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A reassessment on *Luchibang xingzhe*: A still valid istiodactylid pterosaur within a chimera

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ABSTRACT

Recently a new genus and species of istiodactylid pterosaur was named by Hone et al. (2020) based on a very complete skeleton from northern China. Although the possibility that the specimen was a chimera was raised by the authors themselves, checks of the specimen revealed no tampering with the specimen and it was considered genuine. The animal was posited as an unusual member of the clade, but characters from both the head and body supported the general identification as an istiodactylid. However, recent damage to the specimen because of flooding in the museum in which it is housed, has revealed that the rostrum and mandible were in fact added to the back of the skull and rest of the body of a second pterosaur. Here we correct the record on this specimen and suggest that *Luchibang xingzhe* as a taxon is still valid.

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INTRODUCTION

Fossil forgeries are a longstanding issue in Chinese collections (Stone, 2010), although this is neither a modern problem in palaeontology (e.g., see Romano and Pignatti 2021; Rossi et al., 2024) or one limited to China (e.g., Grimaldi et al., 1994; Scheyer et al., 2023). Forgeries by fossil collectors or dealers are created to improve the apparent quality of the material and so increase their value. Many of these are very crude and easy to detect (e.g., see Zipfel et al., 2010) and have been identified and not entered the scientific literature (Rowe et al., 2001), though others more sophisticated and have been described before their later discovery as being composites (Selden et al., 2019). Pterosaurs are among the taxa that have been suggested to be composites, with several specimens from Brazil suspected of being made of multiple constituent animals (e.g., Bennett, 1989; Dalla Vecchia et al., 2014; Cerqueira et al., 2021). It should though be noted that chimeric specimens can contain important scientific material (e.g., 'Archaeoraptor' Zhou et al., 2002) and some have only very minor additions or changes to them (e.g., the rostrum of the holotype of *Microraptor gui* Xu et al., 2003).

Recently, Hone et al. (2020) described and named a new large and complete skeleton of a Chinese istiodactylid, *Luchibang xingzhe* (ELDM 1000), that was purchased from a dealer. Istiodactylids are an unusual group of toothed pterodactyloid pterosaurs characterized by long snouts bearing triangular interdigitating teeth and a large nasoantobrital fenestra (Witton, 2013, p. 148). Numerous istiodactylids have been described from the Jiufotang Cretaceous fossil beds in northeastern China (e.g., Lü et al., 2008; Wang et al., 2008; Zhou et al., 2019) and they are far more common in this region than from other sites.

In the original publication, the possibility was raised that the specimen had been tampered with and was a chimera, but no evidence of manipulation or alterations could be found (Hone et al., 2020, S2). This included examination of the edges and underside of the slab where possible, the presence of bones overlapping with one another between the cranium and various parts of the postcranium. Even some preparation of key areas of the specimen showed no apparent modifications (Hone et al., 2020, S2). The only issue was a mismatch in some of the postcranial anatomy to that of typical istiodactylids (see also Ozeki et al., 2023), although again this had been considered in the original paper and the discussion and analyses therein (Hone et al., 2020).

However, recent damage to the specimen has in fact revealed that the specimen has indeed been altered before it reached the Erlianhaote Dinosaur Museum, and that the specimen is a composite of two separate pterosaur fossils (Figure 1). Here we correct the record on the original specimen and the interpretations that come from this as presented by Hone et al. (2020). As we hold that the original description of the specimen remains an accurate reflection of the slab, and that the taxon *Luchibang xingzhe* remains valid (if restricted to the rostrum) and given the minimal impact on the scientific literature so far of the original paper, we have elected not to retract the original manuscript, but instead to offer this correction.

Institutional Abbreviations

ELDM, Erlianhaote Dinosaur Museum, Erlianhaote, Inner Mongolia, China.

DISCUSSION

Modification to the Specimen

ELDM 1000 was recently on loan to the Inner Mongolia Museum of Natural History and part of the storage facility of the museum was unfortunately flooded and the specimen was submerged in water. The specimen was notably damaged as a result of this incident although there has been some small erosion to the surface of the bones and teeth of the anterior part of the skull. Importantly, the flooding has revealed that there are different matrices between the anterior part of the jaws (hereafter, part A of ELDM 1000) and the back of the skull and the postcranial skeleton (hereafter, part B of ELMD 1000), which strongly suggest this specimen is a chimera (Figure 1). Between the bones of parts A and B, there are four pieces of bones (forming the posterior part of the cranium and mandible), which are clearly not from part A and may, or may not, be from part B (Figure 2).

Evidence of coarse sands (not added by the flood) can be found surrounding the skeleton, which were not present in the shales that are with ELDM 1000A. This naturally suggests that the sands were added artificially and that most of the original matrix was removed during initial preparation before the specimen originally reached the museum. The sands were most likely glued to part A because they have been retained after the water damage from the flooding, and all the matrix of part A covering the mixed layer was lost.

We think that parts A (and the possible a third section between A and B) were prepared nearly

FIGURE 1. The specimen ELDM 1000 as shown in (left) Hone et al. (2020, their figure 1) and in its current state (right) showing the joint between the rostrum and the rest of the skeleton. The area around the rostrum is highlighted in green and the parts of the back of the skull that may also be problematic are in yellow. Scale bar is 10 cm.

free of matrix and added into a major part of B. The specimen was then covered with glue and sand to hold it together. This layer was then covered with a stabilizing piece of plasterboard and then the entire specimen was turned and prepared down from the reverse side. As a result, A appears to be in the same matrix as B and there was no join visible.

