Late Cretaceous bird from Madagascar reveals novel development of beaks

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Mesozoic birds display striking differences in size, flight adaptations, and feather organization\textsuperscript{1–4}, but exhibit relatively conserved patterns of beak shape and development\textsuperscript{5–7}. Neornithine (= crown group) birds exhibit constraint on facial development\textsuperscript{8–9} as well, but also comparatively diverse beak morphologies associated with a range of feeding and behavioral ecologies. Here we report a new, crow-sized stem bird, *Falcatakely forsterae* gen. et sp. nov., from the Late Cretaceous of Madagascar that possesses a remarkably long and deep rostrum, a novel expression of beak morphology previously unknown among Mesozoic birds and superficially similar to that of a variety of crown group birds (e.g., toucans). The rostrum of *Falcatakely* is composed of an expansive edentulous maxilla and a small tooth-bearing premaxilla. Morphometric analyses of individual bony elements and three-dimensional rostrum shape reveal the development of neornithine-like facial anatomy despite the retention of maxilla-premaxilla organization similar to that of nonavialan theropods. The unique patterning and increased height of the rostrum in *Falcatakely* reveals a degree of developmental lability and increased morphological disparity unknown in early-branching avialans. Expression of this novel phenotype (and presumed ecology) within a stem bird underscores that consolidation to the neornithine-like premaxilla-dominated rostrum was not an evolutionary prerequisite for beak enlargement.
Understanding of Mesozoic bird evolution continues to improve, driven predominantly by
discoveries from the Early Cretaceous of China\textsuperscript{1–3,6}. Although these specimens exhibit striking
variation in body size, soft-tissue anatomy, and inferred ecologies\textsuperscript{2–4,10,11}, disparity in Mesozoic
avian cranial shape remains restricted to a relatively limited number of forms considered to be
either generalists or substrate-probing specialists\textsuperscript{5,6,12–15} only distantly related to crown birds. The
Late Cretaceous (~100–66 Myr ago) chapter of avialan evolution remains relatively incomplete
owing to a paucity of new fossil discoveries (although see recent works on birds such as
\textit{Ichthyornis}\textsuperscript{16} and \textit{Asteriornis}\textsuperscript{17}). Thus, new fossils of Late Cretaceous birds are essential for
refining hypotheses relating to avialan morphological evolution and diversification.

The phylogenetic diversity of early branching (non-neornithine) Mesozoic birds is
dominated by enantiornithines, heralded as the first avialan diversification and characterized by a
range of body sizes and inferred habits\textsuperscript{2,14,18–21}. This radiation is notable for its apparent near-
global distribution throughout most of the Cretaceous. An exceptionally well-preserved partial
cranium of a previously unknown enantiornithine (University of Antananarivo [UA] 10015)
from the latest Cretaceous (Maastrichtian) of Madagascar falls within a critical temporal-spatial
gap (i.e., the entire Cretaceous of Afro-Madagascar, for which very few avialans are known).
The specimen expands our knowledge of realized cranial shape disparity, in terms of both
morphological details and proportions of elements, within the enantiornithine radiation and
Mesozoic birds as a whole.

\textbf{Systematic palaeontology}

\begin{center}
Theropoda Marsh, 1881
\end{center}

\begin{center}
Paraves Sereno, 1997
\end{center}
Avialae Gauthier, 1986

Ornithothoraces Chiappe, 1995

Enantiornithes Walker, 1981

*Falcatakely forsterae* gen. et sp. nov.

**Etymology.** “Falcata” (from Latin *falcatus*), meaning armed with a scythe, in reference to shape of rostrum; “kely” (Malagasy), meaning small; “forsterae,” in recognition of Catherine A. Forster’s contributions to work on Madagascan paravians.

**Holotype.** Partial cranium (University of Antananarivo [UA] 10015) consisting of rostrum, palate, and periorbital regions (Fig. 1, Extended Data Figs. 1 & 2, Supplemental Videos 1–8).

