The body plan of *Halszkaraptor escuilliei* (Dinosauria, Theropoda) is not a transitional form along the evolution of dromaeosaurid hypercarnivory (#43616)

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The body plan of *Halszkaraptor escuilliei* (Dinosauria, Theropoda) is not a transitional form along the evolution of dromaeosaurid hypercarnivory

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The dromaeosaurid theropod *Halszkaraptor escuilliei* is characterized by several unusual features absent in other paravians, part of which has been interpreted as diagnostic of a novel lineage adapted to a semiaquatic ecology. Recently, these evolutionary and ecological interpretations have been challenged, and *Halszkaraptor* has been claimed to be a transitional form between non-dromaeosaurid maniraptoriforms and other dromaeosaurids: following that re-evaluation, its peculiar body plan would represent the retention of several maniraptoran plesiomorphies, lost among other dromaeosaurids, and not an adaptation to a novel ecology. This alternative scenario is here carefully investigated and tested. It is shown that most of the statements supporting the alternative scenario are based on invalid homology statements, inaccurate or improper literature reports or on misinterpretation of the anatomical terminology. Once these statements have been corrected, character state transition optimization over a well-supported phylogenetic framework indicates that the large majority of the peculiar features of the *Halszkaraptor* lineage are derived novelties acquired by the latter after its divergence from the last ancestor shared with eudromaeosaurs, and thus are not maniraptoriform plesiomorphies. At least seven novelties of the *Halszkaraptor* lineage are convergently acquired with spinosaurids, and are integrated in semiaquatic adaptations: one of these is reported here for the first time. The amount of morphological divergence of Halszkaraptorinae from the ancestral dromaeosaurid condition is comparable to those of Microraptorinae and Velociraptorinae. The halszkaraptorine *bauplan* is thus confirmed as a peculiar amphibious specialization, and does not represent a “transitional” stage along the evolution of dromaeosaurids.

The body plan of *Halszkaraptor escuilliei* (Dinosauria, Theropoda) is not a transitional form along the evolution of dromaeosaurid hypercarnivory

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INTRODUCTION

The bird-like theropod dinosaur *Halszkaraptor escuilliei* is a based on an almost complete skeleton from the Upper Cretaceous of Mongolia (Cau et al., 2017). Compared to other theropods, *Halszkaraptor* shows several unusual features, supporting the institution of a new lineage of Dromaeosauridae, the halszkaraptorines (Cau et al., 2017; Cau & Madzia, 2018), and suggesting a semiaquatic *bauplan* able to exploit both terrestrial and aquatic resources. Recently, Brownstein (2019) published a review of the interpretations of Cau et al. (2017), and concluded that *Halszkaraptor* was not a semiaquatic form but a "transitional form" between the plesiomorphic maniraptoriform *bauplan* and the hypercarnivorous dromaeosaurids. Here, I show that several statements in Brownstein (2019) are unsupported, inaccurate or contradictory, and that most of the arguments raised by Brownstein (2019) stem from a substantial misinterpretation of the literature (*in primis*, but not uniquely, Cau et al. 2017) or are based on problematic homology statements.

MATERIAL AND METHODS

Brownstein (2019) cited several statements from the literature in support of his arguments: they were carefully checked and when not corresponding to the original source, they were reported and commented. All information from *H. escuilliei* discussed here was acquired by AC at the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, where MPC D-102/109 is temporarily housed (see Cau et al., 2017). First-hand examination of MPC D-102/109 was

integrated with multi-resolution scan data of the fossil, based on propagation X-ray phase-contrast synchrotron microtomography performed in 2016, at the European Synchrotron Radiation Facility in Grenoble, France (see Cau et al., 2017, supplementary information). In order to test the evolutionary and phylogenetic scenario suggested by Brownstein (2019), I used a new version of the data set used in Cau et al. (2017) (Supplementary Files). The data matrix was analyzed using TNT vers. 1.5. (Goloboff et al., 2008), following the same protocol of Cau et al. (2017: a first round of 100 "New Technology" runs, using default setting, was followed by a Tree-Bisection-Reconnection run using the shortest trees saved during the first round as starting topologies). The Triassic dinosaur *Herrerasaurus* was used as root of the trees. Four spinosaurid taxa were included in the sample, to test the distribution of the features shared by *Halszkaraptor* and those non-coelurosaurian theropods (Cau et al., 2017). The "agreement subtree" algorithm implemented in TNT was used to reconstruct the taxonomically most comprehensive fully-dichotomous structure shared by all shortest trees found: for this reconstruction, max tree was set to 50.000 due to memory limitations in TNT. The agreement subtree topology was used as framework for character state reconstruction at nodes and for estimating the minimum length of the recovered branches. Character state transition reconstruction at nodes was performed in PAUP (Swofford, 2002), importing the agreement subtree topology reconstructed in TNT and using the ACCelerated TRANsformation (ACCTRAN) optimisation. Taxonomic nomenclature follows Cau et al. (2017), with emendation of Unenlagiinae following Hartman et al. (2019). The distribution of the reconstructed state transitions along the theropod phylogeny was used to compare the alternative scenarios discussed by Cau et al. (2017) and Brownstein (2019). Institutional abbreviations: MPC, Institute of Paleontology and Geology, Mongolian Academy of Sciences, Ulanbatar, Mongolia; RBINS, Royal Belgian Insitute of Natural Sciences, Brussels, Belgium; YFGP, Yizhou Fossil and Geology Park, Yizhou, China.

RESULTS

Several sentences in Brownstein (2019) are inaccurate or problematic, including mentions to statements in the literature which are actually contradicted by the mentioned references themselves. In the following references, the term "ref./refs." followed by one or more numbers refers to the reference list in Brownstein (2019).

61

62 *Literature misreports and unsupported statements*

63 Brownstein (2019) wrote:

64 "Cau et al. [ref. 32] compared the construction of the skull of *H. escuilliei* to the anterior skulls
65 of modern birds like ducks and geese, with which *Halszkaraptor* was considered somewhat
66 analogous."

67 The above sentence in Brownstein (2019) misreports the mentioned source: Cau et al. (2019) did
68 not compare the skull of *H. escuilliei* with modern birds like ducks and geese, and did not
69 consider any analogy between the skull of this dinosaur and those birds.

70

71 Brownstein (2019) compared the premaxilla of *Halszkaraptor* with those of ornithomimosaurs
72 and therizinosaurians. He wrote:

73 “However, moderately to strongly (=platyrostral) laterally expanded premaxillae are found in a
74 variety of maniraptorans and maniraptoriforms [...]. Among these, the premaxillae of
75 *Erlikosaurus* are the best preserved and are highly reminiscent of the premaxillae of
76 *Halszkaraptor* in their clear lateral expansion in dorsal view [...]”.

77 *Contra* Brownstein (2019), it is unlikely that the platyrostral morphology of *Halszkaraptor* is
78 homologous to those he referred to other coelurosaurs. In *Halszkaraptor*, the platyrostral
79 condition is acquired by the remarkable anteroposterior elongation and dorsoventral flattening of
80 the prenarial region of the premaxilla, which also results in the posterior placement of the narial
81 region relative to the snout anterior tip. In ornithomimosaurs, the platyrostral condition is instead
82 related to the lateral expansion of the perinarial region (e.g., Osmólska et al., 1972; Lee et al.,
83 2014) which is not followed by any significant elongation of the prenarial region. In
84 *Erlikosaurus*, the prenarial part of the premaxilla is taller than long, constrasting with the
85 opposite condition in *Halszkaraptor* (Figure 1). Note that the relative elongation of the prenarial
86 part of the premaxilla and the posterior retraction of the premaxillary margin of the external naris
87 are not co-variant and thus could be considered as independent features (e.g., *Haplocheirus*,
88 Choiniere et al., 2014, figure 4). In *Erlikosaurus*, the narial fossa is expanded laterally and forms
89 the majority of the premaxillary body, whereas in *H. escuilliei* the narial fossa is completely
90 excluded from the participation to the premaxillary body (Figure 1). The “lateral expansion” of
91 the premaxilla, claimed by Brownstein (2019), is thus produced by distinct elements in the two

taxa (i.e., prenarial elongation and depression in *Halszkaraptor*, *vs* sub- and perinarial widening in *Erlikosaurus*), and could not be considered homologous (Figure 1).

Brownstein (2019) wrote:

“It is unclear how Cau et al. [ref. 32] observed retracted nares in *Halszkaraptor*, as the anterior nasals are not preserved in that taxon".

Based on his own statement, Brownstein (2019) assumed that the retraction of the external naris in Cau et al. (2017) was meant as the position of the narial margin of the nasal. As clearly stated in the latter paper, the retraction of the external naris referred to the narial margin of the premaxilla, and not to the narial margin of the nasal. They wrote: “[T]he platyrostral *premaxilla with* a dorsolaterally oriented *external naris that is retracted beyond the oral margin* is unique among theropods, although *in its elongation, the premaxilla* is similar to those of spinosaurids” (Cau et al., 2017; italics added here). Brownstein (2019) thus raised a concern for a feature which actually was not discussed by Cau et al. (2017).

Furthermore, Brownstein (2019) wrote:

"Despite the support for it found here, if *the presence of elongate nares* is not found as the plesiomorphic state for coelurosaurs in future analyses, the presence of them in a variety of theropods that do not show any features for a semiaqautic [sic] lifestyle provides evidence against the argument of Cau et al. [ref. 32], *who argued this feature was indicative of such an ecology*." (Italics added here).

Contra Brownstein's (2019) claim, Cau et al. (2017) did not write that the “elongation” of the naris is present in *Halszkaraptor* or that it is relevant in whatever ecological scenario. The actual feature mentioned by Cau et al. (2017), the retraction of the premaxillary narial margin beyond the premaxillary body, is absent in alvarezsauroids (Choiniere et al., 2014), ornithomimosaurs (Osmólska et al., 1970; Lee et al., 2014), oviraptorosaurs (e.g., Balanoff et al., 2009; Balanoff et al., 2012) and therizinosauroids (Lautenschlager et al., 2014), and is instead comparable to that in baryonychine spinosaurids (e.g., Charig and Milner, 1997; Sereno et al., 1998), and has been linked to a semiaquatic ecology (see Charig and Milner, 1997; Milner, 2003; Rayfield et al., 2007; Ibrahim et al., 2014).

Brownstein (2019) wrote:

"Although *Halszkaraptor* was differentiated from other theropods in possessing a rostral neurovascular system not entirely restricted [to] the lateral portions of the premaxillae [ref. 32], the rostral neurovasculature extends onto the dorsal surface of the body of the premaxilla in basal members of most other maniraptoran clades",

Several statements by Brownstein (2019) inaccurately listed the external distribution and the density of the neurovascular foramina in other theropods. *Contra* Brownstein (2019), the premaxilla of *Shenzhousaurus* is much less extensively pitted than in *Halszkaraptor* (see Ji et al., 2003, ref. 13 cited by Brownstein, 2019). *Contra* Brownstein (2019), the neurovascular foramina in ornithomimosaurus are densely distributed only along the oral margin but are less extensively distributed (if not absent) along the rest of the premaxillary body (see Kobayashi & Lü, 2003; Ksepka & Norell, 2004; Kobayashi & Barsnold, 2005; Lee et al., 2014). The same condition is present in oviraptorosaurs (e.g., Balanoff et al., 2009; Balanoff et al., 2012), where the premaxilla is extensively pitted only along the oral margin and scarcely penetrated in the rest of the bone. In all mentioned examples, the condition in these taxa differs from *Halszkaraptor*, where the density of foramina is greater and their distribution is more extensive all along the bone surface. Among theropods, only spinosaurids show a comparable density and distribution of neurovascular foramina in the premaxilla (Charig and Milner, 1996; Dal Sasso et al., 2005; Ibrahim et al., 2014, fig. S6).

Furthermore, Brownstein (2019) wrote:

“In the more derived therizinosaur *Erlikosaurus*, the same morphology, where the premaxillae harbor neurovascular foramina on both their lateral and mediodorsal surfaces, is clearly present (see Lautenschlager et al. [ref. 19] for clear scans of the premaxillae of *Erlikosaurus*; fig. 1C,D)”.