In the original paper, Hone et al. (2020 S2) discussed the consistency of the specimen and the assessment of its integrity saying "examination and preparation in three distinct locations (between the scapula and mandible, between the right ramus of the mandible and 6th cervical, and finally in the space between the left ramus of the mandible, maxilla and seventh cervical vertebra) by DWEH and an independent observer revealed no evidence of tampering. There was no undercutting of the matrix, no glue or consolidants, and the matrix was entirely consistent in these areas and reached the bone naturally. Between the mandible, maxilla, and 7th cervical, the matrix was removed and revealed bone-to-bone contact between each element". Despite this work and the attention given to the fossil, this was clearly insufficient to detect the changes made to the specimen.

The specimen was recently highlighted by Ozeki et al. (2023) as being potentially a chimera with the skull being separate from the postcranium. Notably, however, the join between ELDM 1000A and B is not as suggested by Ozeki et al. (2023), but actually is at the posterior part of the nasoantorbital fenestra. Even where the specimen was suggested to be a composite, this was so well concealed that the join was no in the place suggested.

Papers on determining if fossils are genuine advocate close examination of the material as a major step in such assessments (Mateus et al., 2008). Other suggested methods to assess specimens for fakes (e.g., CT Scanning, Rowe et al., 2016, UV light and chemical analysis Mateus et al., 2008) are not always practical and in the case of ELDM 1000 for example, the original slab is both large and fragile. Our own observations with UV light and photography have shown specimens from

FIGURE 2. Close up of the join between the sections of ELDM 1000 and showing the rostrum of what remains as *Luchibang xingzhe*. Scale bar is 10 cm.

Liaoning that we know to be genuine can give odd UV reflectance patterns and appear to have been treated or manipulated when they have not.

Taxonomic Identity

The original diagnosis for the taxon was as an "[i]stiodactyloid pterosaur that can be distinguished from others in the group by two unique characters: a large, rectangular sternum with a straight posterior edge, and a long femur that is more than 80% of the length of the ulna. It can be further distinguished from other istiodactylids by the following combination of characters: rostrum with no dorsal expansion anteriorly; very well-spaced teeth in the posterior part of the jaw; a dentary symphysis that is more than four times longer than wide in dorsal view; long and narrow mandibular rami (approximately 20 times longer than wide in dorsal view)" (Hone et al., 2020).

Clearly the two given autapomorphies relate to the postcranium and are now irrelevant as this is from a separate specimen, and indeed potentially not an istiodactylid (see below). However, the combination of traits given in the diagnosis in order to diagnose this animal as being unique all refer to the upper and lower jaws which form a single unique part. As such, we suggest that the name *Luchibang xingzhe* would still be valid, if restricted to a very limited specimen (i.e., ELDM 1000A as shown here in Figure 1). The character of the mandibular rami being 20 times longer than wide in dorsal view becomes problematic as their exact length is not known, although the fact that these are "long and narrow" is clearly still correct since as preserved the rami are still at least 13 times longer than wide.

Other Chinese istiodactylids have been named from similarly limited material (e.g., *Liaoxipterus*, Dong and Lü, 2005) and characters of the jaws and teeth have been important components of defining genera and species in this clade in general (e.g., *Hongshanopterus*, Wang et al., 2008; *Mimodactylus*, Kellner et al., 2019). More recently named taxa such as *Lingyuanopterus* (Xu et al., 2022) show comparisons and diagnoses that would continue to separate *Luchibang* from them and keep it as a valid taxon. As such, despite the limited material here, we suggest that traits are therefore sufficient to diagnose a distinct taxon. *Luchibang xingzhe* would be retained as a valid name, though referring now only to this section of ELDM 1000 (see also Ozeki et al., 2023 who took a similar position treating the skull as a separate and potentially valid unit).

Luchibang xingzhe Hone et al., 2020

Holotype. Rostrum and anterior mandible of ELDM 1000

Revised Diagnosis. Distinguished from other istiodactylids by the following combination of characters: rostrum with no dorsal expansion anteriorly; very well–spaced teeth in the posterior part of the jaw; a dentary symphysis that is more than four times longer than wide in dorsal view; long and narrow mandibular rami (approximately 20 times longer than wide in dorsal view.

Other material. Ozeki et al. (2023) suggest that the postcranial material belongs to the tapejaroid *Sinopterus* or a closely related taxon based on proportional similarities to *Sinopterus*. We agree that this postcranial material represents a tapejaroid, and it does share one feature with *Sinopterus* and other tapejaromorphs to the exclusion of other pterosaurs: a broad tubercle along the coracoid's ventroposterior margin [124(1)]. However, it also possesses several features differing from *Sinopterus* and aligned with those seen in Azhdarchomorpha (all taxa more closely related to the azhdarchids than tapejarids; see Pêgas et al., 2022): a deep flange present on the anteroventral surface of the coracoid [123(1)]; humerus is less than 80% the length of the femur [127(0)]. It does also lack a key feature of the rest of Azhdarchomorpha: mid-cervical vertebrae longer than three times their width [109(2,3)] (as opposed to [109(1)] of this postcranial material, in which the mid-cervicals are longer than wide but their length is not greater than three times their width). Thus, we consider the postcrania to represent an indeterminate member of Azhdarchomorpha.

