ORIGINAL ARTICLE



New cranial material of the earliest filter feeding flamingo Harrisonavis croizeti (Aves, Phoenicopteridae) informs the evolution of the highly specialized filter feeding apparatus

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Received: 10 September 2014 / Accepted: 5 March 2015 / Published online: 26 March 2015 © Gesellschaft für Biologische Systematik 2015

Abstract The Oligo-Miocene flamingo Harrisonavis croizeti represents an intermediate form between the highly specialized extant flamingo cranial morphology and the more generalized ancestral phoenicopteriform one, characterized by the extinct taxon Palaelodus. However, the original description of H. croizeti lacked detail and the lectotypic skull was lost; thus, it is not known how the ancestral phoenicopterid cranial morphology differed from that of recent forms. Here, we describe new cranial material from Oligo-Miocene deposits of France, including a mostly complete skull with an articulated upper bill, a disarticulated upper bill, and pieces of lower bill. We assign this material to H. croizeti and compare it to all previously reported fossil flamingo cranial material as well as to all six living species. We also use 3D computed tomographic data to reconstruct the skull of H. croizeti in three dimensions. The skull and bill of H. croizeti are similar to those of living species, although they display less specialized filter feeding traits, including a straighter bill with less surface area for filtration lamellae and points of articulation with the lower bill which are less developed. The less specialized form of *H. croizeti* suggests the extant *Phoenicopterus* retains a skull morphology more similar to the ancestral condition of crown group flamingos, and the extant *Phoenicoparrus* form is more derived.

Keywords Fossil birds · Miocene · Ecology · Bill morphology · Computed tomography · Saint-Gérand-le-Puy

Introduction

The Phoenicopteridae are a clade of wading birds with a specialized filter feeding ecology. The unique bill of phoenicopterid flamingos is markedly decurved with a lower bill that is much deeper than the upper. The inside margins of the bill are lined with rows of keratinous lamellae which form

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a mesh suited to the filtration of food from the brackish and saline waters of the lakes and lagoons that flamingos inhabit (Jenkin 1957; Zweers et al. 1995). The crown group includes six living species, recognized across two genus-level taxa (Torres et al. 2014), reflecting two general morphologies of the bill: Phoenicopterus, with larger and more compact bills, and *Phoenicoparrus*, with smaller and more bulbous bills (Jenkin 1957). The bill of *Phoenicopterus* has been considered reflective of the morphology ancestral to the crown group (e.g. Jenkin 1957; Olson and Feduccia 1980), but how the highly derived phoenicopterid bill evolved from a generalized straight bill (characterized by Palaelodus ambiguus Milne-Edwards 1863) is not understood. The earliest phoenicopterid Harrisonavis croizeti (Gervais 1852), known from the Late Oligocene to the Middle Miocene (ca. 28–13 Ma; Mlíkovský 2002) of Europe, holds potential to inform our understanding of the ancestral phoenicopterid bill.

H. croizeti was originally reported by Gervais (1852) from a nearly complete skull, but the description was not detailed and the original material was subsequently lost (Cheneval 1984). There have only been two subsequent reports of cranial material attributed to H. croizeti: the rostral half of a lower bill (Harrison and Walker 1976) and the rostral half of an upper bill (Cheneval 1984). In a review of the flamingo fossil record, Olson and Feduccia (1980) included a drawing of a cast of an upper bill and referred it to H. croizeti; this specimen lacks proper description but appears less curved than the bill reported by Cheneval (1984), likely indicating a sub-adult condition (Cheneval 1984). No additional cranial material has been described and how the skull of H. croizeti differs from those of the extant species remains unknown.

Cranial material of fossil flamingos has been reported for only two other taxa, both coeval with *Harrisonavis*. *Palaelodus ambiguus*, a stem group flamingo from the Oligo-Miocene of Europe, displayed a straight bill, a markedly different condition from representatives of Phoenicopteridae and possibly indicating the generalized feeding strategy ancestral to flamingos (Cheneval and Escuillié 1992). The bill of *Leakeyornis* (*"Phoenicopterus"*) *aethiopicus* (Harrison and Walker, 1976), a phoenicopterid from the Early Miocene of Kenya, is known from parts of the upper and lower bills and displayed a general morphology that is similar to the living *Phoenicopterus* (Harrison and Walker 1976).

A paucity of fossil skull material compounded by missing specimens has hindered attempts to understand the evolution of the unique flamingo bill, particularly with respect to the earliest phoenicopterids. As the earliest and best represented phoenicopterid in the fossil record, *H. croizeti* is thus extremely important in addressing this gap in knowledge. Here, we describe new fossil cranial material recovered from the Late Oligocene and Early Miocene of France which we assign to

H. croizeti. Implications for phylogeny, ecology, and the evolution of the highly unique and specialized flamingo filter feeding bill are discussed.