Contra Brownstein (2019), the CT-scanning of *Erlikosaurus* (Lautenschlager et al., 2014) demonstrates that in *Erlikosaurus* both density and number of the external foramina and the relative size of the internal plexus in that therizinosaurid are much less developed than in *Halszkaraptor* (Figure 2). In *Erlikosaurus,* the external foramina are mainly concentrated along the oral margin (Lautenschlager et al., 2014), and are less numerous in both absolute and relative terms than in *Halszkaraptor* (in the latter, the dorsal surface bears at least 20 foramina, distributed over a premaxilla which is about five times shorter than that of *Erlikosaurus*). Furthermore, the relative size of the internal neurovascular plexus (including its main stem) in

Halszkaraptor is significantly larger than in *Erlikosaurus* (Figure 2).

Brownstein (2019) focused his discussion on the tooth replacement patterns in *Halszkaraptor*. He wrote:

"One interesting feature of the premaxillary teeth of *Halszkaraptor* described by Cau et al. [ref. 32] was their delayed replacement rate [sic]. A large amount of research into the loss of teeth in some maniraptoran dinosaurs has found a delayed replacement rate [sic] to be linked to tooth loss in several clades, including therizinosaurs and ornithomimosaurs",

and

"The slowly-replacing [sic] premaxillary teeth of *Halszkaraptor* are also reminiscent of adaptations found in herbivorous theropod lineages like therizinosaurs [refs. 11, 15]".

The above mentioned sentences misinterpreted and misreported the literature. First, Cau et al. (2017) described a "delayed replacement pattern" in *Halszkaraptor*, and not a "delayed replacement rate". Second, refs. 11 and 15 mentioned by Brownstein (2019), i.e., Zanno et al. (2009), and Zanno & Makovicky (2011), do not mention "delayed replacement rate" but instead "low tooth-replacement rate". Brownstein (2019) thus misinterpreted the terminology used by Cau et al. (2017) and assumed that Zanno et al. (2009) and Zanno & Makovicky (2011) referred to the same condition described by Cau et al. (2017). *Contra* Brownstein (2019), the two terms are relative to distinct, non-homologous conditions, and are not synonyms. The term "delayed replacement pattern", used by Cau et al. (2017) for *Halszkaraptor*, refers to the differences between the premaxillary tooth-replacement compared to the maxillary tooth-replacement. The "low tooth-replacement rate" described by Zanno et al. (2009) and Zanno & Makovicky (2011), instead refers to the absence of pronounced replacement waves and gaps between teeth, producing a continuous horizontal cutting surface (Lindsay Zanno, pers. com. , 2019). The "low tooth-replacement rate" (Zanno et al., 2009, and Zanno & Makovicky, 2011) is absent in *Halszkaraptor*, which bears a sinusoid cutting surface along the whole dentition and distinct replacement waves (Figure 3).

Brownstein (2019) also stated that the "delayed replacement rate [sic] is linked to tooth loss". That sentence is not correct: the absence of replacement waves in the teeth is independent to the loss of teeth, as demonstrated by *Pelecanimimus* (Perez-Moreno et al., 1994), parvicursorines (Chiappe et al., 1998) and several troodontids (e.g., Lü et al., 2010), all lacking replacement

185 waves yet retaining a complete set of teeth (Zanno & Makovicky, 2011). Given that
186 *Halszkaraptor* is unique among all dinosaurs in having the largest number of premaxillary teeth
187 (Cau et al., 2017), it shows a condition opposite to the loss of premaxillary teeth seen in
188 therizinosaurids or other omnivorous/herbivorous theropods (Zanno & Makovicky, 2011). In
189 sum, *Halszkaraptor* is not “reminiscent of adaptations found in herbivorous theropod lineages”
190 (*contra* Brownstein, 2019).
191
192 Brownstein (2019) wrote:
193 "Cau et al. [ref. 32] noted the comparatively long neck of *Halszkaraptor* [...]. However, [...], it is
194 unclear why Cau et al. allied this feature to elongate necks in derived semiaquatic avians (e.g.,
195 *Cygnus*)".
196 Cau et al. (2017) did not compared *Halszkaraptor* neck elongation to the condition in derived
197 semiaquatic avians (e.g., *Cygnus*). In the latter study, *Cygnus* is only mentioned once, but in
198 relation to the shape of the interpostzygapophyseal lamina and not because of its neck
199 elongation. Brownstein (2019) misunderstood two distinct sentences in Cau et al. (2017) and
200 combined them improperly.
201
202 Brownstein (2019) wrote:
203 "Despite the fact that Cau et al. [rep. 32] claimed the neck of *Halszkaraptor* composed the
204 greatest percentage of snout-to-sacrum length among *non-avian coelurosaurs*, a large number of
205 clades include taxa that approach, reach, or possibly even exceed that threshold". (Italics added
206 here).
207 The above statement misreports the original sentence of Cau et al. (2017), which instead was:
208 "[c]ompared to body size, the neck is elongate and forms 50% of the snout–sacrum length; this is
209 the highest value found among *Mesozoic paravians* thus far" (italics added here).
210
211 Brownstein (2019) wrote:
212 “If this hypothesized ecomorphology for *Halszkaraptor* is correct, it has major implications for
213 the evolution of bird-like dinosaurs, with *H. escuilliei* representing the first aquatic non-avian
214 maniraptoran and suggesting that the ancestral lifestyle for dromaeosaurids could be one that
215 took place in the water [ref. 32]”.

Contra Brownstein (2019), Cau et al. (2017) (his ref. 32) did not suggest that the ancestral dromaeosaurid lifestyle could be one that took place in the water.

Brownstein (2019) wrote:
"The Djadokhta Formation [...] preserves a highly arid environment [...]. Given this environmental setting, it is hard to envision that specialized, semiaquatic dromaeosaurs would populate this ecosystem".
Other Djadokhtan reptiles show adaptations related to an amphibious lifestyle, like the neosuchian *Shamosuchus diadochtaensis* (a taxon characterized by a platyrostral snout and unserrated subconical dentition; Pol et al. 2009). Even if not the most abundant members, semiaquatic taxa are present in the Djadokhtan faunal assemblages (Lefeld, 1971): their relatively low frequency is in agreement with the presence of ephemeral lacustrine deposits in that Formation (Dingus et al., 2008), but does not constitute a challenge to the ecological interpretation of Cau et al. (2017).

Misreports and misinterpretation of Halszkaraptor *anatomy*
Brownstein (2019) wrote:
"In many dromaeosaurids, including velociraptorines, *Halszkaraptor*, *Deinonychus*, and "*Bambiraptor*" (fig. 5 [sic: this is typo, the actual figure is figure 6]), the anterior end of the ventral surface of the dentary bulges to form a chin (fig. 5B–F), as in some ornithomimosaurs (fig. 6H)".
In dromaeosaurids, the anteroventral margin of the dentary lacks the so-called "chin" or bulging mentioned and indicated in figure 6 of Brownstein (2019): dromaeosaurids are characterized by subparallel dorsal and ventral margins of the dentary which describe a roughly quadrangular outline with the anterior margin of the bone when seen in lateral view (see Turner et al., 2012, figs. 15C, 23A-C, 26, 29A, 38C). In theropod morphology, the term "chin" is used in relation to the presence of a distinct anteroventral process or flange oriented mediolaterally, not involved in the symphysial articulation, and does not describe the mere shape of the anteroventral corner of the dentary (e.g., Brusatte & Sereno, 2007). Furthermore, a "bulge" is expected to be a distinct swelling not related to the mere topographic confluence of the anterior and ventral margins of the bone. Both features are absent in dromaeosaurids, Furthermore, *contra* Brownstein (2019), the

247 shape of the anteroventral margin of the dentary in dromaeosaurids clearly differs from
248 ornithomimosaurs (e.g., Osmólska et al., 1972; Kobayashi & Lü, 2003; Kobayashi & Barsbold,
249 2005; Lee et al., 2014).
250 Brownstein (2019, figure 6D) included a drawing of the anterior end of the dentary of
251 *Halszkaraptor* in lateral view, and depicted a distinctly convex “bulge” at the anterior end of the
252 ventral margin (indicated in that figure by an arrow). That drawing is inaccurate and misleading.
253 The anteroventral end of the dentary in *Halszkaraptor* is eroded (Figure 1B and 1D), so its exact
254 shape, including the presence of the “bulge” illustrated by Brownstein (2019, figure 6D), cannot
255 be determined. Regardless to what actually Brownstein (2019) meant with “bulge” in the
256 dromaeosaurid dentaries, its presence in *Halszkaraptor* is not based on evidence.
257
258 Brownstein (2019) wrote:
259 "On the whole, the skull of *Halszkaraptor* also shares many similarities with basal troodontids,
260 including [...] tightly packed teeth, and recurved, ziphodont, unserrated crowns".
261 The combination of terms "ziphodont” coupled with “unserrated" is a contradiction due to the
262 improper use of the anatomical terminology: "ziphodont" means, literally, tooth with serration
263 (Langston, 1975). The dentition of *Halszkaraptor* is not ziphodont.
264 In *Halszkaraptor*, only the premaxillary teeth are packed, a condition comparable to *Microraptor*
265 but absent in other microraptorines (Xing et al., 2013; Pei et al., 2014). The rest of the dentition
266 (notably, the whole maxilla) in *H. escuilliei* is formed by spaced alveoli with complete
267 interdental septa, differing from troodontids where the anterior maxillary dentition is formed by
268 tightly packed teeth housed in a sulcus often lacking interdental septa (e.g., Lü et al., 2010). The
269 topographical differences between the regions bearing packed teeth suggest that the condition in
270 *H. escuilliei* is not homologous to that in troodontids.
271
272 Brownstein (2019) wrote:
273 "Shortened caudal series. *Halszkaraptor* possesses a highly modified caudal series, a feature that
274 Cau et al. [32] used to support a modified posture in this taxon analogous to some birds".
275 Cau et al. (2017) did not state that the caudal series of *Halszkaraptor* is shortened. The actual
276 number of caudal vertebrae in MPC D-102/109 is unknown, being the distal end of the tail
277 missing. The preserved part of the tail in MPC D-102/109 is comparable to the majority of basal

paravians (e.g., Godefroit et al., 2013b; Lefèvre et al., 2017) in elongation and proportions of the vertebrae, and it is not significantly reduced, as instead seen in pygostilian birds or in some oviraptorosaurs (Zhou et al., 2000; Cau, 2018). Note that Cau et al. (2017) mentioned the tail size in *Halszkaraptor* relatively to the exceptional neck elongation, but did not state any peculiar reduction in the caudal series. Furthermore, Cau et al. (2017) did not write that the unusual features in the caudal vertebrae of *Halszkaraptor* support a modified posture like that in birds: the latter was inferred on the basis of hypertrophied origin and insertion of the *m. ileofibularis* in, respectively, ilium and femur (Cau et al., 2017, supplementary information). Brownstein (2019) thus misinterpreted two distinct and unrelated sentences in Cau et al. (2017), one about the peculiar features of the caudal vertebrae (not related to tail elongation/reduction), and another about the pelvic and femoral adaptations supporting hip-extension.

Brownstein (2019) wrote:
"Therefore, the cross-sectional limb morphology of *Halszkaraptor* provides among the strongest evidence against a partially marine ecology in *H. escuilliei*",
and
"These results were used to support a semiaquatic ecological mode in the taxon, with the forelimb acting as a propulsion device. However, the inferences made by Cau et al. [ref. 32] from the morphometric analyses are flawed, as the forelimb of *Halszkaraptor* looks strikingly unlike the paddles formed by the forelimb bones of plesiosaurs" (Brownstein, 2019).
Brownstein (2019) did not provide any quantitative morphometric analysis in support of his sentences. *Contra* Brownstein (2019), the cross-section geometry of *Halszkaraptor*'s ulna reflects an unusual flattening of the bone (a feature that was first noted in the other halszkaraptorine *Mahakala*, see Turner et al., 2011), and recalls the analogous condition differentiating wing-propelled aquatic birds from other avians (Simpson, 1946). When plotted relative to ulnar length, the mid-shaft mediolateral diameter of *Halszkaraptor* ulnar shaft clusters it among wing-propelled birds and not among other bird groups, and also results proportionally more expanded transversally than in other non-avian theropods (Figure 4): this morphometric feature is consistent with the ecomorphological scenario of Cau et al. (2017).