Locality Information

The locality information for the specimen as hailing from the Yixian Formation in Nei Mongol, northern China was provided with the original material. In the light of the chimeric nature of the specimen, this does further raise issues about the likely origins of both A and B parts. It is impossible to determine the locality and horizon based on the available matrix (some of which has itself been altered). The main part B (potentially an azhdarchomorph pterosaur) is represented by chaoyangopterids in the Jehol Biota. All the known chaoyangopterid specimens were from the Jiufotang Formation (Wang et al., 2023). Istiodactylids are almost from the Jiufotang Formation, except for *Luchibang*, only one reliable individual out of dozens of specimens was reported from the Yixian Formation (Ozeki et al., 2023). Hence, we must be cautious about the original information of the locality and horizon of the holotype, although it remains likely that is it from the Jehol Group of western Liaoning.

Clades

Although Hone et al. (2020) did run separate phylogenetic analyses with just the cranial and postcranial material included, this does not match the split we now know to be present in ELDM 1000. As a result, we took the original analysis and split off the characters from only the rostrum rather than the whole skull and repeated our analysis. The topology recovered here (excluding *Luchibang* and the postcranial material) is almost identical to that recovered in Hone et al., (2020). *Luchibang* is recovered in a polytomy with *Nurhachius ignaciobritoi* and a clade consisting of *Liaoxipterus brachyognathus* and *Istiodactylus* (in Hone et al., 2020, *Luchibang* is recovered as closer to the latter clade than to *N. ignaciobritoi*; this is the case also in Ozeki et al., 2023). The separate postcranial OTU (with a few differences in the coding from the prior iteration, see Supplementary Information) is recovered here as a tapejaroid. The only tapejaroid postcranial synapomorphy (and the only tapejaroid synapomorphy found in the postcranial OTU) is [128(0)], the humerus+ulna length being less than 80% of the femur+tibia length.

Interpretation

This obviously greatly changes the interpretations of the original fossil; however we stand by our original description of the material in this context and the figures and text do accurately describe the anatomical details present. Below we elaborate on the issues that this raises. As the paper describing and naming *Luchibang* was only published recently, it has fortunately had only a limited impact on the technical scientific literature. Of the peer-reviewed papers that have cited Hone et al. (2020), we offer the following comments and clarifications:

Beccari et al. (2021) used the data matrix from Hone et al. (2020) as the basis of their phylogenetic analysis but did otherwise comment on *Luchibang* or istiodactylid relationships and so we do not consider this work to have been negatively affected.

Holgado (2021) cited the results of the phylogeny of Hone et al. (2020) only in terms of the positon of the ornithicheirids *Ornithocheirus* and *Tropeognathus* relative to one another and noting that the results were consistent with other papers, and so we do not consider this work to have been negatively affected.

Jiang et al. (2021) did use characters from Hone et al. (2020) to differentiate this from the pteranodontoid *Yixianopterus jingangshanensis* but based on traits from the dentition and rostrum of

Luchibang, and so this should not affect the taxonomic work or traits used to diagnose the former. Therefore, we do not consider this work to have been negatively affected.

Zhou et al. (2021) cite Hone et al. (2020) only in the context of the problem of assessing fossils for signs of tampering and so we do not consider this work to have been negatively affected.

Hone (2023) in his paper on the diversity of pterosaur sterna included that of ELDM 1000 as an istiodactylid and now considered tapejaroid (see above). This is a clear difference from the original publication.

Xu et al. (2022; naming a new istiodactylid *Lingyuanopterus*) and Ozeki et al. (2023; describing new material of the istiodactylid *Nurhachius*) included *Luchibang* in their phylogenetic analyses. In both analyses *Luchibang* is recovered as an istiodactylid, though Xu et al. (2022) includes the entire composite and Ozeki et al. (2023) the actual *Luchibang* holotype and the cranial portions of the postcranial specimen. Given this and the small differences in coding between the coding of all the cranial material in the composite vs. just those of the holotope, we do not think that the revisions we presented would have notable effects on the topologies of these analyses. Xu et al. (2022) also carried out several taxonomic comparisons and while there are some similarities between the two, the comparisons were based on the cranium and dentition and not the postcranium, and a number of traits present in the rostrum of *Luchibang* still serve to distinguish it from *Lingyuanopterus*. We therefore do not consider this work to have been negatively affected.

Ozeki et al. (2023) noted that they considered ELDM 1000 to be a composite and coded the cranium as separate to the rest of the specimen in their phylogenetic analysis. This should reduce any issues around the inclusion of *Luchibang*, although they considered the entire skull to have been added on ELDM 1000 when in practice this was only the rostrum. However, we do not consider this work to have been negatively affected.

You et al. (2023) cited Hone et al. (2020) in their supplementary data, but *Luchibang* did not feature in their dataset (S4), and it is not clear if any measurements or the phylogeny was included in the published analyses. We therefore do not consider this work to have been negatively affected.

Sweetman (2023) noted that most Chinese istiodactylids are from the Jiufotang Formation with *Luchibang* an apparent exception. As noted above, this may now be incorrect, but we cannot confirm this.

Ecology and Ontogeny

The original ecological interpretation of *Luchibang* as a long-limbed wader (Hone et al., 2020) is not now supported. There is now no reason to think it was any different in general ecology from any other istiodactylid (though the biology of these animals remains uncertain and somewhat contentious, e.g., see Witton, 2013). The diversity of istiodactylid limb proportions also being much broader than previously considered (Hone et al., 2020: figure 9) is similarly not supported. There is no reason to think that the rest of this animal was unusual compared to other istiodactylids.