Materials and methods

Osteological and myological terminology follows Baumel and Witmer (1993) and Vanden Berge and Zweers (1993), respectively. ML StG 203bis was CT scanned at Université Lyon 1 on a GE Phoenix Nanotom 180 at 30 µm resolution. NMB MA 9594, NMB SG 18285a, and NMB SG 18285b were CT scanned at University of Basel on a GE Phoenix Nanotom M at 38 µm resolution. 3D data was rendered in Avizo (version 8; FEI). Reconstruction of the skull of *H. croizeti* from independent models representing the fossil specimens was carried out by eye in Avizo (FEI); models were left in the original scales (i.e., were not resized or rescaled) and were fit in three dimensions.

Institutional abbreviations Collection Faculté des Sciences de Lyon, Université Lyon 1, Villeurbanne, France (FSL); Natural History Museum, London, UK (NMHUK); Musée des Confluences, Lyon, France (ML); Musée National d'Histoire Naturelle, Paris, France (MNHN); North Carolina Museum of Natural Sciences, Raleigh, NC, USA (NCSM); Natural History Museum Basel, Basel, Switzerland (NMB); Smithsonian National Museum of Natural History, Washington, DC, USA (USNM).

Comparative material Recent taxa: Phoenicopterus roseus Greater Flamingo USNM 558422, Phoenicopterus ruber American Flamingo NCSM 10255, Phoenicopterus chilensis Chilean Flamingo USNM 344795, Phoenicopterus minor Lesser Flamingo USNM 488728, Phoenicoparrus jamesi James's Flamingo USNM 502131, and Phoenicoparrus andinus Andean Flamingo USNM 502130. Fossil material: H. croizeti MNHN Av 6544 (cast of lectotype); FSL 442292; NMHUK 2665; L. aethiopicus NMHUK A 4382, A 4384; and P. ambiguus ML StG 60.

Systematic paleontology

Class Aves Linnaeus, 1758
Mirandornithes Sangster, 2005
Order Phoenicopteriformes Fürbringer, 1888
Family Phoenicopteridae Bonaparte, 1831
Genus Harrisonavis Kashin, 1978
Harrisonavis croizeti (Gervais, 1852)
1852 Phoenicopterus croizeti Gervais: 233
1976 Gervaisia croizeti Harrison and Walker: 308
1978 Harrisonavis croizeti Kashin: 146





1980 Phoenicopterus croizeti Olson & Feduccia: 46

1984 Phoenicopterus croizeti Cheneval: 90

2002 Phoenicopterus croizeti Mlíkovský: 106

2009 Harrisonavis croizeti Mayr: 108

Newly referred material ML StG 203bis, a mostly complete skull with articulated caudal half of the upper bill; on display at the Musée des Confluences and erroneously labeled as "P. ambiguus." NMB MA 9594, the rostral extent of an upper bill; originally figured as a drawing of a cast of the original specimen in Olson and Feduccia (1980) but never formally described. NMB SG 18285a, part of the rostral portion of a left mandible. NMB SG 18285b, tip of a right mandible. Though the lectotype skull of H. croizeti is lost and thus is unavailable for comparison, the phoenicopterid fossil record from this locality is well-studied and extensive and can be referred to a single species (Cheneval 1984). Thus, the new phoenicopterid material described here can be reasonably referred to H. croizeti.

Locality and geologic setting The material described here comes from the Saint-Gérand-le-Puy area, Allier, central France, late Oligocene (MP 25)-early Miocene (MN 2). Only NMB MA 9594, recovered from Montaigu (MN 2), can be referred to a specific locality; there is uncertainty regarding the localities from which the other material was collected (see De Pietri et al. 2011). "Saint-Gérand-le-Puy" actually refers to a complex of lacustrine paleo-environments of various ages spanning the Late Oligocene and Early Miocene which comprised alternating humid and dry periods (Wattinne 1999). During dry periods, abundance of *Hydrobia* gastropods suggests that evaporation resulted in brackish lake conditions, likely approximating the habitats favored by extant flamingos.

Remarks Gervais (1852) originally placed *H. croizeti* in the extant genus *Phoenicopterus* which, at the time, contained all living species. Harrison and Walker (1976) moved *H. croizeti* to the newly erected *Gervaisia* based on differences in the bill; Kashin (1978) erected *Harrisonavis* to replace the preoccupied *Gervaisia*.