Brownstein (2019) also stated:

"[...] this taxon [*Halszkaraptor*] was probably not biomechanically suited to live in water, as its skeleton, like other paravians, would have probably been too light to keep the animal submerged.",

and

"The bones of *Halszkaraptor* are clearly internally hollow to a similar extent as other paravian dinosaurs. However, in tetrapods adapted for a semiaquatic or entirely aquatic lifestyle […], pachyostosis, the extreme thickening of cortical bone, occurs in the limbs. Given that pachyostosis is present in the limb bones of both avian and non-avian theropods that took to the water, the absence of such thickening in *Halszkaraptor*, which Cau et al. [ref. 32] posit was well-adapted for a semiaquatic ecology, would be very surprising from a biomechanical standpoint" (Brownstein, 2019).

In the above mentioned statements, Brownstein (2019) challenges Cau et al. (2017) arguing that vertebrates with hollow long bones and a highly pneumatized postcranial skeleton could not be adapted to some aquatic lifestyle, and implicitly claims that pachyostosis is a necessary requisite for a semiaquatic lifestyle. Both Brownstein's (2019) assumptions are falsified by several modern birds, e.g., the pelicans, characterized by an extensively-pneumatized skeleton (Richardson, 1939), and that are nonetheless well-adapted to piscivory, to exploit the aquatic environment and to a wing-propelled swimming style (Hinić-Frlog & Motani, 2010). It is noteworthy that the degree of internal bone cavitation and pneumatization in the skeleton of pelicans (e.g., Simons & O'Connor, 2012, fig. 3; Wedel, 2014; Wedel, 2018) is more extensive than in *Halszkaraptor*.

Brownstein (2019) then questioned the analysis of morphospace occupation of Cau et al. (2017) which focused on the proportions of the medial fingers (I-II-III) in reptiles.

Brownstein (2019) wrote:

"*Halszkaraptor* lacks the 'paddle' in plesiosaurs, *Araripemys*, and other aquatic vertebrates like ichthyosaurs, wherein the hand contains many closely appressed phalanges (fig. 2). In contrast, the forelimbs of marine reptiles, such as mosasaurs, plesiosaurs, and ichthyosaurs, consist of a massive number of flattened, heavily modified phalanges that form a distinctive paddle shape entirely distinct from the theropod manus (fig. 3B)".

Both aquatic chelonians and penguins show that a flipper- or paddle-like shape could evolve without hyperphalangy (Simpson, 1946; Walker, 1973; Clark & Bemis, 1979; Carpenter et al.,

2010). The hands of wing-propelled birds have only three fingers, with a phalangeal formula even more reduced than in *Halszkaraptor* (Simpson, 1946). Thus, different skeletal morphologies may produce a functional paddle, which is not constrained to a five-fingered pattern and to hyperphalangy. To test if the hand of *Halszkaraptor* fits the overall proportions of a paddle, Cau et al. (2017) compared the proportions of the three medialmost fingers (fingers I-II-III) in reptiles. These fingers define the outline of the leading edge of the paddle, which is a key parameter in any flipper morphology (Combes & Daniel, 2001). The morphometric analysis showed that 1) there is not significant overlap between theropods and other reptiles in finger proportions, 2) *Halszkaraptor* does not cluster among the other theropods, and 3) the outline of the medial/leading edge of the hand in *Halszkaraptor* is more similar to those of aquatic reptiles than those of the other theropods.

Brownstein (2019) failed to explain why *Halszkaraptor* shows so unusual finger proportions: the finger proportions in *Halszkaraptor* are not plesiomorphic for Maniraptora, and are not shared with herbivorous or omnivorous theropods, and thus do not fit Brownstein's (2019) hypothesis. *Contra* Brownstein (2019), the forelimb of *Halszkaraptor* markedly deviates from those of other dromaeosaurids (e.g., *Deinonychus*, Ostrom, 1969; *Microraptor*, Hwang et al., 2002) in several features, including the overall stouter proportions of the bones, the marked flattening of the ulna, the significant reduction of the size of the first finger, the presence of a more robust third metacarpal, and the significant elongation of the phalanges of the third finger: it is noteworthy that all these features differentiate the forelimb of wing-propelled birds (e.g., penguins) from other (i.e., non-swimming) avians (Simpson, 1949).

Brownstein (2019) wrote:

“Their resultant reconstruction of the glenoid facing laterally in *H. escuilliei* is therefore also unsubstantiated”.

The rationale for the inference of a laterally-facing glenoid in *H. escuilliei* is explained by Cau et al. (2017), where it is stated: “Although the fragmentary preservation of the pectoral region prevents a detailed reconstruction of forelimb range of motion, on the basis of phylogenetic bracketing, we infer that the glenoid in *Halszkaraptor* faces laterally, as it does in forelimb-assisted swimming tetrapods”. A laterally-facing glenoid is a paravian symplesiomorphy inherited by dromaeosaurids (Turner et al., 2012) and thus, in absence of contrary evidence and

based on phylogenetic bracketing, it is the most plausible condition for *Halszkaraptor*. Given that such a feature is also an adaptation necessary for any form of forelimb-assisted swimming (Carpenter et al., 2010), the plesiomorphic glenoid condition of paravians which is assumed for *Halszkaraptor* is also a potential exaptation for a forelimb-assisted swimming style.

Brownstein (2019) wrote:
"Cau et al [32] noted that the 'sickle' claw on pedal digit II is heavily reduced in *Halszkaraptor* compared to other dromaeosaurids (fig. 2A,E)".
The above-mentioned statement misreports Cau et al. (2017), who instead wrote: "The second toe is half the length of the third (Fig. 3e), with a stout phalanx II-2 and a *large falciform ungual, similar to those in other paravians*". (Italics added here). *Contra* Brownstein (2019), when pedal ungual II size of *Halszkaraptor* is plotted against femur length (a frequently-used proxi of body size in theropod research), there is no significant difference between *H. escuilliei*, the other dromaeosaurids, and other basal paravians (Figure 6).

Inaccurate or unsupported references to other taxa
Brownstein (2019) wrote:
"As in basal members of the Ornithomimosauria like *Nqwebasaurus* [ref. 67] […], *Halszkaraptor* possesses a large number of premaxillary teeth".
According to Choiniere et al., 2012 (reference 67 in Brownstein, 2019), the premaxillary teeth of *Nqwebasaurus* are not preserved, so their actual number is unknown.

Brownstein (2019) wrote:
"Members of basal clades in the Dromaeosauridae, *including microraptorans* and unenlagiines, also possess a large number (20+) of teeth in their maxillae". (Italics added here).
All known microraptorans have less than 20 teeth in their maxillae, not more (e.g., Turner et al., 2012, figure 23; Xing et al., 2013; Pei et al., 2014). Note that assuming (erroneously) a larger number of maxillary teeth in microraptorans has significant implications for the number of maxillary teeth inferred at the root of Dromaeosauridae (see below).

Brownstein (2019) wrote:

"The complete connection of the postzygapophyses by bone surface [as in *Halszkaraptor*] is present in the basal-most ornithomimosaur *Nqwebasaurus* and the basal-most therizinosaur *Falcarius*, and is present to a lesser extent in basal alvarezsaurs like *Aorun* and *Haplocheirus*, the basal ornithomimosaur *Pelecanimimus*, and the basal tyrannosauroid *Guanlong*."
Contra Brownstein (2019), all the above-mentioned taxa bear distinct postzygapophyses not-completely merged medially, and show posteriorly-concave interzygapophyseal laminae excavated dorsally by the ligament fossa (Choiniere et al., 2010, Zanno, 2010; Choiniere et al., 2012), and thus lack the autapomorphic complex of *H. escuilliei*.

Brownstein (2019) wrote:
"*Microraptor* was an arboreal glider [ref. 21]".
Turner et al. (2012; ref, 21 of Brownstein, 2019), does not mention and does not discuss any arboreal and/or gliding adaptation for *Microraptor* (see also Dececchi & Larsson, 2011).

Brownstein (2019) wrote:
"Although it is clear that the prominence of the supratrochanteric process in *Halszkaraptor* is greater than in these unenlagiines, the supratrochanteric process in many anchiornithids is similarly developed [91, 92]."
Brownstein's (2019) references 91 and 92, i.e., Godefroit et al. (2013a) and Godefroit et al. (2013b), do not mention the supratrochanteric process in anchiornithids. Both *Eosinopteryx* (Godefroit et al., 2013a) and *Aurornis* (Godefroit et al., 2013b, Figure 5A) lack a prominent supratrochanteric process like that claimed by Brownstein (2019) (pers. obs., 2015). The supratrochanteric process of the anchiornithids is no more developed in shape and extent than the tuber-like process present in other paravians (e.g., compare *Aurornis*, Figure 5A, or *Anchiornis*, Hu et al., 2009, fig. S4b, with *Rahonavis*, Turner et al., 2012, fig. 55B) and is much less prominent than in *Halszkaraptor*, where it forms a peculiar large shelf-like lateral projection overhanging the ilium (Fig. 5B).

Methodological weakness and non-reproducibility of the phylogenetic analysis

Brownstein (2019) provided a data matrix in the supplementary information of his paper.

Unfortunately, the phylogenetic results described in Brownstein (2019) could not be obtained using the provided data matrix (i.e., the topology resulted using that data set is identical to that in Cau et al., 2017: extended data figure 10). Even more puzzling is the list of characters that Brownstein (2019) claimed to form the diagnosis of the clade formed by halszkaraptorines and unenlagiines, that he obtained in his analysis. He wrote:

"This clade is united by five characters: 27 (0, maxillary fenestra situated at anterior border of antorbital fossa), 107 (1, Sacral vertebrae number is six), 193 (1, ascending process of astragalus short and slender), 580 (0, sagittal crest of parietal comprised of two parallel crests), and 828 (0, Meckelian groove centered)" (Brownstein, 2019).

Note that character numeration does not follow entirely the original character list (supplementary information of Brusatte et al., 2014): character statements #27, #107, #580 and #828 in Brownstein (2019) are instead statement #28, #108, #581 and #829 in Brusatte et al. (2014).

Three of the above-listed character states could not be unambiguous synapomorphies of the "Halszkaraptorinae + Unenlagiinae" node, because they are actually absent among halszkaraptorines:

The maxillary fenestra is only known in *Halszkaraptor* among halszkaraptorines (Cau et al., 2017). In this taxon, it is placed posterodorsally on the antorbital fossa and not "at anterior border of antorbital fossa": thus, character 28 of Brusatte et al. (2014) cannot be scored as "0" in any halszkaraptorine.

The ascending process of the astragalus is only known in *Mahakala* among halszkaraptorines (Turner et al., 2011). In this taxon, the ascending process is wide and covers the whole anterior surface of the tibia (state 0 of character 193 of Brusatte et al., 2014), and is not slender and restricted over the lateral half of the tibia as in the state 193.1 of Brusatte et al. (2014).

The parietal is only known in *Halszkaraptor* among halszkaraptorines (Cau et al., 2017). In this taxon, the bone entirely lacks a sagittal crest, and thus, following the description of the character in Brusatte et al. (2014), character 581 is inapplicable in *Halszkaraptor*.

The cause of these bizarre results cannot be determined based on the data provided.