Similarly, although the main part of the specimen is clearly a young animal showing numerous signs of immaturity (Hone et al., 2020), this is less apparent for the rostrum and mandible alone. Aside from the bone surface texture, there are few traits used to classify the ontogenetic status of pterosaurs that could be seen in this part of the skeleton (Kellner, 2015). Thus, although the skull and mandible here are clearly not of a very young animal, it is impossible to say how old the individual may have been or how large it could grow. It is clearly a good fit size-wise for the postcranium to which it is attached and not dissimilar in size to other istiodactylids suggesting a moderate wingspan of c. 3 m, but this should no longer be considered a young animal that would have been much larger in adulthood.

CONCLUSIONS

Fossil forgeries remain a clear, though likely small, problem for palaeontology. Fossils continue to be purchased or donated to collections that were not collected and documented by academics and their exact origins are unknown or uncertain. As seen here, even close examination of material while searching for evidence of fabrication can miss such tampering given the detail of the work done. Although suspicion had been cast on this specimen before, it may not have been discovered that this had been altered were it not for the accidental damage to ELDM 1000, and it is not always possible or practical to heavily prepare or otherwise alter fragile specimens to search for changes made to them.

In this case, despite our checks and concerns, the original authors were deceived by the changes made to the specimen. We hope that this work serves to correct the record on this specimen and any echoes that the original paper has had on the scientific literature. The original authors are chastened by this experience and trust that this serves a timely warning for others assessing the validity of specimens offered to them.

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SUPPLEMENTARY INFORMATION

We took the phylogenetic analysis of pterosaur relationships by Hone et al. (2020) and modified it such that the holotype of *Luchibang xingzhe* and the now distinct postcranial material were coded as separate OTUs (see below). As in Hone et al. (2020), the OTU for *Linlongopterus jennyae*, which was pruned in the final analyses of Kellner et al. (2019) due to its status as a “wild card taxon,” was retained within our analysis for the sake of thorough sampling. Following the addition of these changes, we performed a phylogenetic analysis with the software TNT v 1.5 (Goloboff et al., 2018) using the TBR heuristic searches performed using maximum parsimony. Following Kellner et al. (2019), the search for the most parsimonious trees (MPTs) was conducted via Traditional Search (TBR swapping algorithm), 10,000 replicates, random seed, 20 trees to save per replication, and collapsing trees after search.

Changes made to the coding of the original Hone et al., 2020 analysis for revision are as follows:

3. Changed (1) to (?) as we don’t have enough to show a nasoantorbital fenestra is present.

22. Changed (0) to (?) as we don’t have enough to confidently say that the dorsal margin of the skull is entirely “nearly straight”.

42. Changed (0) to (?) because the absence of a posterior ventral expansion on the maxilla cannot be demonstrated with this portion of the skull.

43. Changed (0) to (?) because the absence of maxilla-nasal contact cannot be demonstrated.

44. Changed (-) to (?) for the reasoning in [43].

76. Changed (1) to (?) because the ratio cannot be determined with this fragment of mandible.

Removed all coding between 106–150 (?1?11????????102000?201??40??1??????212222120) as it is considered a separate specimen. This coding was moved to a new OTU, “Luchibang_postcrania”, with 1–105 coded as (?) because these cannot be coded for this specimen.

Postcranial OTU Changes

119. Changed (1) (“stout, with constructed shaft”) to (?) as this cannot be assessed.

124. Changed (0) to (1) as it is present.

128. Changed (1) to (0).

131. Changed (4) (“enlarged, warped”) to (5) (“long, proximally placed, curving ventrally”); there is no warping to the deltopectoral crest, and it best matches the condition of state (5).

