that of modern Grues; as in the latter, there is a wide proximal metacarpal symphysis.

As in modern Gruidae but contrary to Aramidae, the phalanx digiti alulae lacks a claw. The phalanx proximalis digiti majoris (Fig. 3) bears no distally protruding process which, within Gruoidea, is a derived characteristic of the Gruidae. In concordance with modern Grues, the crus longum of the os carpi ulnare is very long.

The pelvis (Fig. 3) is similar to that of living Grues in its proportions, although the alae praeacetabulares ilii are more strongly protruding in craniolateral direction. The cranioventral surface of the synsacrum exhibits no longitudinal ridge (contrary to Psophiidae) and the vertebral sutures are not visible (contrary to Gruidae).

The femur (Fig. 3) resembles that of *Aramus* in its proportions. The crista trochanteris is more weakly developed than in the Gruidae. The crista supracondylaris medialis is small and there is a marked impressio ansae musculi fibularis.

The tibiotarsus is similar to the corresponding bone of modern Grues and the trochlea cartilaginis tibialis is proximo-distally low, with pronounced cristae.

The tarsometatarsus (Fig. 3) is proportionally shorter than that of extant Grues. Whether there was a large eminentia intercotylaris as in the latter cannot be discerned. The crista lateralis hypotarsi appears to be well developed as in the Aramidae, whereas it is strongly reduced in the Gruidae. The distal end of the bone resembles the distal tarsometatarsus of Aramidae and *Balearica*; the trochlea metatarsi II is much shorter than the tr. met. III but not as short as in the Gruinae.

The three anterior toes (Fig. 3) are proportionally longer than those of the Gruidae although the pedal phalanges are less slender and elongated than in the Aramidae. The hallux is also distinctly longer than in the Gruidae, though not as elongated as in the Aramidae, where the proximal phalanx of the hallux is as long as the third phalanx of the third toe. The os metatarsale I is small and stout, and of similar proportions to the corresponding ossicle of *Balearica*, whereas it is less elongated than in *Aramus*. The proximal end of the first phalanx of the fourth toe bears a marked medially protruding projection, which appears to be a synapomorphy of the Gruoidea (Fig. 3). The claws are similar to those of the Aramidae, whereas that of the hallux is more reduced in the Gruidae.

Ossified tracheal rings and tendons of the hind limb are scattered over the slab. Ossified tendons are also preserved along the cranial margin of the carpometacarpus and the distal section of the ulna.

Discussion

Figure S2 depicts a hypothesis on the phylogenetic position of the Parvigruidae fam. nov. The new taxon is unequivocally identified as a member of the Grues by the derived presence of (1) beak with very long narial openings (absent in Psophiidae); (2) sternum elongated and narrow, without deep incisions in its caudal margin (otherwise known only for Psophiidae and Rhynochetidae [kagu]); (3) trochlea metatarsi II plantarly deflected and reaching much less far distally than trochlea metatarsi III (absent in Psophiidae); (4) medially protruding projection on the proximal end of the first phalanx of the fourth toe (otherwise known only for Psophiidae); and (5) numerous ossified tendons along the leg bones (also in some rails and galliform birds). Unfortunately, the preservation of the fossil does not allow recognition of the characters listed by Livezey (1998: Tab. 3) as synapomorphies of the clade (Gruidae + Aramidae).

The Parvigruidae are shown to be outside crown group Grues by (1) the proportionally shorter beak, (2) medial surface of extremitas cranialis of scapula without large pneumatic foramen (listed as a synapomorphy of the clade [Gruidae + Aramidae] by Livezey 1998: Tab. 3), and (3) more rail-like limb bone length proportions (e.g., ulna shorter than humerus, femur as long as humerus). With respect to these plesiomorphic features, the new species corresponds with Rallidae and Psophiidae.

P. pohli exhibits no obvious autapomorphic specializations and may thus be similar to the stem species of the Grues. A major evolutionary modification in the stem lineage of Aramidae was elongation of the beak as an adaptation to feeding on snails. The significant size increase in the stem lineage of the Gruidae, with correlated changes in limb bone proportions, appears to be an adaptation for probing and walking in open grass and marshlands and may be related to the opening of early Paleogene forested environments and spread of grasslands during the Oligocene and Miocene (e.g., Janis 1993; Jacobs et al. 1999).

As detailed elsewhere (Mayr 2005), there is no evidence for the presence of crown group members of modern "families" in pre-Oligocene fossil deposits, and occurrence of stem lineage Grues in the Lower Oligocene of Europe is in concordance with this observation.

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