Phylogenetic test

The phylogenetic analysis performed here reconstructed >99.999 shortest trees of 6566 steps (CI

464 =0.2333, RI =0.5558). The agreement subtree topology (Figure 7) is formed by 158 of the
465 included 185 operational taxonomic units, indicating a relatively stable and well-supported
466 framework among the majority of the taxa. The relationships among the main coelurosaurian
467 clades are in agreement with the previous iterations of this data set (e.g., Cau et al., 2017; Cau,
468 2018). The analysis supports the sister group relationships between halszkaraptorines and
469 unenlagiines, as found in Cau (2018), Gianechini et al. (2018), Hartman et al. (2019), and
470 advocated by Brownstein (2019). This clade is supported by 11 unambiguous synapomorphies
471 (Supplementary Files). Note that the result of this analysis confirms only one of the five
472 synapomorphies suggested by Brownstein (2019) in support of this clade (the presence of six
473 sacral vertebrae).
474 Part of the features discussed by Brownstein (2019) and claimed in *H. escuilliei* are falsified by a
475 careful analysis of the morphology of *Halszkaraptor* and other taxa, and do not support
476 Brownstein's (2019) scenario (e.g., *Halszkaraptor* actually lacks the “low tooth-replacement
477 rate”, a “short tail”, or a “reduced” second toe ungual). Other purported features listed by
478 Brownstein (2019) cannot be considered as shared morphological character statements because
479 the condition in *Halszkaraptor* is not topographically homologous to those in non-paravian
480 maniraptoriforms (e.g., the “platyrostral” premaxilla of *Halszkaraptor* cannot be homologous to
481 those in ornithomimosaurus or therizinosauroids). Once these features are removed from the list
482 of phylogenetically significant features forming the Halszkaraptorine body plan, the latter is
483 described by 17 morphological character statements (Table 1).
484 Character state transition optimization indicates that the majority of the features (11 over 17) are
485 evolutionary novelties acquired along the “Halszkaraptorinae + Unenlagiinae” clade after its
486 divergence from the other dromaeosaurids (Table 1, Figure 7). Seven of these halszkaraptorine
487 novelties are convergently acquired by spinosaurids (Figure 8A). *Contra* Brownstein's (2019)
488 scenario, only two among the 17 features discussed (i.e., the absence of serration in the
489 premaxillary dentition, and the presence of a robust metacarpal III) are maniraptoromorph and
490 paravian symplesiomorphies, conserved in *Halszkaraptor* and lost along the “microraptorine-
491 eudromaeosaurian” lineage.
492

493 ## DISCUSSION

494 The quality of the arguments provided in Brownstein (2019) is dramatically weakened by 1) a

long series of inaccurate reports, improper, wrong or contradictory citations, 2) the misreports and misuse of the anatomical and morphological terminology, 3) the use of inaccurate figures that in some cases explicitly illustrated non-existent features, and 4) the non-reproducibility of the claimed results. As shown above, most of this rebuttal paper has been necessarily devoted to identify and correct all these problematic statements, most of which are fundamental in Brownstein's (2019) alternative scenario, and to remove them from the proper comparison of the two hypotheses.

Brownstein (2019) systematically misinterpreted several sentences in Cau et al. (2017) and thus provided a largely inaccurate and misleading depiction of the latter. Several statements that Brownstein (2019) referred to Cau et al. (2017) are actually absent in the latter. The frequent referral to fully-aquatic reptiles in Brownstein's (2019) discussion is misleading and unnecessary, because Cau et al. (2017) did not suggest such an extreme form of aquatic adaptation in *H. escuilliei.* The absence of polydactyly and the lack of pachyostosis in *Halszkaraptor* are not valid arguments challenging the evolution of a semiaquatic ecology, because several tetrapod lineages (including some wing-propelled diving birds like pelicans) evolved such an ecology in absence of those anatomical features. Given that Cau et al. (2017) did not suggest a “partially marine ecology” [sic] for *Halszkaraptor*, and did not suggest a plesiosaur-like locomotory style or a plesiosaur-like forefin morphology in *Halszkaraptor*, it is unclear why Brownstein (2019) had focused to that peculiar fully-aquatic *bauplan*. Note that all aquatic and diving birds (both flying and flightless) lack the plesiosaur-like features in the forelimb listed by Brownstein (2019), so the absence of a plesiosaur-like paddle or a plesiosaur-like swimming style do not necessarily invalidate locomotion in water or a semiaquatic ecology in a maniraptoran theropod. Note that Cau et al. (2017) described the locomotory style of *Halszkaraptor* using the relatively neuter term “forelimb-assisted swimming” instead of any stronger term that may indicate a peculiar locomotory style more closely analogous to those of, for example, penguins or plesiosaurs. Thus, *contra* Brownstein (2019), focusing on the absence of fully-aquatic in *Halszkaraptor* does not affect the arguments discussed in Cau et al. (2017). Most of Brownstein's (2019) paper appears thus devoted to demolish his own arbitrary deformation of the hypothesis of Cau et al. (2017), and could hardly be considered a valid review of the latter paper.

Brownstein (2019) suggested that most of the features forming the unusual body plan of *Halszkaraptor* are maniraptoriform or maniraptoran plesiomorphies which were subsequently

lost along the lineage leading to Eudromaeosauria. As shown above, a significant part of the features listed by Brownstein (2019) in support of that hypothesis are not valid, being based on inaccurate reports not supported by the literature cited therein. In most cases, those statements are based on misinterpretation of the anatomical terminology, or are grounded on problematic homology statements. In the most problematic cases, the mention of those features is merely false, being them absent in the holotype of *H. escuilliei* (e.g., the so-called "dentary chin" is not present in MPC-D 102/109). Once tested quantitatively, the remaining character statements mentioned by Brownstein (2019) are in large part inferred as synapomorphies of the halszkaraptorine lineage or, at most, as synapomorphies of the clade also including the unenlagiines (e.g., Gianechini et al., 2011, Gianechini et al., 2017; Gianechini et al., 2018), and were acquired by that lineage after its divergence from the other dromaeosaurids. Contra *Brownstein* (2019), the most parsimonious scenario places the loss of serration in the lateral dentition, the increased number of lateral teeth, the elongation of the neck, and the development of the prominent supratrochanteric shelf, as novelties acquired along the "halszkaraptorine-unenlagiine" lineage: all these features were not inherited from maniraptoriform ancestors, and were not secondarily lost in eudromaeosaurs. The majority of the similarities with some maniraptoriforms are homoplastic convergences (a phenomenon widespread among theropod dinosaurs, see Holtz, 2001; Figure 8A). At least seven of the halszkaraptorine novelties are convergently acquired by spinosaurids, and are integrated in a semi-acquatic and piscivorous ecology (Charig and Milner, 1997; Ibrahim et al., 2014; Cau et al., 2017). One of these features, reported here for the first time, is the "festooning pattern" in the upper dentition size variation, which recalls semi-aquatic crocodilians (see Charig and Milner, 1997; Dal Sasso et al., 2005; Pol et al., 2009). In *Halszkaraptor*, the anteriormost two maxillary teeth (and corresponding alveoli) are smaller and much slender than the other anterior maxillary teeth and also smaller than the largest premaxillary teeth: this condition produces a distinct sinusoidal ("festooning") oral margin due to the presence of two zones bearing elongate fang-like teeth, one in the premaxilla and one in the anterior half of the maxilla, separated by a zone bearing reduced teeth (Figure 3). This condition is markedly different from the straight and uniform cutting surface present in the oral margin of the herbivorous theropods (Zanno & Makovicky, 2011; see Figure 1A), and has been interpreted as an adaptation for foraging efficiently in aquatic environments and for grabbing evasive prey items (Vullo et al., 2016). This snout morphology is frequently associated

with the presence of numerous neurovascular pits opening on most of the premaxillary surface (Vullo et al., 2016), which is also shared by *H. escuilliei* and spinosaurids.

Assuming that the peculiar halszkaraptorine features are maniraptoriform plesiomorphies (as claimed in Brownstein, 2019) is not the most parsimonious explanation of the evidence, because it would require the secondary loss of all these claimed ancestral states in oviraptorosaurs, in the "avialan-troodontid" lineage (Averaptora) and in the "eudromaeosaur-microraptorine" lineage. The scenario supported here confirms the hypothesis that, during their evolution, different coelurosaurian lineages converged to a non-ziphodont, multitoothed, and long-necked body plan independently each other (Zanno & Makovicky, 2011; Choiniere et al., 2014). It is noteworthy that the result of the current study is obtained setting ambiguous character optimization to favor reversals over convergences (accelerated transformation optimization), and thus endorsing a possible "deep" (maniraptoriform) origin of the halszkaraptorine features and their later reversal among eudromaeosaurs (as suggested by Brownstein, 2019): even with that optimization, the majority of the discussed features are recovered as synapomorphies of the halszkaraptorine lineage, and cannot be interpreted as maniraptoriform plesiomorphies (*contra* Brownstein, 2019).

Brownstein (2019) consistently re-interpreted most of the features of *Halszkaraptor* listed by Cau et al. (2019) as plesiomorphic conditions of clades more inclusive than Halszkaraptorinae: careful comparison of the terms used in the two papers shows that the character descriptions used by Brownstein (2019) differ from those in Cau et al. (2017) in not distinguishing neomorphic and transformational character statements (Sereno, 2007). For example, Brownstein (2019) did focus on *the presence* of the supratrochanteric process of the ilium (a neomorphic character state shared by many paravians and therizinosauroids) to challenge Cau et al. (2017), whereas the latter did discuss *the development of the shelf-like* supratrochanteric process (a transformational character state present uniquely among the halszkaraptorine-unenlagiine lineage). As a consequence of such misinterpretation, what is a genuine apomorphy of the halszkaraptorines is erroneously claimed to be a maniraptoran plesiomorphy. Similarly, Brownstein (2019) did focus on *the presence* of the interpostzygapophyseal lamina in the cervical vertebrae (a neomorphic character state widespread among maniraptoriforms), whereas Cau et al. (2017) did discuss *the development of the expanded and fan-shaped* interpostzygapophyseal lamina in the cervical vertebrae (a transformational character state autapomorphic of *H. escuilliei*): the plesiomorphic status of the neomorphic state does not invalidate the autapomorphic status of the

transformational one.

It should be remarked that Brownstein's (2019) scenario failed to provide an evolutionary explanation for the autapomorphic features that even the latter paper recognizes as being present in *Halszkaraptor*. The mere assertion of a “transitional” morphology in *Halszkaraptor* does not provide an explanation for its autapomorphies, because the latter, by definition, are not states intermediate between non-dromaeosaurids and later-diverging dromaeosaurids, but are instead novel features acquired uniquely along the terminal branch. All these features are unexplained under Brownstein's (2019) scenario, because they are not maniraptoran plesiomorphies and are not correlated to an herbivorous/omnivorous ecology (see Zanno and Makovichy, 2011). Given that these features are observed among piscivorous and aquatic amniotes, as discussed by Cau et al. (2017), and in absence of an alternative explanation for their presence in *Halszkaraptor*, the ecomorphological hypothesis discussed by the latter study keeps being valid even under the revised phylogenetic framework advocated by Brownstein (2019). Paradoxically, the sister-taxon relationship between Halszkaraptorinae and Unenlagiinae suggested by Brownstein (2019) (but see it discussed also in Cau, 2018; Gianechini et al., 2018; and Hartman et al., 2019), weakens the so-claimed “transitional” status for the morphology present in *Halszkaraptor*, because it removes the latter taxon from a more direct basal divergence near the ancestral dromaeosaurid node, and places it nested among a disparate branch of non-eudromaeosaurian dromaeosaurids (Novas et al., 2009; Gianechini et al., 2018). Furthermore, the amount of morphological divergence of the halszkaraptorines from the ancestral paravian root is comparable to those of microraptorines and velociraptorines (Figure 8B): asserting that *Halszkaraptor* is "likely representative of the morphological transition from the ancestral body plan of maniraptorans to the one [sic] that characterized dromaeosaurids" (Brownstein, 2019) is thus unjustified. In sum, even under the phylogenetic framework advocated by Brownstein (2019), there is no reason for assuming that the disparate morphologies represented by *Halszkaraptor* and the unenlagiines were “plesiomorphic” or “transitional” between the basal maniraptoran *bauplan* and other dromaeosaurids. The evolutionary scenario suggested by Brownstein (2019) is thus falsified by its own phylogenetic structure.