**Locality and horizon.** Locality MAD05-42, Berivotra Study Area, Upper Cretaceous (Maasrichtian; 72.1–66 Myr ago) Anembalemba Member, Maevarano Formation, Mahajanga Basin, northwestern Madagascar.

**Diagnosis.** Differs from other paravians based on the following combination of features (*indicates autapomorphies): extended, high maxilla that forms dorsal contour of rostrum*; dimpled texture on nasal and lacrimal, particularly on triangular caudodorsal process of latter*; lacrimal with caudally expanded ventral process*; large, flat jugal process of postorbital*. Further differs from most avialans by: long, straight quadratojugal process of jugal; antorbital fenestra nearly as long as tall. Further differs from other enantiornithines by: premaxilla slots into extended V-shaped sulcus of maxilla*; narrow rostrum (width at premaxilla-maxilla junction estimated at ~15% maximum width at rostral margin of orbit); nasal with distinct fossa near rostral end*.
Remarks. Avialae and Neornithes are used herein to delimit increasingly less inclusive monophyletic assemblages of theropod dinosaurs. Avialae (= “birds”) refers to all theropods closer to living birds than to dromaeosaurids and troodontids (i.e., a stem-based monophyletic group containing *Passer domesticus* and all theropods closer to it than to *Dromaeosaurus* or *Troodon*). Neornithes represents the crown group of birds and is the equivalent of Aves (sensu ref. 23); see Supplementary Information for additional phylogenetic definitions.

Cranial Osteology

UA 10015 pertains to an enantiornithine bird (estimated cranial length = 8.5 cm) with a high, but extremely narrow, preorbital region (Fig. 1). The lightly built face consists of a long, high edentulous maxilla and a short, tooth-bearing premaxilla, forming a rostrum unlike that of any known bird. The external nares are rostrally positioned and widely separated from a large, parallelogram-shaped antorbital fenestra. The premaxillae are fused rostrally and exhibit a short frontal process as in some other enantiornithines5,24,25. The maxillary process is short and slots into a V-shaped concavity on the maxilla (Fig. 1b, c; Extended Data Figs. 1f, 2c). A single, conical, unserrated tooth is preserved in the left premaxilla; the presence of additional premaxillary teeth is uncertain due to incomplete preservation.

The maxilla (<1 mm thick) of *Falcatakely* is unique among avialans in being extremely high and long, and forming at least 90% of the reconstructed pre-orbital rostrum height (Fig. 1c). It is unfenestrated, a condition shared with Enantiornithes (Supplementary Information), and lacks an antorbital fossa; it also preserves detailed vascular sulci over its surface indicating the presence of an expansive keratinous rhamphotheca (beak) in life26 (Fig. 1a, Supplemental 3D PDF S1). The premaxillary process is well developed and forms part of the ventral border of the
external naris. An elongate, tapering caudoventral projection contributes to the jugal bar, delimiting the ventral border of the orbit where it underlies the lacrimal boot. The elongate nasals expand in width caudally and are unique in possessing dorsomedially positioned fossae near the external nares (Extended Data Fig. 1b). The mid-portion of the nasals are broad and vaulted, as in bohaiornithid enantiornithines and,27 and express surface dimpling on the lateral margin near the articulation with the lacrimal (Extended Data Fig. 1b–d). µCT-mediated reconstruction of *Falcatakely* reveals a nearly complete right lacrimal (Fig. 1c, Supplemental 3D PDF S2). The dorsal half of the element is T-shaped, as in avialans such as *Archaeopteryx, Pengornis,* and *Parapengornis*. The rostrodorsal process is considerably longer than the caudodorsal process and is most similar to the condition in pengornithid enantiornithines (e.g., *Parapengornis*). The caudodorsal process is unique among avialans in morphology, being sub-triangular in shape, dimpled, and pneumatic (Extended Data Fig. 1d). The ventral ramus is longer than either the caudodorsal or rostrodorsal process, and is extensively excavated, as in pengornithids and bohaiornithids. The ventral ramus terminates as a caudally expanded boot that sits just dorsal to the overlapping portions of the jugal and maxilla (Fig. 1c).