Results

Measurements ML StG 203bis: maximum length as preserved, 110.08 mm; maximum width across processus postorbitales, 29.75 mm; width across rostralmost part of frontal, 18.98 mm; depth from ventral face of os basisphenoidale to dorsalmost point of skull, 25.32 mm; depth of upper bill at midpoint of nares, from dorsal surface to apex of maxillary keel, 11.75 mm; depth of upper bill at rostral end of nares, from dorsal surface to apex of maxillary keel, 10.89 mm; and

maximum length of nares, 37.73 mm. NMB MA 9594: maximum length as preserved, 75.44 mm; maximum width, 16.86 mm; length along dorsal surface as preserved, 79.55; length along ventral surface as preserved, 55.68 mm; and depth of upper bill at rostral end of nares, from dorsal surface to apex of maxillary keel, 9.69 mm. NMB SG 18285a: maximum length as preserved, 53.36 mm, and maximum depth as preserved, 14.82 mm. NMB SG 18285b: maximum length as preserved, 51.18 mm, and maximum depth, 16.66 mm. All depths were measured perpendicular to the long axis. In all cases, "maximum length as preserved" refers to the distance between the two most distant points on each fossil.

Description The cranial morphology of flamingos is highly conserved across the living taxa. Variation is most obvious in the bill and follows generic division: the bill of species of *Phoenicopterus* is larger and more compact while that of species of *Phoenicoparrus* is smaller and more bulbous (Jenkin 1957). ML StG 203bis comprises a nearly complete cranium missing the lacrimals and the entire mandible. The upper bill is broken off just rostral to the nares and is also missing. In size and general morphology, it is similar to living flamingos, from which it differs in features of the upper bill, the tomial profile of both the upper and lower bills, the articulation of the lower bill, and the base of the skull. It is much larger and morphologically different from the coeval stem group phoenicopteriform *Palaelodus ambiguus* (Palaelodidae), which displayed a straight, pointed upper bill.

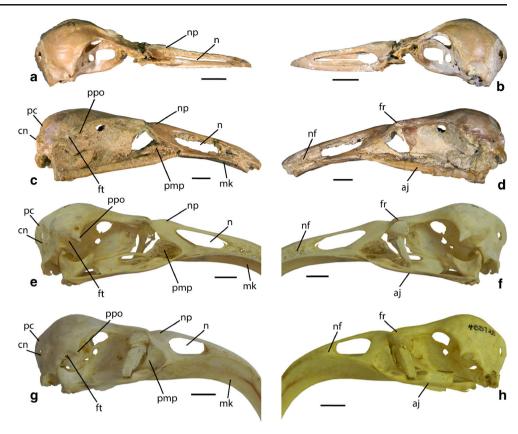
The general shape and size of the caudal part of the upper bill is very similar to Phoenicopterus roseus, and both differ from Phoenicoparrus minor in the same respects: a shallow maxillary keel (though shallower than in *P. roseus*) along the ventral surface of the upper bill with the crista tomialis forming a broad surface on either side (Fig. 1c-f; Fig. 2c-f); by contrast, the keel of P. minor is dorsoventrally very deep, imparting a wedge-like cross section to the entire upper bill (Fig. 1g, h; Fig. 2h). In ML StG 203bis, the breadth of the ventrolateral surface of the crista tomialis is slightly reduced and the depth of the maxillary keel is greatly reduced compared to both L. aethiopicus and P. roseus. The ventral face of the crista tomialis of P. ambiguus (Fig. 2b) forms a ventrolateral lip, creating two broad grooves proceeding along the length of the bill bordered by the crista tomialis and the midline, a condition vastly different from both ML StG 203bis and modern flamingos.

In ML StG 203bis, shallow furrows proceed rostrally from the holorhinal nares, as in the living species (Fig. 1c–h); these furrows are missing in *P. ambiguus* (Fig. 1a, b), which differs from members of Phoenicopteridae in having nares which span nearly the entire length of the bill. The nares themselves are longer relative to skull length, extending rostrally well past the start of the curve of the upper bill, approaching the inflection point (Fig. 1c, d); by contrast, the nares of the living





Fig. 1 Skull of Harrisonavis croizeti (Gervais 1852), from the Late Oligocene of the Auvergne region in central France. compared with the extinct Palaelodus ambiguus and extant flamingos Phoenicopterus roseus and Phoenicoparrus minor in lateral views. P. ambiguus (ML StG 60) in right lateral (a) and left lateral (b) views. H. croizeti (ML StG 203bis) in right lateral (c) and left lateral (d) views. P. roseus in right lateral (e) and left lateral (f) views. P. minor in right lateral (g) and left lateral (h) views. aj arcus jugalis, cn crista nuchalis, fr frontal ridges, ft fossa temporalis, mk maxillary keel, n nares, nf nasal furrow, np nasal prominence, pc prominentia cerebellaris, pmp processus maxillopalatinus, ppo processus postorbitalis. Scale bars 1 cm