CONCLUSIONS

The hypothesis that the body plan of *Halszkaraptor* represents a “transitional” condition

intermediate between non-paravian maniraptoriforms and eudromaeosaurians is based on a series of non-rigorous homology hypotheses, on the misinterpretation of several character statements describing the coelurosaurian diversity, and has been erected over a problematic list of literature misreports and misquotes. *Halszkaraptor* markedly diverged from the other maniraptorans, and careful investigation of the character state distribution among coelurosaurs confirms that the large majority of the peculiar features of *H. escuilliei* are not maniraptoran symplesiomorphies, and cannot define the ancestral dromaeosaurid body plan. A quantitative analysis of the morphological divergence among these taxa falsifies Brownstein's (2019) scenario, dismissing a "transitional" status for the halszkaraptorines relative to other dromaeosaurids. Furthermore, that hypothesis is unable to interpret the peculiarities of the halszkaraptorines which are absent in the herbivorous/omnivorous maniraptoriforms, and fails to explain the similarities between *Halszkaraptor*, semiaquatic birds and piscivorous reptiles.

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Figure 1

Comparison between the skull of the therizinosaurid *Erlikosaurus andrewsi* (A, C) and the paravian *Halszkaraptor escuilliei* (B, D), in left lateral (A, B) and dorsal (C, D) views.

Key differences in snout morphology: prenarial part of premaxilla taller than long (a1) or longer than tall (a2); platyrostral condition produced by perinarial widening (a1) or prenarial flattening (a2); complete loss of premaxillary dentition (c1) or supranumerary premaxillary dentition (c2); maxillary dentition lacking replacement waves (d1), or bearing distinct replacement waves (d2); narial fossa widely overlapping premaxillary oral margin (e1) or narial fossa not overlapping premaxillary oral margin. Scale bars in mm. Figures A and C provided by S. Lautenschlager (used with permission); figures B and D modified from Cau et al. (2017).

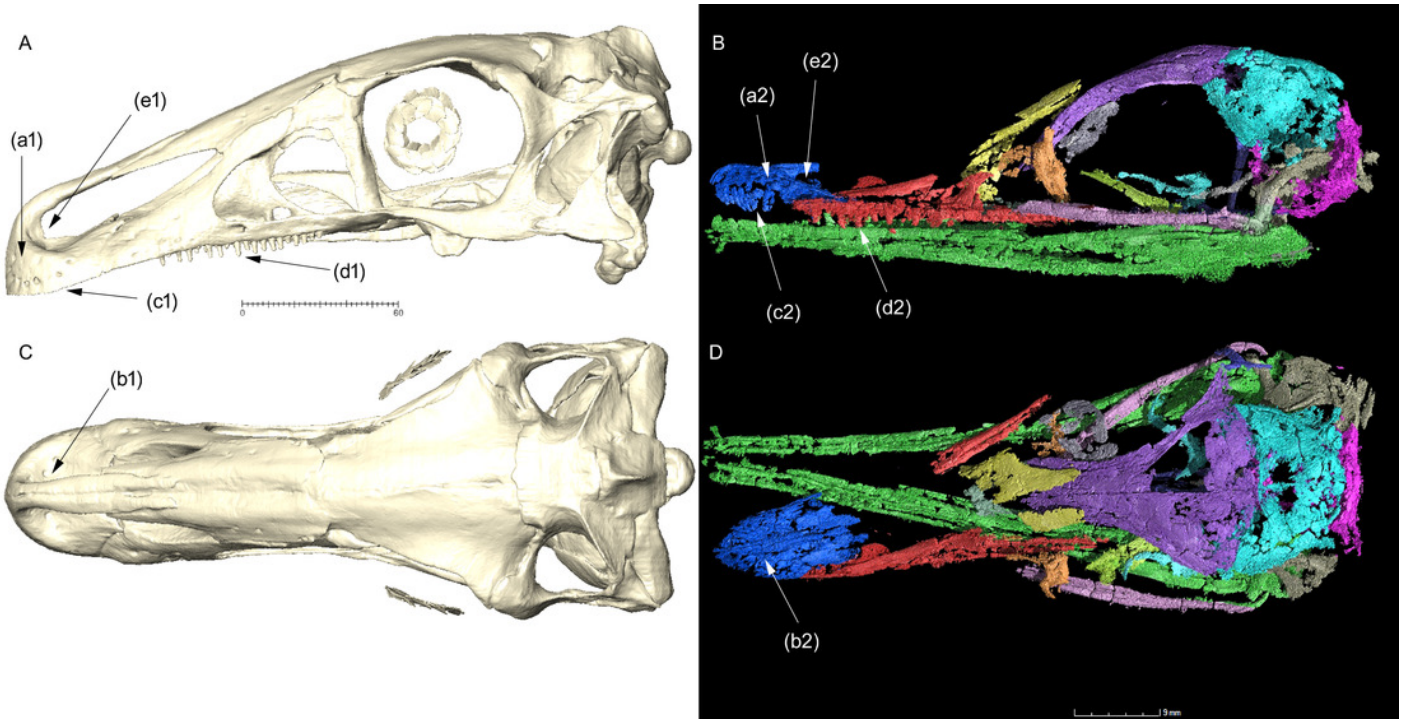


Figure 2

Development of the premaxillary neurovascular plexus in some archosaurs.

Semitransparent rendering of premaxilla of *Erlikosaurus andrewsi* (A, B) in lateral (A) and dorsal (B) views. Semitransparent rendering of premaxillae of *Halszkaraptor escuilliei* (C, D) in lateral (C) and dorsal (D) views. Semitransparent rendering of anterior end of snout in *Crocodylus sp.* (E), *Halszkaraptor escuilliei* (F) and *Erlikosaurus andrewsi* (G) in dorsal view. Semitransparent rendering of snout in cf. *Spinosaurus aegyptiacus* (H, I) in lateral (H) and dorsal (I) views. Figures in (A-D) and (E-I) rescaled at same width for comparison. In red, rendering of the neurovascular plexus. Arrows in E-I indicate the level of the anterior margin of the external naris. Figures A, B and G modified from images provided by S. Lautenschlager (used with permission). Figures C-F modified from Cau et al. (2017). Figures H, I modified from images provided by D. Iurino (used with permission). Abbreviations: en, external naris; nps, basal stem of the neurovascular plexus; pnr, prenarial part of premaxilla.

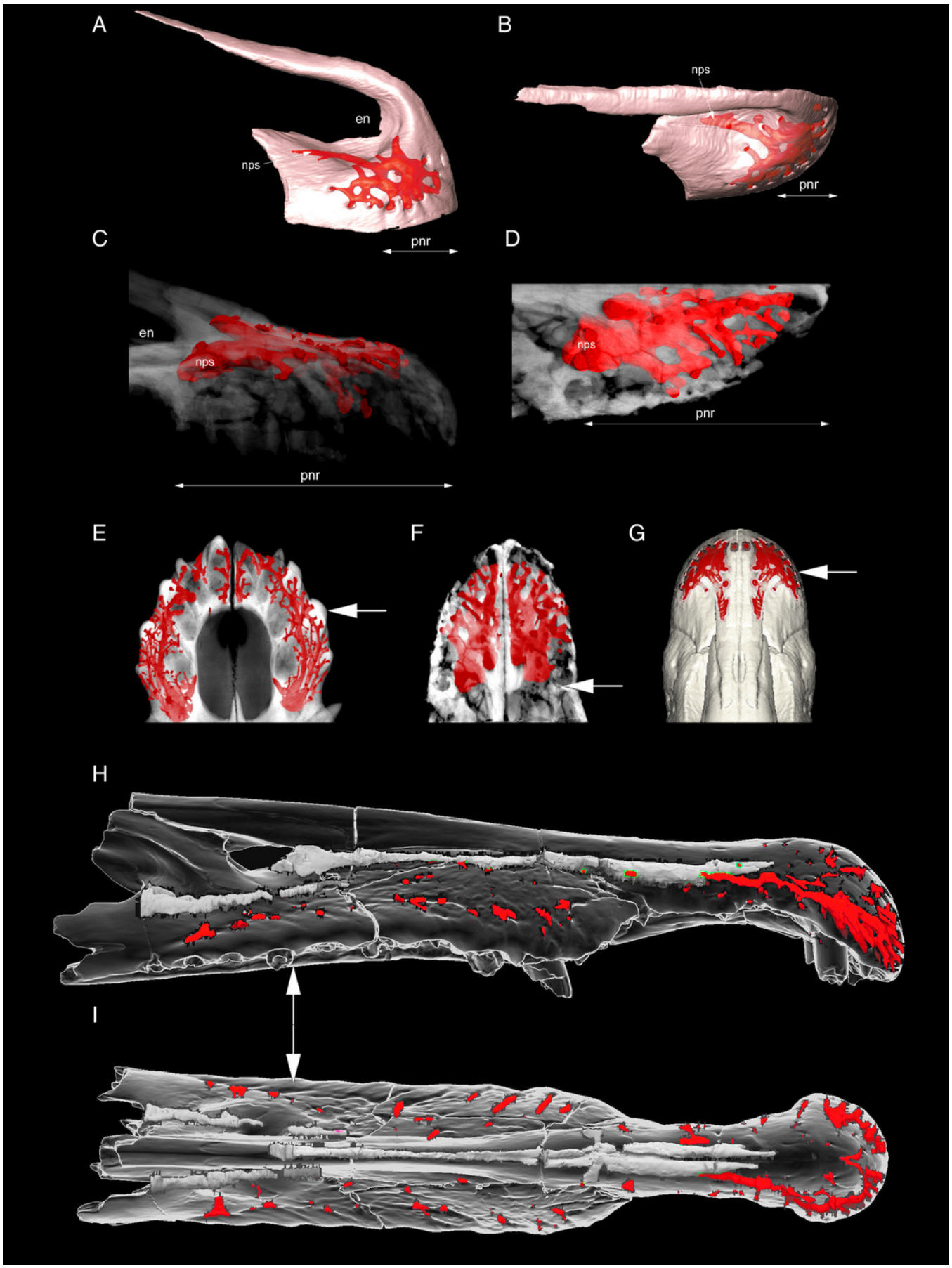

A
en
nps
pnr
B
nps
pnr
C
en
nps
pnr
D
nps
pnr
E
F
G
H
I

Figure 3

Premaxillae and maxillae of *H. escuilliei* MPC D-102/109 in right lateral view.

In A, the different bones are colored to help the identification of the distinct elements forming the rostrum. Note that the majority of the right maxilla is lost (light blue), revealing most of the left maxilla (pink) in medial view (in his figure 1, Brownstein, 2019, misinterpreted the preservation of the maxillae and depicted most of the lateral surface of the right maxilla based on the medial side of the left one). In B, semi-transparent reconstruction of the same elements, showing the tooth roots and the “festooning” pattern in tooth size variation. Scale bar in mm. Abbreviations: lmx, left maxilla; lpmx, left premaxilla; m1-2, first and second maxillary tooth; pdl, paradental lamina; rmx, right maxilla; rpmx, right premaxilla.