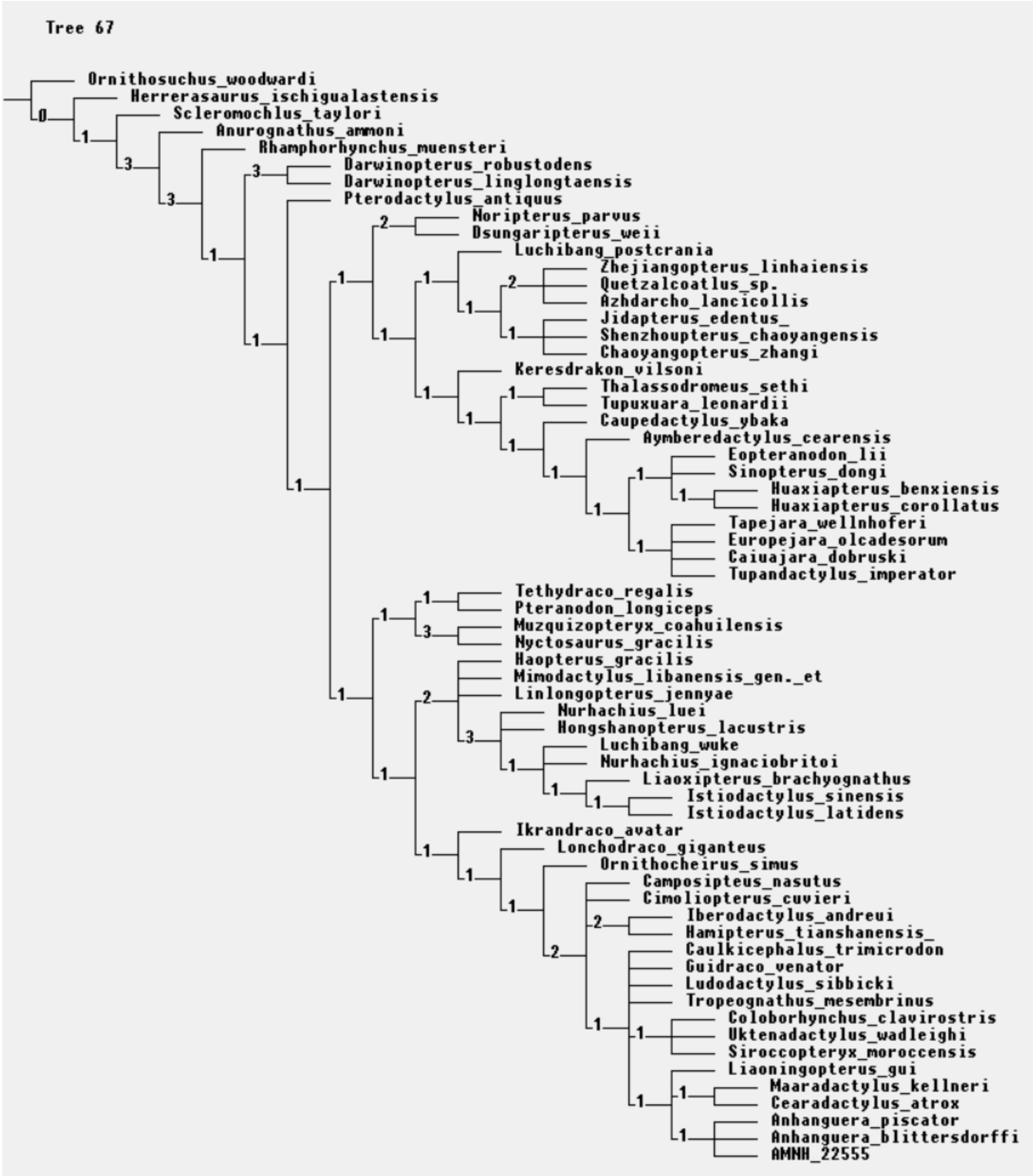
132. Changed (0) to (1,2).

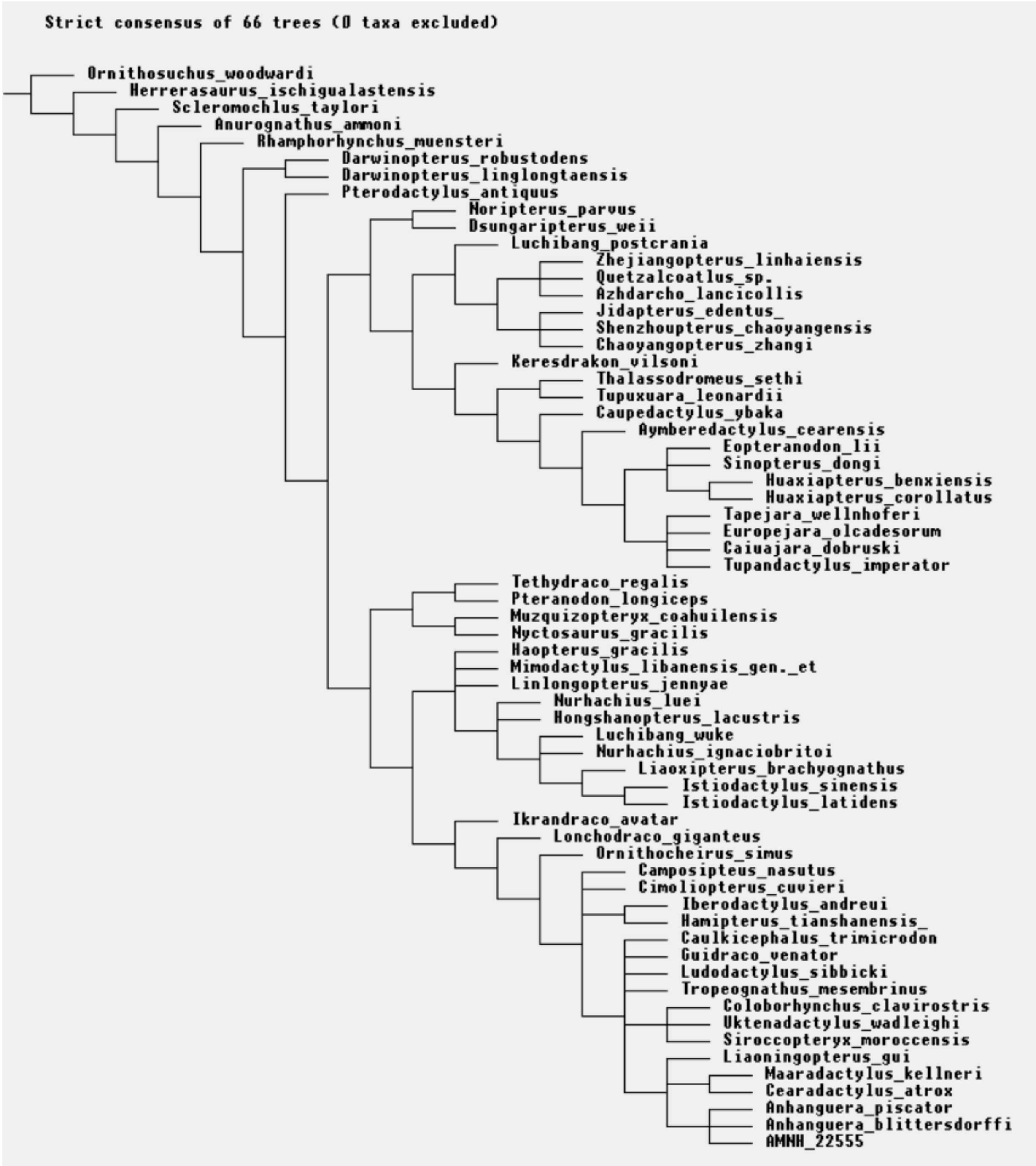
142. Changed (2) to (3).