species do not proceed past the start of the curve, ending well before the inflection point (Fig. 1e-h). The os nasale of ML StG 203bis is broader relative to the width of the upper bill, with a less steep mediolateral slope, than in the living species, but is on par with *Palaelodus* (Fig. 2). The slight prominence at the caudal part of the processus frontalis of the nasal (Fig. 1c, d) is reduced and more caudally positioned compared to the modern species (Fig. 1e-h). The processus maxillopalatini of the ossa maxillaria are fused along the midline as in extant flamingos but are more dorsoventrally shallow (Fig. 1c, d) compared to *P. roseus* and very shallow compared to *P. minor* (Fig. 1e-h), contributing to the general shallowness of the bill compared to the modern species.

The os frontale is very similar to the modern flamingos, with a pair of dorsoventrally high ridges just caudal to the nasal and shallow fossae glandulae nasales dorsal to the orbits (Fig. 2c, e, g). These features are lacking in *P. ambiguus*, which instead has two shallow grooves between the orbits which are set apart by short ridges (Fig. 2a); Cheneval and Escuillié (1992) interpreted these as grooves for nasal glands. The fossae glandulae nasales in ML StG 203bis are broader and proceed caudally past the base of the processus postorbitalis in dorsal view (Fig. 2c, d), unlike the living species (Fig. e–h). In *P. ambiguus*, the grooves do not proceed caudally past the orbits (Fig. 2a, b). The os parietale is more similar to *P. roseus* than *P. minor*, with a marked crista nuchalis transversa which flares laterally towards the base of

the skull (Fig. 2c–f). By contrast, the crista nuchalis of *P. minor* is far less developed (Fig. 2g, h). The crest in *Palaelodus* is even more poorly developed (Fig. 2a, b).

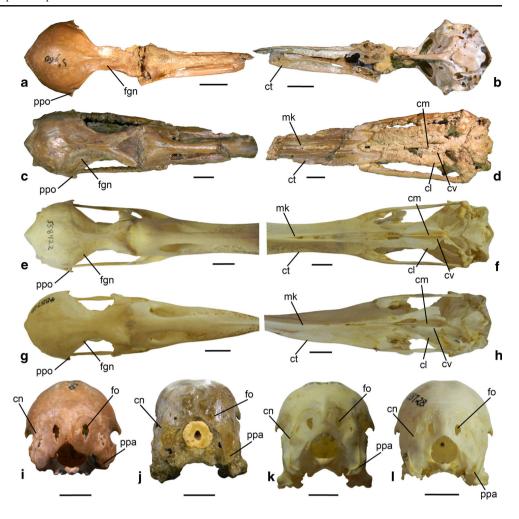
The processus postorbitalis of the os squamosum is somewhat worn but appears to be blunt and broad with a ventral orientation (Fig. 1c, d; Fig. 2c); by contrast, the processus postorbitales of the living species are ventrorostrally oriented (Fig. 1e-h; Fig. 2e, g). In *P. ambiguus*, they share the ventral orientation of ML StG 203bis but flare slightly ventrolaterally and appear to be blunter still (Fig. 1a, b; Fig. 2a). The processus zygomaticus of ML StG 203bis is well-developed, as in modern flamingos, but is poorly preserved (Fig. 1). The fossa temporalis is as broad and deep as in *P. ruber* (Fig. 1c–f), reaching farther caudally than in P. minor (Fig. 1g, h). The prominentia cerebellaris is greatly reduced and does not extend as far caudally from the cranium as the crista nuchalis transversa (Fig. 1c, d). In the living species, and particularly P. roseus, the prominentia cerebellaris is very well-developed and extends caudally well past the crista nuchalis transversa (Fig. 1e-h). The processus paroccipitalis is ventrally oriented as in the modern species but is not so mediolaterally broad (Fig. 2i-1). ML StG 203bis displays paired fonticuli occipitales, as in *Palaelodus* and the living species, but they are poorly preserved.