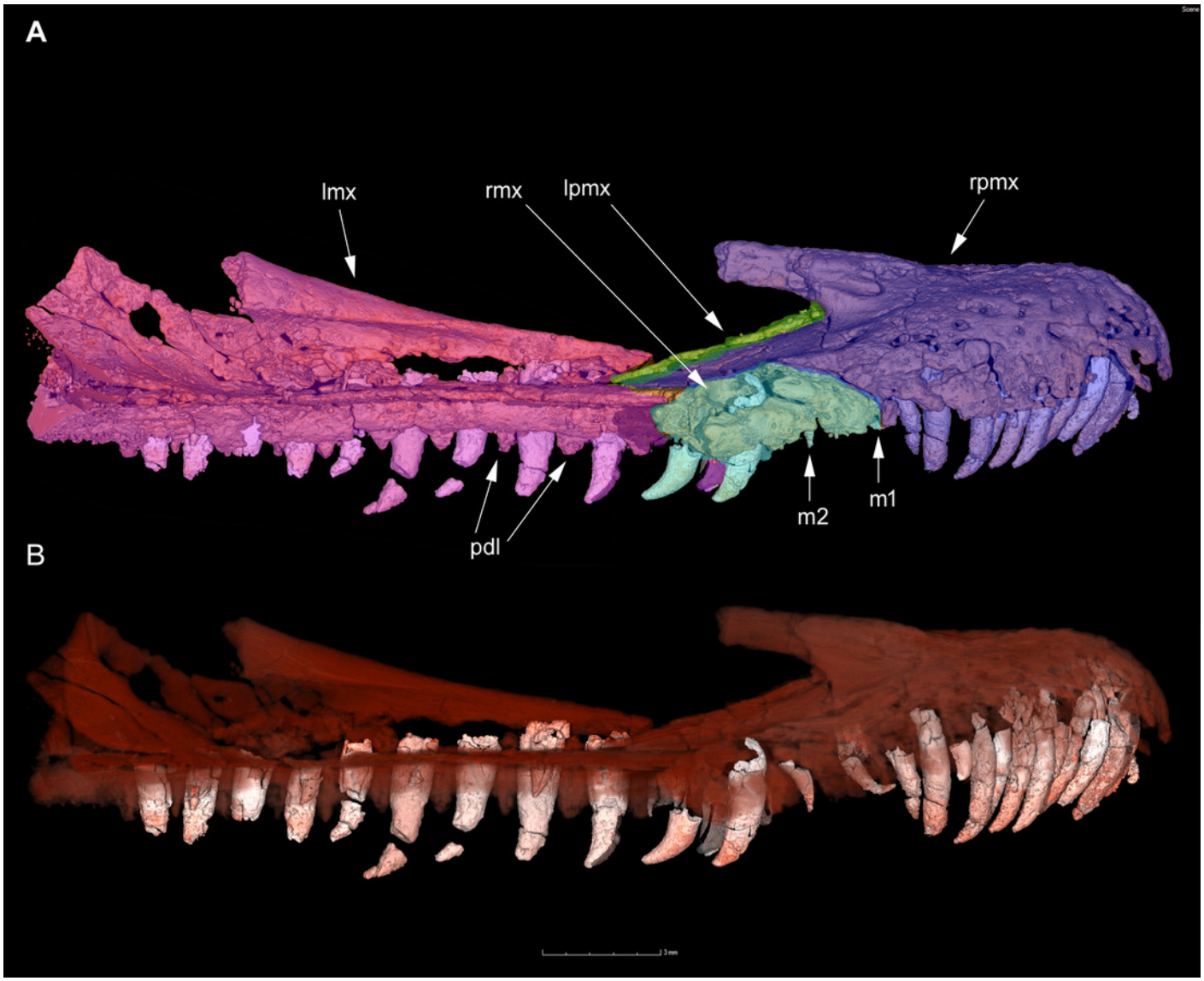
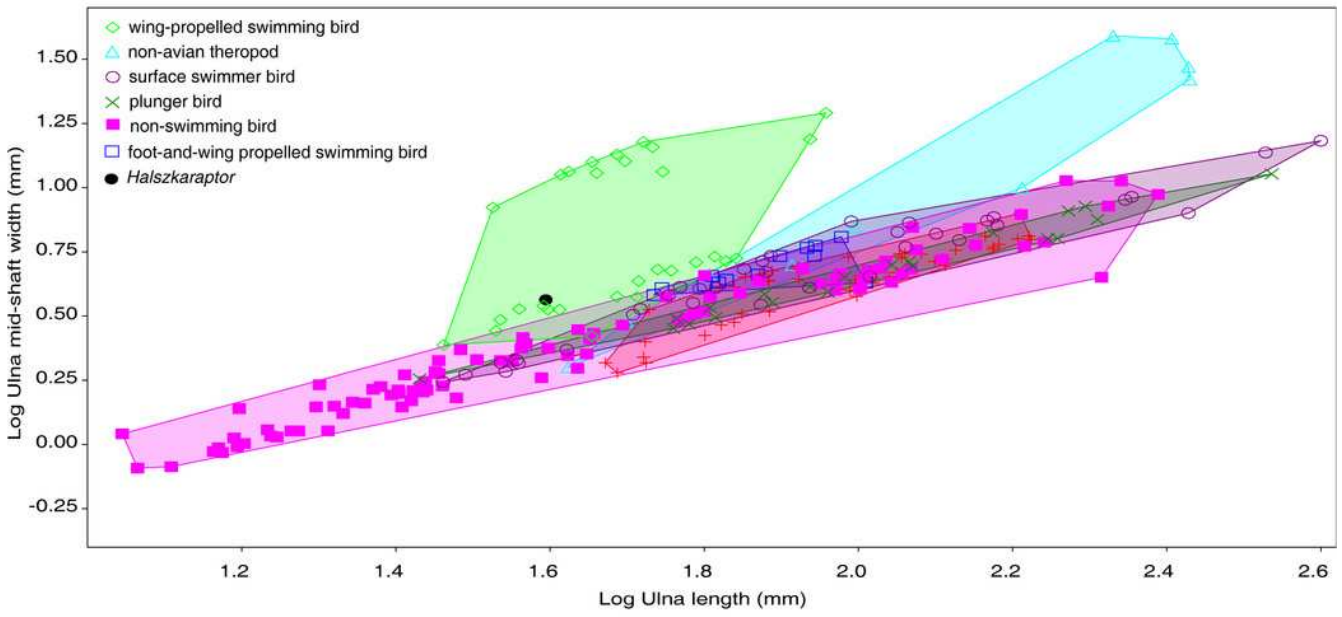

A
lmx
rmx
lpmx
rpmx
m2
m1
pdl
B

Figure 4

Plot of ulna mid-shaft width relative to ulnar length in theropods.

A, full sample. B, same sample but reduced to non-avian theropods and wing-propelled birds. Data in Supplementary Files.

A



B

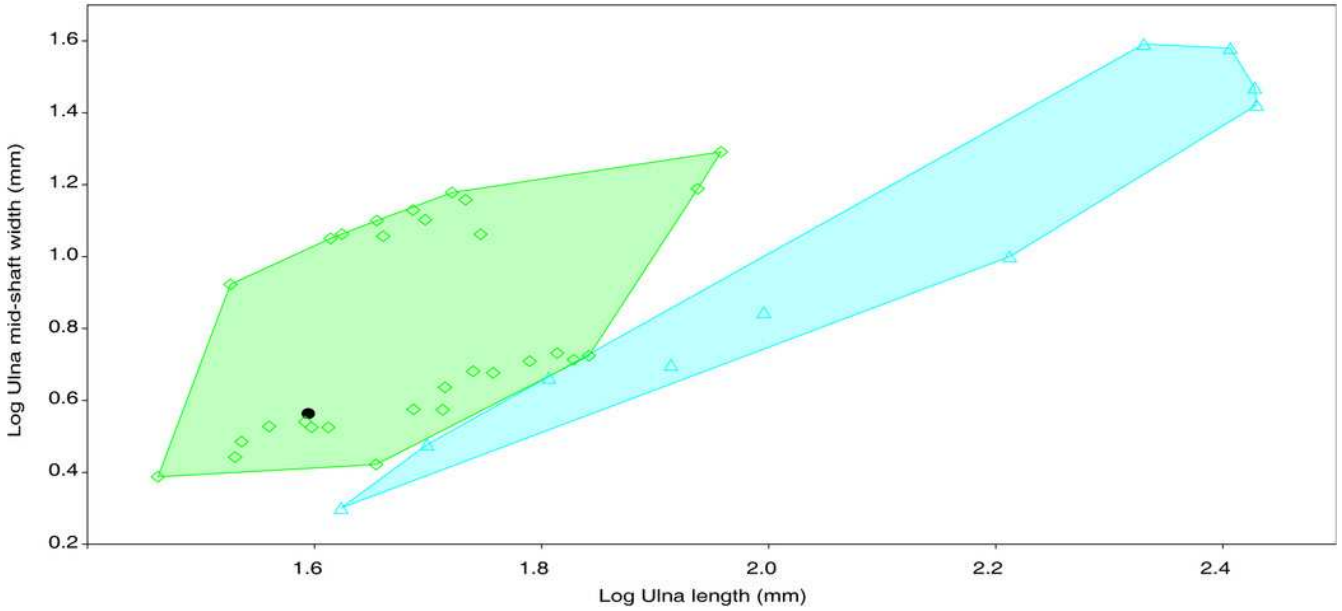
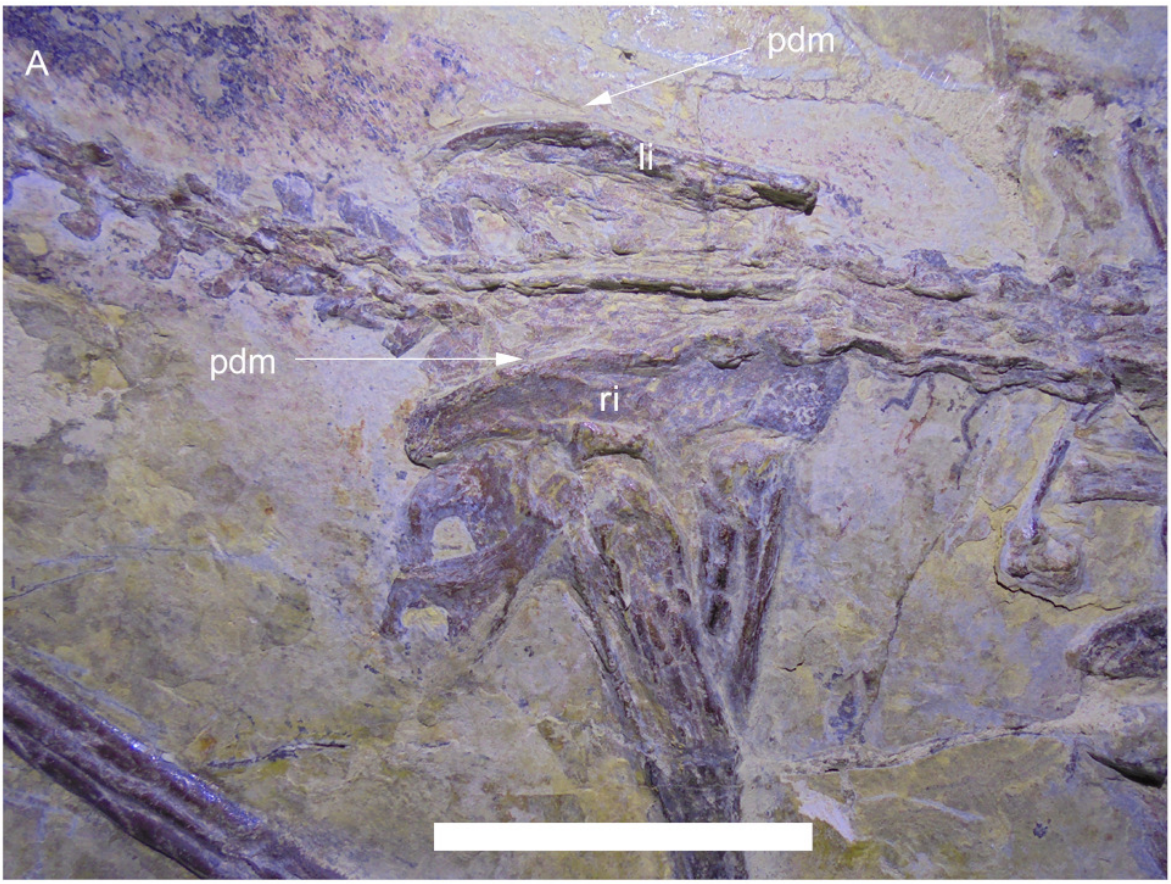


Figure 5

Development of the supratrochanteric process in the paravian theropods *Aurornis xui* YFGP-T5198 and *Halszkaraptor escuilliei* MPC D-102/109.

A, pelvic region of the anchiornithid *Aurornis* in lateral view. Note that the left ilium is exposed dorsally, showing the thickness of the dorsal margin of the bone. B, pelvic region of *H. escuilliei*, in dorsomedial view. Note the prominent supratrochanteric process which overhangs the lateral surface of the ilium. Scale bars = 30 mm. Abbreviations: li, left ilium; pdm, posterodorsal margin; ri, right ilium.