146. Changed (2) to (3).

Consistency index: 0.630

Retention index: 0.872


Tree 67
Ornithosuchus_woodwardi
Herrerasaurus_ischigualastensis
Scleromochlus_taylori
Anurognathus_ammoni
Rhamphorhynchus_muensteri
Darwinopterus_robustodens
Darwinopterus_linglongtaensis
Pterodactylus_antiquus
Noripterus_parvus
Dsungaripterus_weii
Luchibang_postcrania
Zhejiangopterus_linhaiensis
Quetzalcoatlus_sp.
Azhdarcho_lancicollis
Jidapterus_edentus_
Shenzhoupterus_chaoyangensis
Chaoyangopterus_zhangi
Keresdrakon_vilsoni
Thalassodromeus_sethi
Tupuxuara_leonardii
Caupedactylus_ybaka
Aymberedactylus_cearensis
Eopteranodon_lii
Sinopterus_dongi
Huaxiapterus_benxiensis
Huaxiapterus_corollatus
Tapejara_wellnhoferi
Europejara_olcadesorum
Caiuajara_dobruski
Tupandactylus_imperator
Tethydraco_regalis
Pteranodon_longiceps
Muzquizopteryx_coahuilensis
Nyctosaurus_gracilis
Haopterus_gracilis
Mimodactylus_libanensis_gen._et
Linlongopterus_jennyae
Nurhachius_luei
Hongshanopterus_lacustris
Luchibang_wuke
Nurhachius_ignaciobritoi
Liaoxipterus_brachyognathus
Istiodactylus_sinensis
Istiodactylus_latidens
Ikrandraco_avatar
Lonchodraco_giganteus
Ornithocheirus_simus
Camposipteus_nasutus
Cimoliopterus_cuvieri
Iberodactylus_andreui
Hamipterus_tianshanensis_
Caulkicephalus_trimicrodon
Guidraco_venator
Ludodactylus_sibbicki
Tropeognathus_mesembrinus
Coloborhynchus_clavirostris
Uktenadactylus_wadleighi
Siroccopteryx_moroccensis
Liaoningopterus_gui
Maaradactylus_kellneri
Cearadactylus_atrox
Anhanguera_piscator
Anhanguera_blittersdorffi
AMNH_22555



Matrix:

xread

150 64

Ornithosuchus_woodwardi000000200000100010000000100000-00000--00--0100---000000000000--0-
0000000000?0000000--00-00000000000000000000000000000000000000000000000000000000

Herrerasaurus_ischigualastensis0000100000000000010000001000000-00000--00--0100---000000000000--
0-000000000000000000--00-
0000000000000000000000000000000000000000000000000000000000000020

Scleromochlus_taylori0000100000000000010000201000000-00000--00--0100---00001?020??0--0-
00????0000000?0000--00-00?000?000??000000???00??0000??0?000???00??0???0???00?0000000??

Anurognathus_ammoni00000010000000001100120100000-00100--00--0110---000110010??0--0-
000000000100000000--00-0010001001000000000???0???01000?0???0??0110?100000??1001122?0011

Rhamphorhynchus_muensteri1100100000011001010000130000-00000--00--0100---000000021000--0-
000000001002012010--00-001000100000010000000000000100000100011110020000100?100122221012

Darwinopterus_linglongtaensis10110000000011??????0001100000-0000?20000000-1010100010021?00--
0-00?00?00????010000--00-
0010001?1000000000???10??001?0?00?000?1110?100?10??100311111022

Darwinopterus_robustodens101100?00?011??????0001100000-0000?20000000-1010?00010021?00--0-
00?00?00????010000--00-0010001?1000000000???1???001?0?00??0??111??100?10??10031111102?

Pterodactylus_antiquus1010000000011??0???0001100000-00000--00--00-1001000010031?00--0-
10?00000???2010000--00-00100010100000000000002110010000001000121100500?100?100312222020

Dsungaripterus_weii1010000101111041120000130000-0100111000010-?---
0000100211012211011101001012012000--11-12--
0110000000000001111100110?000???0?2210??5?001001??13122?2120

Noripterus_parvus1010000101111??????0001300000-0100111000010-?---
000010021?01221101?10?00?0?2012000--?1-12--
01100000000000?11??0?????????????????????????0?001????????????

Keresdrakon_vilsoni101????????????????00?1300000-?00?0--00--?0-
???????????2????????????0000???301200101?3------------------
?111?00?????00020011?0?01520?1???????????????

Tupuxuara_leonardii10110020020210511210001300100-0000134000000-
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11111001???00002001?2100152011001?01313??2???

Thalassodromeus_sethi1011002002021?611210001300100-0000134000000-
1110000110022101271101100300101?0120011313------------------
??

Caupedactylus_ybaka1011002002021?511210021310100-0000134000000-
?????00?210221?12711011?000010130120011013------------------
???????????00002001????015200???????????????

Aymberedactylus_cearensis
????????????????????00??31???20120011?1
3------------------???