The jugal is triradiate with a long, dorsoventrally restricted maxillary process, a distinct postorbital process, and an extended, bar-like quadratojugal process (Extended Data Fig. 1e). In contrast to most avialans,21,28 the quadratojugal process is long and directed straight caudally, forming the ventral border of the infratemporal fenestra. The quadratojugal process is not bifurcated as in most non-avialan theropods and some phylogenetically early-branching birds like *Sapeornis*. The right postorbital (Extended Data Fig. 1e) is represented only by its ventral process, which is flat and tapering, and quite unlike any known amongst avialans, or paravians.
generally. At least 15 scleral ossicles are present, enough to estimate the external diameter of
the scleral ring at 16–18 mm (Fig. 1c).

The digitally reconstructed palate of UA 10015 (Extended Data Fig. 2) reveals a
substantial level of detail not typically observable in Mesozoic avialans. The palatine is
triradiate, with a long, thin rostral process that abuts the maxilla (Extended Data Fig. 2a). The
palatine does not contact the jugal and only modestly contacts the pterygoid, but shares an
elongate contact with the ectopterygoid. A dorsomedially directed choanal process sweeps
toward the midline to join its antimere. UA 10015 preserves only the thin rostral processes of the
pterygoids; these are in close association with the palatines (Extended Data Fig. 2a). The
ectopterygoid, an element that is unknown in most Cretaceous avialans, is represented by a
robust body and a thin, elongate, uncinate process that contacts the jugal bar (Extended Data Fig.
2a). The vomers are represented by two thin, dorsoventrally restricted laminar plates that extend
rostrally between the two maxillae (Extended Data Fig. 2a, c). Thin sheets of bone are present
just rostral to the pterygoids, potentially representing the expanded caudal end of the vomer,
reminiscent of the condition in *Gobipteryx*.

**Mosaic Evolution in the Avian Beak**

Our phylogenetic analyses recover *Falcatakely* nested within Enantiornithes (Fig. 2,
Extended Data Figs. 3, 4). The long, deep, and narrow rostrum of *Falcatakely*, dominated by an
expanded maxilla, stands in stark contrast to the premaxilla+maxilla-formed facial region of
other enantiornithines and more crownward non-neornithines. Even among rostrally elongated
ornithothoracine taxa such as *Longipteryx*, *Longirostravis*, and *Dingavis*, this morphology is
achieved through concomitant reduction in premaxillary and maxillary height as bones elongate along the rostrocaudal axis$^{5,6,12,14,15}$.

Quantitative assessment of non-avialan and avialan (including Neornithes) facial shape demonstrates the unique combination in *Falcatakely* of a derived cranial phenotype (i.e., a neornithine-like expanded rostrum) formed by an underlying plesiomorphic paravian skeletal framework. We used 2D geometric morphometrics (Fig. 3) to compare maxillary and premaxillary shape in UA 10015 with that of a sample of fossil non-avialan theropods, as well as the crown birds *Gallus gallus* (red junglefowl) and *Nothoprocta pentlandii* (Andean tinamou). Principal component analysis (PCA) reveals that species group together based on the ratio of maxillary to premaxillary size (PC axis 1) and the ratio of rostrocaudal length to dorsoventral height of both elements (PC axis 2). Despite having maxillary and premaxillary proportions similar to those of non-avialan theropods (e.g., paravians, oviraptorosaurs, ornithomimosaurs), *Falcatakely* exhibits an overall rostrum phenotype convergent upon a number of neornithine groups.