A
pdm
li
pdm
ri


B
pdm
li

Figure 6

Pedal ungual II size among paravians.

Plot of pedal ungual II length relative to femur length dismisses Brownstein's (2019) claim that *Halszkaraptor*'s ungual is reduced compared to other dromaeosaurids. Data in Supplementary Files.

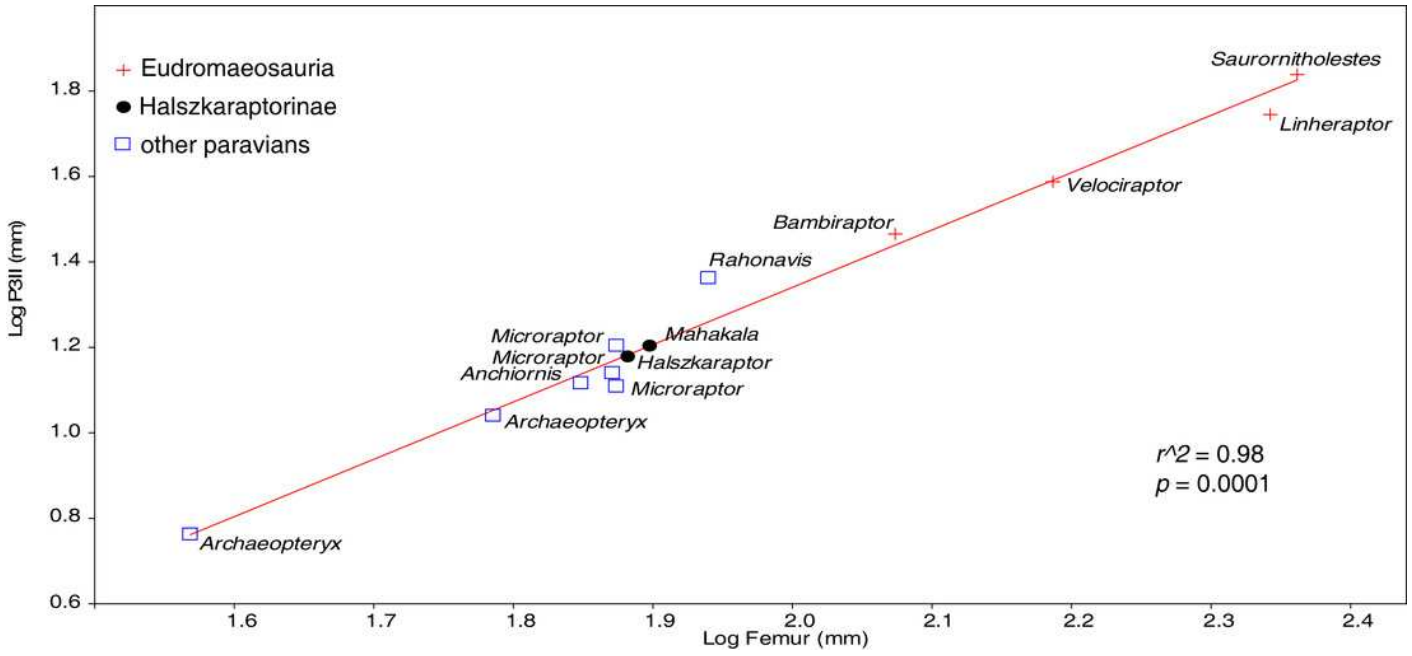


Figure 7

Phylogeny of the tetanuran theropods focusing on maniraptoriforms.

Agreement subtree of 50.000 shortest trees reconstructed by the phylogenetic analysis, used as framework for character state transition optimization. Numbers at branches indicate the morphological features listed in Table 1.

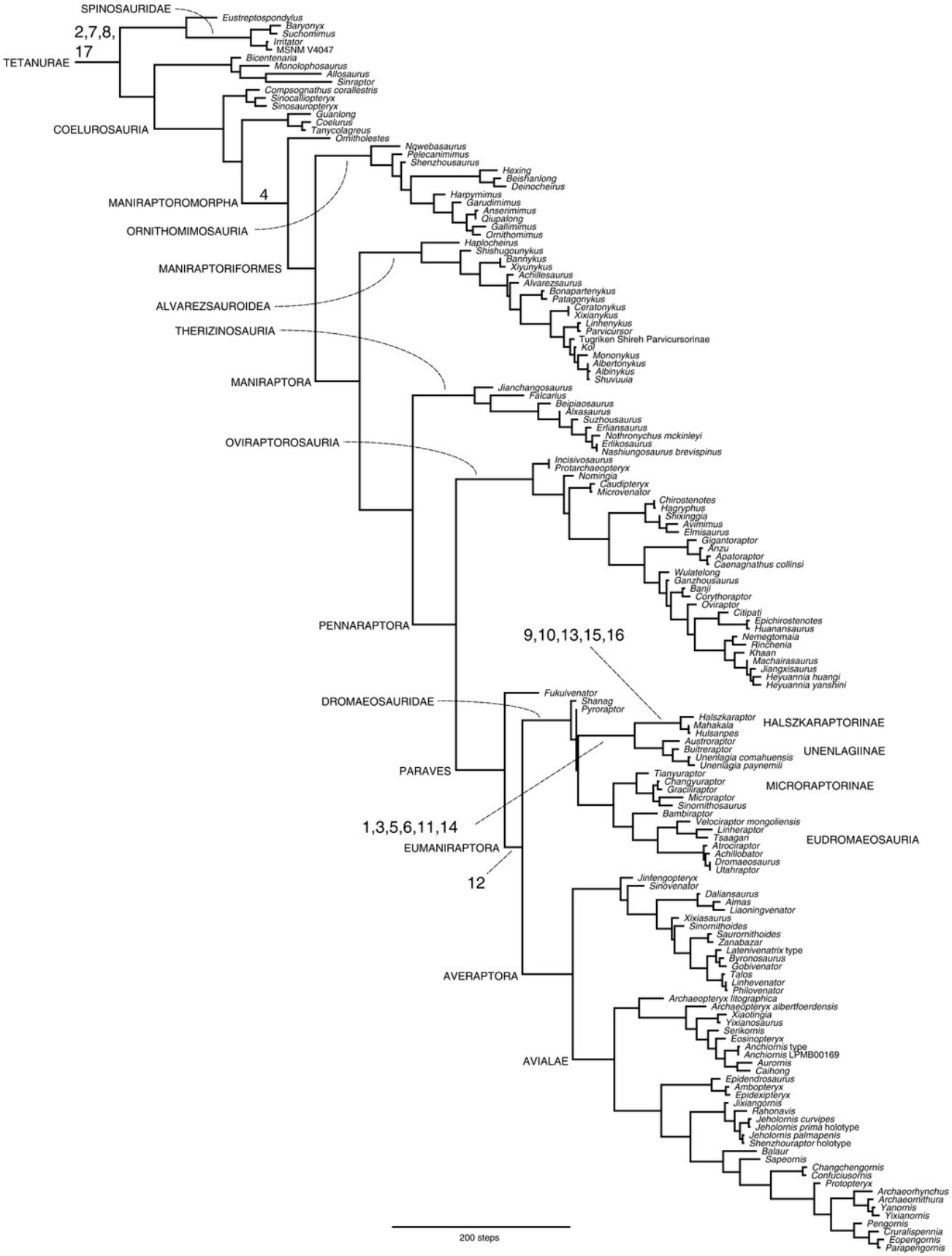
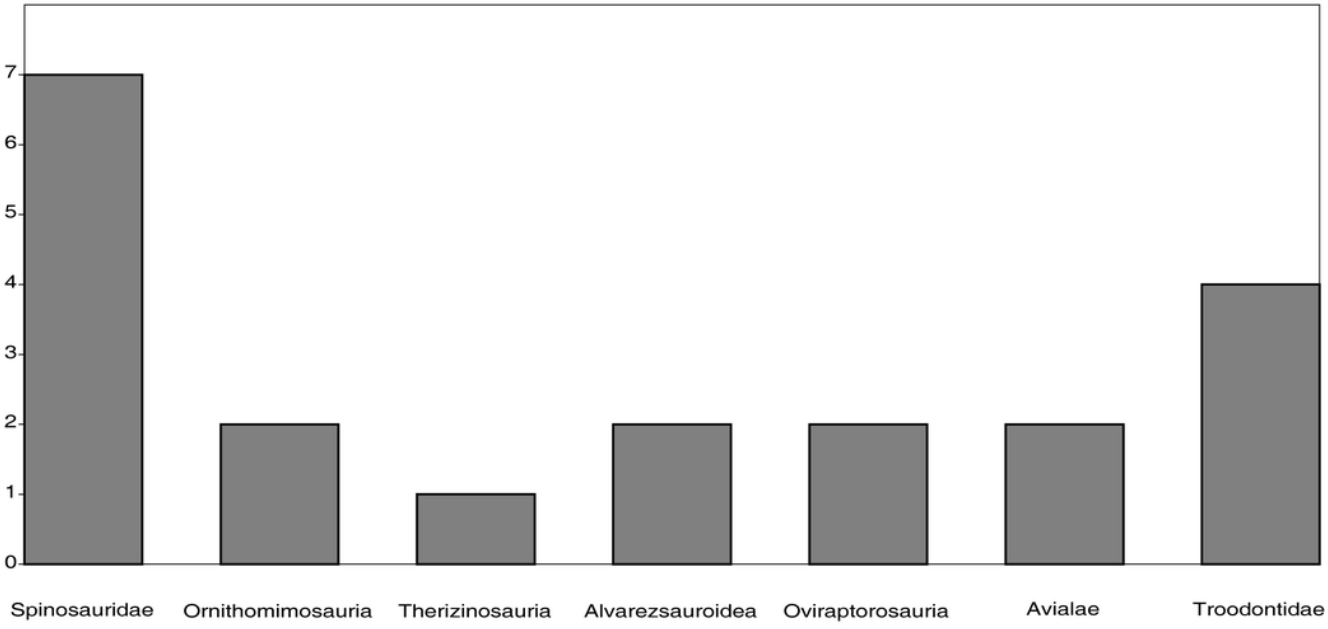