Tupandactylus_imperator1011002002021??????102131?100-0000133100000-
??????0110?22?01221101????0????201210112?3------------------
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Caiuajara_dobruski1011002002021??????1021311100-?000133100000-
???????1?00220?1221101101001??120121011213------------------
?1111000?0?00002?01?21?11520?1??120??????????

Europejara_olcadesorum
??????2???021???????0????????????????????0??????????????220?12???0???????1?1201?10112?
3------------------???

Tapejara_wellnhoferi101100200202102????1021311100-0000133000000-
?????1011002200122110110100110120121011213------------------
?1111000?0?00002001?210115200100120?31???2120

Sinopterus_dongi1011002002021??????1021311000-1000133000000-
1100010110022?11211101?0??01???20121011013------------------
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Huaxiapterus_corollatus101????????????????102131?000-1000133010000-
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?1?11??0???000???0??211??5??????????3132321??

Huaxiapterus_benxiensis1011002002021??????102131?000-1000133010000-
???????110022??1211101????01???201210110?3------------------
?1?11??0?????????????2????????????20?3122?2120

Eopteranodon_lii101??0???2?????????1021311000-100013300??00-
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????????????????????21???5??????????3?22?2???

Chaoyangopterus_zhangi101??1?0???????????001130?000-?00????00--00-
???????????????1??????????00????012000--?3------------------
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Shenzhoupterus_chaoyangensis1010012002021??????001130?000-0001155000000-
?????0??2???2?01241101????00???2012000--?3------------------
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Jidapterus_edentus_101?????????????????0011300000-?001???00--00-
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?1?2110??????0???1??200??5?0?100????312232120

Azhdarcho_lancicollis???????????????????00??3?000???0??????0?--?0-
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11031221???????????????015?0?????????????????

Quetzalcoatlus_sp.10100020020????????0001300000-?00014?00--00-0---
000010??210?????????000010?3012000--13------------------
11031221?0?00002010?20?0152001001???4132?2??20

Zhejiangopterus_linhaiensis10100020020?1??????0001300000-00000------00-0---0000100?2?00--0-
01??0?00????012000--?3------------------1??31221?0?000???10?200??5???100?20?413??2???

Nyctosaurus_gracilis10101000000110101100012300000-00000------00-?????00011021100--
1200?000001013012000--13------------------11?110111000?00100013110130?011122123222?20??

Muzquizopteryx_coahuilensis?01010?000011???????0?????????0?00???????00-?????0001?021?00--
1200????0??????????0???3------------------???11011????1????????11??30??111?21???????1??

Pteranodon_longiceps10100020000111302310012300000-00000------00-
112?0000110231012311001000001013012000--03------------------
111110111011101200012110141111112202322232020

Tethydraco_regalis
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???014111????????????????

Lonchodraco_giganteus1??????????????????00??200000-
?0??1??0000???????????????????????????010?????110?01?0?????1000101000000001??????????
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Ikrandraco_avatar1010000000110????10001200000-00000------00-11001?01000311?0--0-
00?00100101211000112?0-00100010100?0000001111101??????????????2????41??2112201??2??????

Ornithocheirus_simus10??????????????????0??100?00-
?0????????????????????????????????????0?0???????????????0-
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Cimoliopterus_cuvieri1???????????????????0??100010-
?0??1?20000????????????????????????????011???????????????0-
?0?000???000???000???

Camposipteus_nasutus
1?????????????????????0?10001110????????00???????????????????????????011??????????????
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Hamipterus_tianshanensis_10100020000?1011111000110001110000121001100-?????001010211?0--0-
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Iberodactylus_andreui
????????????????????0??100?111?0??1?10011???????????????????????????011???????????????
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Tropeognathus_mesembrinus101000200001101011100?110001110000102000000-
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AMNH_2255510101020000110101110011100012?0000102000000-
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Anhanguera_blittersdorffi1010102000011010111001110001210000102000000-
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Anhanguera_piscator1010102000011?1????001110001210000102000000-
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Liaoningopterus_gui

101?0?2000011???????0??1000121?00?1020000?????????0110211??????????0110????0?0??1010
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Siroccopteryx_moroccensis
1???????????????????0??0000113?0??1??0000???????????????????????????011??????????????
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Uktenadactylus_wadleighi
1???????????????????0??0000113?0?????0000??????????????????????????011??????????????
0-???100?0?000???010???

Coloborhynchus_clavirostris
1???????????????????0??0000113?0?????0000??????????????????????????011??????????????
0-???100???000???010???

Ludodactylus_sibbicki1010000000110?????001110001??0000???000000-
1100101001021101161100?00110??1201000101?0-
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Guidraco_venator10?0000000011??????001110001??0000???000000-
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Caulkicephalus_trimicrodon
10????0??0??????????01?100?12?00??1020000??????????????????11611????011??0???????????
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Cearadactylus_atrox
10100??0010?101????0?11100?121?00?1020000?????00??1011?211??????????011010?2010000--
00-0111101000000110 1??