In the modern species, the arcus jugalis twists laterally at its midpoint resulting in a dorsoventrally flat shape at the midpoint (Fig. 1e-h). By contrast, in ML StG 203bis, the arcus





Fig. 2 Skull of Harrisonavis croizeti (Gervais 1852), from the Late Oligocene of the Auvergne region in central France. compared with the extinct Palaelodus ambiguus and extant Phoenicopterus roseus and Phoenicoparrus minor in dorsal, ventral, and occipital views. P. ambiguus (ML StG 60) in dorsal (a), ventral (b), and occipital (i) views. H. croizeti (ML StG 203bis) in dorsal (c), ventral (d), and occipital (j) views. P. roseus in dorsal (e), ventral (f), and occipital (k) views. P. minor in dorsal (g), ventral (h), and occipital (l) views. cl os palatina, crista lateralis; cm os palatine, crista medialis; cn crista nuchalis; ct crista tomialis: cv os palatine. crista ventralis; fgn fossa glandularis nasalis; fo fonticulus occipitalis; mk maxillary keel; ppa processus paroccipitalis; ppo processus postorbitalis. Scale bars 1 cm



jugalis remains straight and retains a dorsoventrally tall shape in cross section at its midpoint (Fig. 1c, d). The jugal-maxillary articulation of ML StG 203bis is similar to that of *P. roseus*, forming a thin, mediolaterally broad, slightly concave up face (Fig. 1c–f). In *P. minor*, this face is deeply concave with a groove proceeding along the jugal much farther caudally than in either *P. roseus* or ML StG 203bis (Fig. 1g, h). Much of the caudal part of the ossa palatina are obscured, but well-developed cristae ventralis, medialis, and lateralis are visible, as in the modern species (Fig. 2d, f, h). The remaining ventral face including the otic region, the ossa quadrata, the ossa pterygoidea, and the vomer are entirely obscured by matrix. Digital "preparation" of these regions using CT data was unfeasible due to difficulties with reliably distinguishing bone from surrounding matrix.

NMB MA 9594 represents the distal portion of a sub-adult flamingo upper bill, including the rostral part of the nares (Fig. 3a, b, n). The bill is very shallow and broad as in *P. roseus* (Fig. 3e, f, l), tapering towards a blunt tip; by contrast, the rostral part of the upper bill in *P. minor* is extremely narrow with a spoon-shaped tip (Fig. 3g, h, m). The nares are dorsoventrally narrow, and furrows lined with foramina proceed

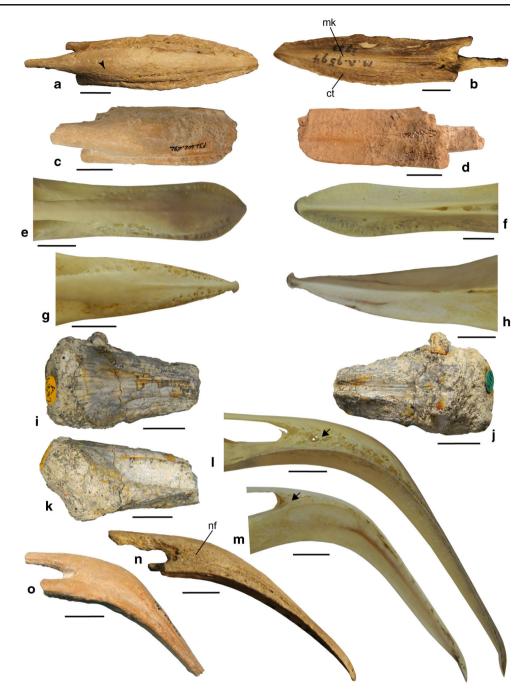
rostrally from the nares to the tip, as in modern flamingos (Fig. 3i–o). However, unlike modern flamingos, the bone's surface at the rostral margin of the nares and along the furrows proceeding rostrally from the nares of NMB MA 9594 is mostly solid, with little reticulation (Fig. 3n). This area is poorly preserved in ML StG 203bis, but the upper bill previously assigned to *H. croizeti* by Cheneval (1984) displays a similar condition (Fig. 3o). In representatives of *Phoenicopterus*, this area is highly reticulated (Fig. 3l). In members of *Phoenicoparrus*, reticulation of this area is reduced but retains a pitted appearance (Fig. 3m) which is not present in *Harrisonavis croizeti* (Fig. 3n–o).

The ventral face of the bill is marked by a very shallow maxillary keel (Fig. 3b, n). This keel is extremely reduced compared with the living species (Fig. 3f, h, l, m) but congruent with the shallow keel of ML StG 203bis (Fig. 1c, d; Fig. 2d). The keel is double ridged at the caudal extent and broadens and flattens into a shallow single ridge proceeding to the tip of the bill (Fig. 3b). The texture of the caudal part of the dorsal surface of NMB MA 9594 is fibrous (Fig. 3a), unlike the reticulation of adult living flamingos (Fig. 3e, f) but resembling texture identified in long bones as indicating areas of