SPINOSAURIDAE
Eustreptospondylus
2,7,8,
17
Baryonyx
Suchomimus
Irritator
MSNM V4047
TETANURAE
Bicentenaria
Monolophosaurus
Allosaurus
Sinraptor
Compsognathus corallestris
Sinocalliopteryx
Sinosauropteryx
Guanlong
Coelurus
Tanycolagreus
COELUROSAURIA
Ornitholestes
Nqwebasaurus
Pelecanimimus
Shenzhousaurus
Hexing
Beishanlong
Deinocheirus
MANIRAPTOROMORPHA
4
Harpymimus
Garudimimus
Anserimimus
Qiupalong
Gallimimus
Ornithomimus
ORNITHOMIMOSAURIA
Haplocheirus
Shishugounykus
Bannykus
Xiyunykus
MANIRAPTORIFORMES
Achillesaurus
Alvarezsaurus
Bonapartenykus
Patagonykus
ALVAREZSAUROIDEA
Ceratonykus
Xixianykus
Linhenykus
Parvicursor
THERIZINOSAURIA
Tugriken Shireh Parvicursorinae
Kol
Mononykus
Albertonykus
Albinykus
Shuvuuia
MANIRAPTORA
Jianchangosaurus
Falcarius
Beipiaosaurus
Alxasaurus
Suzhousaurus
Erliansaurus
Nothronychus mckinleyi
Erlikosaurus
OVIRAPTOROSAURIA
Nashiungosaurus brevispinus
Incisivosaurus
Protarchaeopteryx
Nomingia
Caudipteryx
Microvenator
Chirostenotes
Hagryphus
Shixinggia
Avimimus
Elmisaurus
Gigantoraptor
Anzu
Apatoraptor
Caenagnathus collinsi
Wulatelong
Ganzhousaurus
Banji
Corythoraptor
Oviraptor
Citipati
Epichirostenotes
Huanansaurus
Nemegtomaia
Rinchenia
Khaan
Machairasaurus
Jiangxisaurus
Heyuannia huangi
Heyuannia yanshini
PENNARAPTORA
9,10,13,15,16
DROMAEOSAURIDAE
Fukuivenator
Shanag
Pyroraptor
Halszkaraptor
Mahakala
Hulsanpes
HALSZKARAPTORINAE
Austroraptor
Buitreraptor
Unenlagia comahuensis
UNENLAGIINAE
Unenlagia paynemili
PARAVES
Tianyuraptor
Changyuraptor
Graciliraptor
MICRORAPTORINAE
Microraptor
Sinornithosaurus
Bambiraptor
1,3,5,6,11,14
Velociraptor mongoliensis
Linheraptor
Tsaagan
EUDROMAEOSAURIA
EUMANIRAPTORA
Atrociraptor
Achillobator
Dromaeosaurus
Utahraptor
12
Jinfengopteryx
Sinovenator
Daliansaurus
Almas
Liaoningvenator
Xixiasaurus
Sinornithoides
Sauornithoides
Zanabazar
Latenivenatrix type
Byronosaurus
Gobivenator
Talos
Linhevenator
Philovenator
AVERAPTORA
Archaeopteryx litographica
Archaeopteryx albertfoerdensis
Xiaotingia
Yixianosaurus
Serikornis
Eosinopteryx
Anchiornis type
Anchiornis LPMB00169
Aurornis
Caihong
AVIALAE
Epidendrosaurus
Ambopteryx
Epidexipteryx
Jixiangornis
Rahonavis
Jeholornis curvipes
Jeholornis prima holotype
Jeholornis palmapenis
Shenzhouraptor holotype
Balaur
Sapeornis
Changchengornis
Confuciusornis
Protopteryx
Archaeorhynchus
Archaeornithura
Yanornis
Yixianornis
Pengornis
Cruralispennia
Eopengornis
Parapengornis
200 steps

Figure 8

Comparison between the halszkaraptorine body plan and other theropod clades.

A, number of halszkaraptorine novelties convergently acquired by non-dromaeosaurid lineages. B, anagenetic distance (in steps) from the paravian node based on the minimum branch length of the agreement subtree in Figure 7. Note that spinosaurids acquired the largest number of similarities with halszkaraptorines, and that halszkaraptorine divergence from the ancestral dromaeosaurid body plan is comparable to those of other clades.

A


7
6
5
4
3
2
1
0
Spinosauridae
Ornithomimosauria
Therizinosauria
Alvarezsauroidea
Oviraptorosauria
Avialae
Troodontidae

B

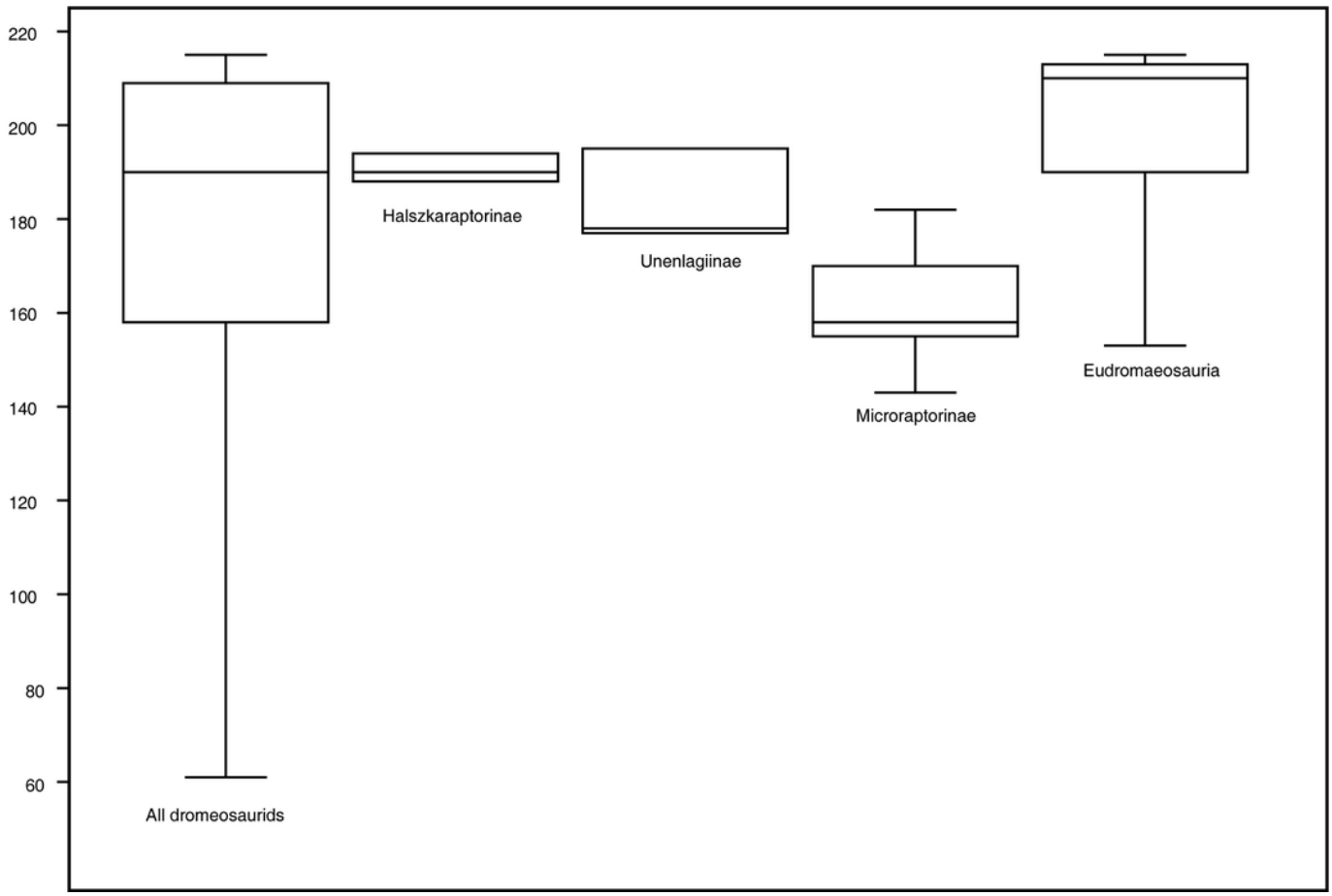

220
200
180
160
140
120
100
80
60
All dromeosaurids
Halszkaraptorinae
Unenlagiinae
Microraptorinae
Eudromaeosauria

Table 1(on next page)

Phylogenetic status of 17 key features of *Halszkaraptor*.

Nodal optimisation of the morphological features of *Halszkaraptor* body plan, based on the agreement subtree topology. Character numeration refers to the character list of the phylogenetic analysis, with described state indicated by number in brackets. Ambiguously optimized state changes based on accelerated transformation (marked by *). “Novelty” means that the character state in *H. escuilliei* is optimized as evolving among Halskzaraptorinae or at most among “Halszkaraptorinae + Unenlagiinae” under accelerated transformation optimisation.

1

Character statement and Homoplasy Index (hi)	**# char.**	**Nodes**	**Status in *Halszkaraptor***
1) Premaxillae fusion; hi = 0.833.	11(1)	"Halszkaraptorinae + Unenlagiinae"*. Pygostylia. Oviraptoroidea.	Novelty. Convergent with pygostylians, oviraptoroids and spinosaurids.
2) Premaxillary narial margin placed posterior to mid-lenght of premaxillary oral margin; hi = 0.941.	27(1)	Averostra. Lost in: "Microraptorinae + Eudromaeosauria"*, Troodontidae, among jeholornithids, among ornithomimosaurs, in Allosauroidea, in Tyrannosauroidea.	Averostran plesiomorphy. Note that *Halszkaraptor* shows a novel state: the narial margin placed more posterior then the whole premaxillary body (convergent with avialans and spinosaurids).
3) Number of premaxillary teeh >4; hi = 0.8.	14(1)	"Halszkaraptorinae + Unenlagiinae"*. Ornithomimosauria*. Spinosauridae.	Novelty. Convergent with basal ornithomimosaurs and spinosaurids.
4) Premaxillary teeth unserrated; hi = 0.875.	15(1)	Maniraptoromorpha. Lost in some troodontids, and in "Eudromaeosauria + Microraptorinae". Re-gained in some microraptorines.	Maniraptoriform symplesiomorphy. Convergent with spinosaurines.
5) Lateral teeth unserrated; hi = 0.917.	159(1)	Alvarezsauroids more derived than *Haplocheirus**. Pannaraptora*. Lost at Dromaeosauridae root*. Re-gained in "Halszkaraptorinae + Unenlagiinae". Homoplastic in Troodontidae. Spinosaurinae.	Novelty. Convergent with non-dromaeosaurid pennaraptorans and spinosaurines.
6) >20 maxillary teeth; hi = 0.9.	34(1)	Maniraptoriformes. Lost in Pennaraptora. Re-gained in "Halszkaraptorinae + Unenlagiinae". Re-gained in "Sinovenatorinae + Troodontinae". Baryonychinae*.	Novelty. Convergent with non-pennaraptoran maniraptoriforms and baryonychines.
7) Premaxillary teeth incisiviform; hi = 0.917.	16(1)	Averostra*. Lost in Alvarezsauroidea*, Averaptora and Oviraptoroidea*. Homoplastic in Eudromaeosauria and Troodontidae.	Averostran symplesiomorphy.
8) Lateral teeth labiolingually compressed; hi = 0.875.	599(0)	Theropoda. Lost in Spinosauridae.	Theropod plesiomorphy.
9) Cervical vertebrae elongate (centrum more than twice longer than deep); hi = 0.875.	222(1)	Halszkaraptorinae*. *Fukuivenator*. "Caudipterydae + Oviraptoroidea"*. Lost in heyuannines*. *Falcarius*. "Deinocheiridae + Ornithomimidae". Spinosauridae.	Novelty. Highly homoplastic among other maniraptoriforms. Convergent with spinosaurids.

10) Horizontally-oriented caudal zygapophyses; hi = 0.	1726(1)	Halszkaraptorinae	Novelty.
11) Prominent caudal prezygocostal laminae; hi = 0.857.	626(1)	Neotetanurae. Lost in derived ornithomimosaurs, some alvarezsauroids, oviraptorids, and in Eumaniraptora. Re-gained in "Halszkaraptorinae + Unenlagiinae".	Novelty. Homoplastic among other maniraptoriforms.
12) Robust metacarpal III; hi = 0.95.	322(0)	Eumaniraptora*. Lost in "Microraptoria + Eudromaeosauria"*. Homoplastic among microraptorines. Lost in "*Balaur* + Pygostylia" Lost among Anchiornithinae. Derived therizinosaurids.	Eumaniraptoran symplesiomorphy.
13) Elongate manual phalanx p1-III; hi = 0.933.	292(0)	Lost in Tetanurae*. Re-gained in Microraptoria*, Halszkaraptorinae*, Scansoriopterygidae and Pengornithidae*.	Novelty. Convergent with some paravian lineages.
14) Shelf-like iliac supratrochanteric process; hi = 0.5.	1773(1)	"Halszkaraptorinae + Unenlagiinae"*, lost in *Unenlagia*.	Novelty.
15) Elongate posterolateral crest on femur; hi = 0.75.	693(1)	Ceratonykini*. Halszkaraptorinae. Late-diverging troodontids*.	Novelty. Convergent with a few maniraptorans.
16) Markedly convex extensor surface of metatarsal III; hi = 0.5.	1616(1)	Halszkaraptorinae. *Balaur*.	Novelty.
17) Unconstricted proximal end of metatarsal III; hi = 0.941.	483(0)	Theropod plesiomorphy. Homoplastically lost among alvarezsauroids. Homoplastic in Oviraptorosauria. Lost in Ornithomimidae, Microraptorinae, Unenlagiinae and Troodontidae.	Theropod plesiomorphy.

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