The configuration of the individual skeletal elements in *Falcatakely* is more similar to the non-avialans *Microraptor* and *Zanabazar* than to ornithuromorphs (including neornithines) due to the expanded maxilla and relatively small premaxilla. Nonetheless, the three-dimensional shape of the pre-orbital facial skeleton closely resembles that of some extant birds (Extended Data Figs. 5, 6), as assessed using 3D geometric morphometrics to compare the shape of the maxilla, premaxilla, and nasal within a sample of 349 extant birds (Supplementary Information)$^{32}$. PCA of rostrum shape reveals that *Falcatakely* occupies a position in whole-rostrum morphospace that is quantitatively similar to those of a number of unrelated neornithines, including members of Ramphastidae (toucans), Phaethonidae (tropicbirds),
Columbidae (pigeons and doves), and Tyrannidae (tyrant flycatchers) (see interactive 3D plot associated with online materials).

The discovery of *Falcatakely* expands the realized cranial morphology among known non-neornithine birds considerably. Analysis of its three-dimensional anatomy reveals a stem bird occupying a previously unrealized position in rostrum morphospace and potentially exploiting an ecology not again seen until the diversification of crown-group birds in the mid-Cenozoic. A partial emancipation of the palate from the facial skeleton (i.e., loss of jugal contact with the palatine) concurrent with heretofore unappreciated rostrum elaboration suggests that these regions are functionally and developmentally integrated\(^\text{16,31,33}\). Interestingly, a mosaic pattern of palatal release is exhibited among stem avialans, at least insofar as the functional demands of the rostrum/beak in *Falcatakely* appears to have required reinforcement of the connections to the rear of the face. These connections are maintained through both the ectopterygoid and with retention of the robust postorbital linkage, despite the loss of the mid-face palatine connection to the jugal bar. Such an arrangement was likely necessary for stabilizing the mid-portion of the cranium and the long, high, and extremely narrow rostrum. Although incomplete, the presence of a robust postorbital further indicates a rigidly enforced caudal region of the cranium\(^7\).

The maxilla-dominated facial skeleton of *Falcatakely* reveals two important insights for the evolutionary history of birds. First, the ancestral developmental patterning of rostrum construction in basal avialans has generated neornithine-like cranial phenotypes not recognized in the fossil record until now. Second, the developmental reduction of the maxilla previously inferred for Ornithothoraces\(^7,9\) was not a fixed trait, at least among enantiornithine birds. Thus, consolidation to a premaxilla-dominated rostrum, a hallmark of all living birds, was not an
evolutionary prerequisite for rostrum, and thus, beak enlargement. More generally, this is consistent with a growing appreciation for the flexibility of underlying developmental mechanisms that may be responsible for generating convergent morphology among distantly related forms. With *Falcatakely*, this appreciation can now be extended to the deep time avialan record. The discovery of *Falcatakely* expands the ecomorphological potential realized by enantiornithines and Mesozoic birds more generally. This new appreciation of avialan anatomy underscores the potential for significant variability in trophic ecology during the first great diversification of the group during the Cretaceous Period.

**Online Content**

Detailed methods, along with additional Extended Data display items, Source Data, Nature Research reporting summary, details of authors contributions and competing interests statement, etc. are available in the online version of the paper at https://XXXX XXXX XXXX; references unique to these sections appear only in the online paper. Additional supporting information (e.g., interactive PDFs; matrices and executable files) are available on DRYAD at: https://doi.org/10.5061/dryad.mkkwh70wg.


**MAIN FIGURE LEGENDS:**
Fig. 1 | Cranium of the Cretaceous enantiornithine bird *Falcatakely forsterae* (UA 10015, holotype). a, Photograph of specimen, with right lateral view of pre-orbital region (right side of image) and ventral view of palatal region (left side of image); b, Digital polygon reconstruction from µCT scan of specimen in a; c, Digital polygon reconstruction of specimen with most elements in b placed in near-life position in right lateral view; d, Line drawing reconstruction (not to scale) illustrating preserved (in white) elements of cranium. Left and right sides indicated as (l) and (r), respectively. AOF, antorbital fenestra; ect, ectopterygoid; EN, external nares; ITF, infratemporal fenestra; jpmx, jugal process of maxilla; ju, jugal; lc, lacrimal; mpmx, midline premaxilla; mx, maxilla; na, nasal; pal, palatine; pmx, premaxilla; po, postorbital; pter, pterygoid; qj, quadratojugal; sr, scleral ring; to, tooth. [Planned for column width (89 mm); colour]