Fig. 3 Sub-adult and adult upper bills from Harrisonavis croizeti compared to extinct Leakeyornis aethiopicus and adult extant Phoenicopterus roseus and Phoenicoparrus minor. Sub-adult H. croizeti (NMB MA 9594) in dorsal (a), ventral (b), and right lateral (n) views. Adult H. croizeti (FSL 442292) in dorsal (c), ventral (d), and right lateral (o) views. Adult P. roseus in dorsal (e), ventral (f), and right lateral (l) views. Adult P. minor in dorsal (g), ventral (h), and right lateral (m) views. L. aethiopicus (NMHUK A 4382) in dorsal (i), ventral (j), and right lateral (k) views. ct crista tomialis, mk maxillary keel; nf nasal furrows. Arrows indicate reticulated surface unique to extant flamingos. Arrowhead indicates fibrous texture on dorsal surface of NMB MA 9594, suggesting the bill belonged to a subadult individual. Scale bars 1 cm



active bone growth (Tumarkin-Deratzian et al. 2006; Watanabe and Matsuoka 2013); thus, the bill curve preserved by NMB MA 9594 indicates a sub-adult morphology, in contrast to the adult and more curved FSL 442292 (Fig. 3c, d, o), agreeing with the diagnosis of Cheneval (1984) (Fig. 3). Although sub-adult, NMB MA 9594 shows the shallow maxillary keel and reduced curve characteristic of *H. croizeti*.

NMB SG 18285b represents the right part of the tip of a lower bill (Fig. 4c, d). The dorsal edge is highly curved and the lateral face displays marked ridging characteristic of modern flamingos. NMB SG 18285a represents a middle portion of

the left side of a flamingo bill (Fig. 4a, b). The bill is dorsoventrally very deep and highly mediolaterally compressed and displays a marked downward curve, all diagnostic of the clade Phoenicopteridae. The material is congruent in size and morphology to the cast of the skull described by Gervais (Fig. 5c) and the lower bill described by Harrison and Walker (1976) (Fig. 4g). The lower bill of *H. croizeti* is not so dorsoventrally deep or as inflated as living species (Fig. 4e, f). The lateral profile created by the upper and lower bills of *H. croizeti*, when closed, is less curved than the living species and is congruent with a shallower maxillary keel.





Fig. 4 Material representing lower bills of Harrisonavis croizeti compared to extinct Leakevornis aethiopicus and extant Phoenicopterus roseus and Phoenicoparrus minor. H. croizeti (NMB SG 18285a), middle part of the left side, in right lateral (a) and internal (medial; b) views. H. croizeti (NMB SG 18285b), tip of the right side, in lateral (c) and internal (medial; d) views. P. roseus in right lateral (e) view. P. minor in right lateral (f) view. H. croizeti (NMHUK A 2665) in right lateral (g) view. L. aethiopicus (NMHUK A 4384) in right lateral (h) view. Arrow indicates ridging characteristic of flamingo bills. Scale bars 1 cm



Discussion

The skull of Harrisonavis croizeti closely conforms to the highly conserved phoenicopterid skull, particularly that of representatives of the extant genus *Phoenicopterus*. Osteological variation from the modern morphology is almost exclusively characterized by poor development of features associated with the unique specialized filter feeding behavior. The beak of H. croizeti differs from the living species by the following: (1) an upper bill with a broader and shallower os nasale and a much broader tip, (2) a shallower maxillary keel, (3) a shallower lower bill, (4) a less curved tomial profile (formed by the upper and lower bills) in lateral view, (5) longer nares relative to point of curvature of the upper bill, and (6) no reticulation of the surface of the bone at the rostral end of the nares. The shape of the bill is integral to flamingo filter feeding. The ventral face of the upper bill, including the maxillary keel, and the margins of the lower bill support the keratinous lamellae which comprise the filtration mesh (Jenkin 1957; Zweers et al. 1995). The deep lower bill facilitates an enlarged tongue, considered by Olson and Feduccia (1980) to be the initial adaptation to filter feeding. The curvature of the bill and prominence of the maxillary keel are proportionate with surface of insertion for filtering lamellae, facilitating the upside-down feeding characteristic of flamingos (Jenkin 1957; Zweers et al. 1995). In all these respects, *H. croizeti* is less specialized than the extant species.