Fig. 2 | Mosaic evolution of the avialan facial skeleton as depicted among selected early-branching forms. Phylogenetic analysis places *Falcatakely forsterae* among enantiornithine birds. Illustration for *Xinghaiornis(*) placed near its approximate position in the phylogeny and based on ref. 15. Illustrations not to scale. Colour coding: premaxilla, red; maxilla, green; nasal, yellow; lacrimal, lavender; dentary, blue. Images for *Archaeopteryx, Ichthyornis, Hesperornis*, and *Gallus* modified from ref. 16 (see Supplementary Information for additional details for included taxa and phylogenetic analyses). [Planned for 1 ½ column width (136 mm); colour]

Fig. 3 | Geometric morphometric analyses of facial shape in *Falcatakely forsterae* among paravians. Plot of first two principal components of 2D landmark analysis of maxillary (blue
line segments) and premaxillary (red line segments) morphology of select theropod taxa. Unique
configuration of maxilla and premaxilla in *Falcatakely* is more similar to that of non-avialans in
a two-dimensional analysis focused on fossil taxa, although overall three-dimensional rostrum
phenotype occupies morphospace converged upon by subsequent radiations of neornithine birds
(hyperlink to HTML file). See Supplementary Information for analytical protocols. [Planned for
column width (89 mm); colour]

EXTENDED DATA FIGURES

**Extended Data Fig. 1 | Rostrum of the Cretaceous enantiornithine bird *Falcatakely*
forsterae** (UA 10015, holotype). a, Line drawing reconstruction (not to scale) illustrating
preserved (in white) elements of cranium; b, Digital polygon surface reconstruction (from µCT
scans) of right nasal in rostroventral view (caudal to top) highlighting midline depression and
dimpled surface texture; c, Digital polygon surface reconstruction of right nasal in dorsal view
illustrating dimpled architecture on frontal and rostral portions, which extends laterally onto
lacrimal; d, Digital polygon surface reconstruction of right facial elements in right lateral view to
illustrate shape and inter-element relationships of nasal, maxilla, and lacrimal (note surface
texture of right maxilla with neurovascular sulci broadly expressed over lateral surface, deep to
inferred keratinous covering (i.e., beak)); e, Digital polygon surface reconstruction of lower
lateral face to highlight arrangement of maxilla, lacrimal, jugal, and postorbital (all elements
from right side); f, Digital polygon surface reconstruction of left maxilla and premaxilla
articulation (rostral to left). AOF, antorbital fenestra; cdp, caudodorsal process of lacrimal; cp,
choanal process of palatine; ect, ectopterygoid; EN, external nares; ITF, infratemporal fenestra;
fpn, frontal process of nasal; inb, internarial bar; jpmx, jugal process of maxilla; ju, jugal; lbo,
lacrimal boot; lc, lacrimal; ld, lacrimal dimpling; le, lacrimal excavation; lf, lacrimal foramen; mpx, midline premaxilla; mx, maxilla; mpj, maxillary process of jugal; na, nasal; nd, nasal dimpling; nf, nasal fossa; nvs, neurovascular sulci; pal, palatine; pmx, premaxillary process of maxilla; pmx, premaxilla; po, postorbital; qj, quadratojugal; rdp, rostrodorsal process of lacrimal; rpn, rostral process of nasal; tm, tomial margin; to, tooth; vr, ventral ramus of lacrimal. [Planned for page width; greyscale]

Extended Data Fig. 2 | Palatal and lateral facial regions of the Cretaceous enantiornithine bird Falcatakely forsterae (UA 10015, holotype). a, Digital polygon surface reconstruction (from µCT scans) of palate and lateral face in ventral view; b, Reconstructed outline drawing of Falcatakely in palatal view (shaded regions not preserved); c, Digital polygon surface reconstruction of internal aspect of left facial skeleton (premaxilla, maxilla, nasal) and palate in right lateral view. Left and right sides indicated as (l) and (r), respectively. Dashed line in c represents approximate contour of caudal margin (i.e., ventral ramus of lacrimal) of antorbital fenestra. Scale bar in image serves for both 2a and 2c; reconstruction in 2b not to same scale. AOF, antorbital fenestra; bs, basisphenoid rostrum; cp, choanal process of (right) palatine; ect, ectopterygoid; EN, external nares; jpmx, jugal process of maxilla; mpx, midline premaxilla; mx, maxilla; na, nasal; pal, palatine; pmx, premaxilla; pter, pterygoid; to, tooth; up, uncinate process of ectopterygoid; vm, vomers. [Planned for 2/3 page width; colour]

Extended Data Fig. 3 | Majority rule tree of Falcatakely among coelurosaurians from Bayesian analysis of the Theropod Working Group matrix (TWiG). Clades outside of
Avialae are collapsed for brevity. Posterior probabilities are placed above nodes. [Planned for page width; colour]

Extended Data Fig. 4 | Majority rule tree of *Falcatakely* among avialans from Bayesian analysis of modified Wang and Zhou (2019) matrix. Posterior probabilities are placed above nodes. [Planned for page width; colour]

Extended Data Figure 5 | Geometric morphometric analysis of rostrum shape in *Falcatakely forsterae* among avians. Plot of first two principal components of 3D landmark analysis of total rostrum shape of *Falcatakely* and extant avian taxa. Whereas unique configuration of maxilla and premaxilla in *Falcatakely* is more similar to those of non-avialan paravians (Fig. 3), overall three-dimensional rostrum phenotype occupies morphospace converged upon by subsequent radiations of neornithine birds (hyperlink to HTML file). See Supplementary Information for analytical protocols. [Planned for column width (89 mm); colour]

Extended Data Figure 6 | Landmarking procedure for 3D geometric morphometric analysis in dorsal (a) and lateral (b) views. Red points represent anatomical (Type I) landmarks, yellow points are sliding semi-landmarks. [Planned for 2/3 page width; colour]

Supplemental Data File: Interactive morphospace plot of 3D rostrum shape. Plot of first two principal components of 3D landmark analysis of rostrum of *Falcatakely forsterae* and extant
METHODS

Temporal and Stratigraphic context. UA 10015 was recovered in 2010 at locality MAD05-42 in the Berivotra Study Area of the Mahajanga Basin Project. The bone-bearing horizon lies within Facies 2 of the Anembalemba Member in the Upper Cretaceous (Maastrichtian) Maevanaro Formation\textsuperscript{22} (Supplementary Information). Many specimens, including UA 10015, recovered from the Anembalemba Member were entombed as part of rapid debris flows, often resulting in spectacular preservation with only minimal displacement and taphonomic distortion during burial\textsuperscript{38,39}.

Phylogenetic methods. Given the extremely derived condition in *Falcatakely* and the notable amount of homoplasy among non-avialan paravians and basal avialans, we employed a two-tiered dataset approach in an effort to best constrain the phylogenetic affinities of *Falcatakely* (Supplementary Information). First, we utilized the densely sampled, coelurosaur-wide Theropod Working Group matrix (TWiG)\textsuperscript{40,41} to broadly assess and confirm the position of *Falcatakely* among paravians (Extended Data Fig. 3, Supplementary Information). Next, we employed a modified version of a well-established Mesozoic avialan-focused matrix (WEA\textsuperscript{25}), along with modifications from ref. \textsuperscript{16}, to further examine the relationship of *Falcatakely* among avialans (Fig. 2, Extended Data Fig. 4). Bayesian inference (BI) trees were estimated for each dataset using MrBayes v3.2\textsuperscript{42}. The standard model (Markov $k$-state variable model [Mkv]\textsuperscript{43}) was specified with gamma-distributed rate variation (see ref. \textsuperscript{44}). A subset of characters was set as ordered, following the prior usage of the included datasets. During the analysis, Markov Chain
Monte Carlo (MCMC) convergence was assessed using the average standard deviation of split frequencies and examining the trace files in Tracer\textsuperscript{45}. Convergence to stationarity was assumed for split frequencies below 0.01 and effective sample size (ESS) values >200. All analyses were performed with two runs of four chains each, run for 10 million generations, sampling parameters every 1000 generations. The first 25\% of samples were discarded as burn-in. Results are summarized using a majority rule consensus (MRC) tree\textsuperscript{46}. MRC trees for both datasets depict *Falcatakely* as a member of Enantiornithes. The TWiG dataset set recovers it as the sister taxon to *Pengornis*, whereas the WEA matrix finds it in a large polytomy with other enantiornithines (Extended Data Figs. 3, 4). Given the denser avialan sampling in the WEA dataset, the phylogenetic results from this matrix are used here as the primary results. Clade support was assessed using the estimated posterior probabilities from the BI trees. Morphological character support was established for MRC trees using the *map* and *apo* commands in TNT\textsuperscript{47–49}. Additional details of phylogenetic results and clade support are presented in the Supplementary Information.