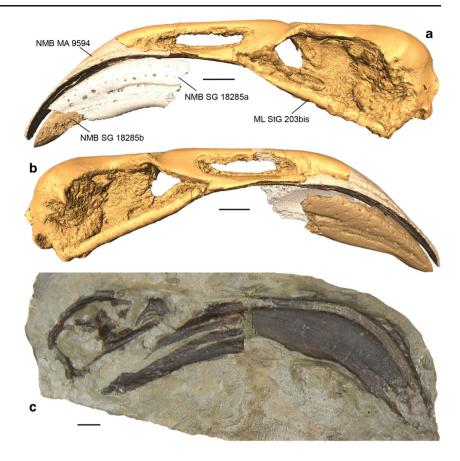
The upper bill reported here (NMB MA 9594; originally figured as a drawing of a cast by Olson and Feduccia 1980) represents the first description of a sub-adult bill of *H. croizeti*. Cheneval (1984) referred FSL 442292, a likely fully adult partial upper bill, to *H. croizeti*. NMB MA 9594 is similar in size to FSL 442292 and adult individuals of *P. roseus*, suggesting the bill described here was already capable of filter feeding; young of *P. roseus* develop a functional filter feeding apparatus at least 5 weeks before achieving adult size (Uys et al. 1963). Additionally, the growth pattern of the bill of *P. roseus* indicates that the bills of sub-adult flamingos, as in NMB MA 9594, can have adult size but retain sub-adult curvature (Uys et al. 1963; MvT unpublished data).

For the first time, we identify morphological variation in the cranium proper between *H. croizeti* and the living species, particularly with respect to articulation of the lower jaw. The pars ventralis of m. adductor mandibulae externus, which is responsible for adduction of the lower jaw, partially inserts on the processus postorbitalis. M. depressor mandibulae, responsible for depression of the lower jaw, is supported by the processus paroccipitalis. Both the processus postorbitalis and the processus paroccipitalis are less developed in *H. croizeti* compared to the extant species. How development of these





Fig. 5 Digital reconstruction of Harrisonavis croizeti comprising newly reported material compared with the cast of the lectotype of *H. croizeti*. Reconstruction in left (a) and right (b) views. Cast of the lectotype skull of H. croizeti (NMNH Av 6544) (c). In addition to other characters (see text), the new upper bill is less curved compared to the previously reported and presumably adult bill, suggesting a sub-adult condition for NMB MA 9594. In the reconstruction of H. croizeti (a, b), the component fossils (indicated by specimen number and by color) have not been modified from their original scales and were fitted by eye in threedimensional space. Some overlap occurs where the specimens preserve the same region of the skull. Scale bars 1 cm



morphological features correlates to the development of the associated musculature is uncertain. However, it is likely that these morphological differences indicate differences in the associated functions. Motion of the bill is integral to flamingo filter feeding, including driving the filtration mechanism and fine-tuning the size selectivity of the functional mesh (Zweers et al. 1995). A number of muscles responsible for positioning the head relative to the neck are associated with the crista nuchalis, including m. biventer cervicis, m. complexus, and m. rectus capitis lateralis. The crista nuchalis is poorly developed in H. croizeti relative to the living species, suggesting the related muscles are also reduced. Though it is uncertain how reduction in these muscles might affect motion of the head, cranial movement is particularly important to both filter feeding (Zweers et al. 1995) and mating display (del Hoyo 1992). Together, these characters suggest H. croizeti was a less specialized filter feeder than the living species.

The less pronounced curvature of the bill and the reduced surface area available for lamellae attachment in *H. croizeti* likely indicate that the filter feeding apparatus was less developed than in the living species. Also, the straighter bill of *H. croizeti* may have been held more vertically during feeding as opposed to the upside-down position of the extant species. Thus, *H. croizeti* illustrates an intermediate evolutionary stage between ancestral filter feeding birds with upright, forward facing bills, and the extant forms.

The feeding ecology of the palaelodids is controversial, and the bill is known only for *P. ambiguus*. Aspects of the leg bones and pedal phalanges have been used to alternately predict that *P. ambiguus* was a wader (Worthy et al. 2010) and a swimmer (Mayr 2014a, b). Cheneval and Escuillié (1992) considered the tall bill of *P. ambiguus* indicative of an enlarged tongue and correlated this with filter feeding behavior in recent taxa such as the crustacean feeding penguins (Spheniscidae) and auks (Alcidae), which also show modifications of the bill for feeding on plankton and the filter feeding

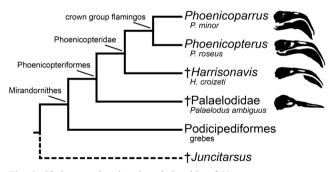


Fig. 6 Cladogram showing the relationship of *Harrisonavis croizeti* to other members of Mirandornithes (flamingos and grebes; Sangster, 2005). *H. croizeti* is placed outside of the crown group based on apomorphic data presented in this study. The relationships of the crown clade are from Torres et al. (2014). The placement of *Juncitarsus* (Olson and Feduccia 1980) is uncertain (indicated by a *dashed line*); treatment here follows Mayr (2014a). Extinct taxa denoted by *dagger symbols*





prions (*Pachyptila*, Procellariidae). Mayr (2014b) disagreed, noting narrower mandibular margins (which serve as surfaces of attachment for filter feeding lamellae in phoenicopterids) in *P. ambiguus* than in the living species. Mayr (2014b) also observed general similarities between the bills of *P. ambiguus* and of juvenile living flamingos, which are straight, lacking the filter feeding modifications of adults. However, Mayr (2014b) acknowledged that the diet of *P. ambiguus* likely comprised abundant invertebrates, the diet presumed to be ancestral to the highly specialized diet of phoenicopterids. It is possible that filter feeding then arose in early diverging phoenicopterids as a more efficient means of capturing smaller and more abundant prey.