To further interrogate the robustness of our inferred trees, three sensitivity analyses were run examining the influence of cranial vs. postcranial data and the potential impact of cranial data-only taxa on tree inference. These analyses reveal no significant topological alterations relative to the standard analysis detailed above, lending support to the primary results placing *Falcatakely* among enantiornithine birds. Moreover, additional explicit hypothesis testing via Bayes Factors comparisons was conducted with *Falcatakely* constrained to stemward positions (e.g., with *Falcatakely* excluded from Pygostylia), which resulted in suboptimal solutions. Details for these analyses and the specifics of the results are provided in the Supplementary Information.
Information, with executable files for the sensitivity and alternative hypothesis testing available on DRYAD at: https://doi.org/10.5061/dryad.mkkwh70wg.

References specific to online-only materials


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preparation of the specimen; J.R.G. and P.M.O. conducted μCT digital preparation/interpretation
and rapid prototyping of UA 10015; R.R.R. and L.J.R. provided geological data and taphonomic
interpretation; P.M.O., A.H.T., J.R.G., and R.N.F. completed lab work on the fossil and digital
representation thereof and provided input on descriptions and comparisons; A.H.T. and P.M.O.
contributed to the character coding and phylogenetic analysis; R.N.F. completed the
morphometric analyses; P.M.O., A.H.T., and J.R.G. developed the manuscript, with
contributions and/or editing from all authors.

Additional Information

Supplementary Information is available in the online version of the paper at http://XXXX

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Data Availability
UA 10015 is cataloged into the collections at the Université d’Antananarivo. Details regarding digital file development and derivatives of files (e.g., DICOM, PLY) used as part of the study are included in the Supplementary Information and archived on the MorphoSource website (https://www.morphosource.org/Detail/ProjectDetail/Show/project_id/7894). Phylogenetic character information and parameters used in the analyses are provided in the Supplementary Information. Executable files for phylogenetic analyses, interactive 3D morphospace plot, and interactive 3D PDFs are hosted on DRYAD: https://doi.org/10.5061/dryad.mkkwh70wg. This published work, including the novel genus (urn:lsid:zoobank.org:act:5BA26059-B428-4896-BFEA-2475419C61FC) and species (urn:lsid:zoobank.org:act:69314771-F0D8-4C15-946C-524164385FB7) along with the associated nomenclatural acts, have been registered in ZooBank: urn:lsid:zoobank.org:pub:4595D69E-FE12-4DAD-B155-89F084254F73.
O’Connor et al. Extended Data Figure 1—Full-page width—greyscale.
O’Connor et al. Extended Data Figure 2—Full-page width—Colour.
O’Connor et al. Extended Data Figure 3—Full-page width—Colour.
O'Connor et al. Extended Data Figure 4—Full-page width—Colour.
O’Connor et al. Extended Data Figure 5—1 ½ column width—Colour.
O’Connor et al. Extended Data Figure 6—column width—Colour.