The 3D digital reconstruction of the skull of *H. croizeti* (Fig. 5a, b) represents the first mostly complete glimpse of the skull of an ancestral phoenicopterid since the loss of the original skull described by Gervais (1852). Although the bill of the reconstruction is sub-adult, the general curvature of the bill is very similar to that of the cast of the lectotype (Fig. 5c). The skull of *H. croizeti* informs the state of flamingo cranial morphology between the much more generalized form characterized by P. ambiguus and the more specialized form of representatives of crown group Phoenicopteridae (Fig. 6). Filter feeding flamingos (Phoenicopteridae) show the following modifications from the more generalized morphology displayed by P. ambiguus: dorsoventral deepening of the cranium, a maxillary keel along the ventral face of the upper bill, a highly curved bill, a lower bill which is much deeper and morphologically different than the upper bill, nares which do not span the entire length of the upper bill, furrows proceeding rostrally from the nares, ridges at the nasofrontal articulation, and expansive salt glands over the orbits. In addition to the features of the beak mentioned above, the following conditions unrelated to the bill are unique to crown group flamingos (Phoenicopterus and *Phoenicoparrus*) and support placement of *H. croizeti* outside the crown group (Fig. 6): a well-developed cerebellar prominence which protrudes caudally past the nuchal crest, less expansive salt glands which do not proceed caudally past the orbits, and twisting at the midpoint of the jugal arch. This placement is congruent with molecular studies which have predicted a Plio-Pleistocene age for the crown group, precluding inclusion of the Oligo-Miocene H. croizeti (Sibley and Ahlquist 1990; Torres et al. 2014). Taxonomically comprehensive comparisons of the post-cranial skeleton among the extant and extinct species will likely reveal additional apomorphies for the crown group.

Conclusions

The close morphological similarity of the skull between *H. croizeti* and the extant genus *Phoenicopterus* has led some to predict a close relationship between these species, to the

exclusion of species of *Phoenicoparrus* (e.g., Olson and Feduccia 1980). However, as shown here, similarities between H. croizeti and species of Phoenicopterus are likely plesiomorphic for crown group Phoenicopteridae. The more specialized strategy of species of *Phoenicoparrus* of feeding primarily on very small food items (e.g., diatoms and cyanobacteria) is thus derived within flamingos. This study supports the hypothesis that the phoenicopterids very likely achieved a highly specialized filter feeding ecology by the Late Oligocene. The skull of H. croizeti was similar to, but less specialized than, the skull of species of the extant genus Phoenicopterus, indicating little novelty in ecology over the ~20 Ma between H. croizeti and the relatively recent divergence of Phoenicopterus from Phoenicoparrus; rather, the progression of the phoenicopterid lineage is marked by likely increased specialization and filtering efficiency through time. The Phoenicopterus-Phoenicoparrus divergence marks an apparent acceleration in innovation in the flamingo skeleton, particularly the bill, resulting in the higher degree of specialization observed in species of Phoenicoparrus.

Acknowledgments We thank the following individuals for specimen access: D. Berthet (Museé des Confluences, Lyon, France), S. Chapman (Natural History Museum, London, UK), L. Costeur (Natural History Museum, Basel, Switzerland), J. Gerwin (North Carolina Museum of Natural Sciences, Raleigh, NC, USA), C. Milenski (National Museum of Natural History, Washington, DC, USA), A Prieur and E. Robert (Faculté des Sciences de Lyon, Villeurbane, France), and F. Vigouroux (Museé des Confluences, Lyon, France). We thank the following individuals for aid with collection of CT data: C. Charles (ENS de Lyon, Lyon, France), J. Hinton (National Museum of Natural History, Washington, DC, USA), S. Robinson (North Carolina State University, Raleigh, NC, USA), and G. Schultz (University of Basel, Basel, Switzerland). For helpful discussion, we thank J. Clarke (University of Texas at Austin, Austin, TX, USA), S. Emslie (University of North Carolina at Wilmington, Wilmington, NC, USA), D. Ksepka (North Carolina State University, Raleigh, NC, USA), G. Mayr (Senckenberg Museum, Frankfurt, Germany), and T. Worthy (Flinders University, Adelaide, Australia). We thank three anonymous reviewers for comments on the manuscript.

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