Maaradactylus_kellneri
101?0?2001011???????0??1000?21?00?1020000?0?1??????0110211?1????????0110??????0??1010
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Linlongopterus_jennyae101000?0000?1??????0001200000-00000------00-
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Mimodactylus_libanensis_gen._et_sp._nov.?????????????030??000??200000-?0???????????0-
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Haopterus_gracilis1010???????????????0001200000-?0000------00-
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Hongshanopterus_lacustris?????????????03001000?1200??0-?0???????--
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Liaoxipterus_brachyognathus
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Istiodactylus_latidens1011000111111??????0000100010-00000------00-1110001121133O?0--0-
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Istiodactylus_sinensis1011000111111??????0000100010-00000------00-?????011211330?0--0-
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Nurhachius_ignaciobritoi10110020?10?1??????0001200010-00000------00-??1??01111033000--
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Nurhachius_luei1011002001?11??????0001200010-00000------00-0----0????031?00----
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Luchibang_wuke10??????????????????00??0000?0-?00?0------
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Luchibang_postcrania
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?????????????????????1?11?????????02010?201??5[1 2]??1??????312232120

;

cnames

{0 External_naris_(or_nasoantorbital_fenestra),_position_relative_to_the_premaxilla_ main_part_dorsal_to_the_ventral_margin_of_the_premaxilla main_part_displaced_posterior_to_the_premaxilla;

{1 External_naris,_dorsoventrally_compressed absent present;

{2 External_naris_and_antorbital_fenestra,_configuration_ separated confluent,_forming_a_nasoantorbital_fenestra;

{3 External_naris_and_antorbital_fenestra_(or_nasoantorbital_fenestra),_ventral_margin_length_relati
ve_the_skull_length shorter_than_40%_of_the_skull_length_ longer_than_40%_of_the_skull_length;

{4 Antorbital_(or_nasoantorbital)_fenestra,_posterior_margin,_shape_ straight_ concave_;

{5 Nasoantorbital_(or_antorbital)_fenestra_extending_dorsal_to_the_orbit_ absent present;

{6 Orbit,_shape_ subcircular quadrangular_(broad_base) piriform_(dorsoventrally_elongated)_;

{7 Orbit,_comparatively_small absent_ present_;

{8 Ventral_margin_of_the_orbit closed open;

{9 Orbit,_position
middle_of_the_skull,_with_the_ventral_margin_of_the_orbit_below_the_middle_of_the_antorbital_(or_nasoantorbital)_fenestra_and_the_dorsal_margin_of_the_orbit_above_the_dorsal_margin_of_the_antorbital_(or_nasoantorbital)_fenestra

high_in_the_skull,_with_the_ventral_margin_of_the_orbit_the_same_level_or_above_the_middle_of_the_antorbital_(or_nasoantorbital)_fenestra low_in_the_-skull,_with_the_entire_orbit_lower_than_the_dorsal_margin_of_the_antorbital_(or_nasoantorbital)_fenestra;

{10 Suborbital_opening absent_ present_;

{11 Lower_temporal_fenestra,_shape_ comparatively_broad,_with_extensive_subhorizontal_ventral_margin piriform,_with_dorsal_portion_wider_than_ventral__ reduced_(slit-like);

{12 Lower_temporal_fenestra,_position_relative_to_orbit posterior_to_orbit reaches_under_posterior_margin_of_orbit;

{13 Choanae,_separation separated_by_vomer confluent;

{14 Postpalatine_fenestra,_shape_ quadrangular/subtriangular oval egg-shaped elongated_eggshaped_kite-shaped,_rounded_margin elliptical reduced,_slit-like;

{15 Secondary_subtemporal_fenestra absent present;

{16 Interpterygoid_fenestra,_size_ORDERED extremely_reduced smaller_than_subtemporal_fenestra larger_than_subtemporal_fenestra;

{17 Interpterygoid_fenestra,_shape_ compressed_laterally broad,_longer_than_wide compressed_anteroposteriorly,_wider_than_long round;

{18 Pterygoid_fenestra absent_ present;

{19 Upper_and_lower_jaw,_marked_gap_during_occlusion absent_ present;

{20 Upper_and_lower_jaw,_shape laterally_compressed_ comparatively_broad_;

{21 Skull,_main_part_of_dorsal_margin,_curvature_excluding_cranial_crest nearly_straight concave_ convex;

{22 Length_of_the_rostrum_(pm-naof)_relative_to_the_skull_length_(pm-sq)_ORDERED reduced_ elongated_(about_or_less_than_half_of_skull_length)_ extremely_elongated_(more_than_half_of_-skull_length);

{23 Rostrum,_anterior_end,_shape_ flat_surface rounded pointed sharp_tip;

{24 Rostral_end_of_premaxillae/maxillae_downturned absent_ present_;

{25 Rostrum,_distinct_concavity_on_occlusal_surface absent present;

{26 Rostrum,_anterior_portion_forming_a_high_ossified_plate absent present;

{27 Rostrum,_anterior_tip_with_a_slight_dorsal_reflection absent present;

{28 Premaxilla,_anterior_expansion absent present;

{29 Premaxilla,_anterior_expansion,_shape_in_horizantal_plane_ absent elliptical anteriorly_expanded quadrangular;

{30 Premaxilla,_posterior_dorsal_process,_curved_upward absent present;

{31 Premaxillae,_anterior_end_rodlike absent present;

{32 Premaxillary_process_separating_the_external_nares,_thickness_ wide narrow_;

{33 Premaxilla,_posterodorsal_margin_of_nasoantorbital_fenestra_(including_nasal),_width_ wide thin;

{34 Premaxillary_sagittal_crest absent present;

{35 Premaxillary_sagittal_crest_position confined_to_the_anterior_portion_of_the_skull_
starting_anterior_to_the_anterior_margin_of_the_nasoantorbital_fenestra,_extending_beyond_occipi-
tal_region
starting_at_about_the_anterior_margin_of_the_nasoantorbital_fenestra,_reaching_the_skull_roof_above_t
he_orbit_but_not_extending_over_the_occipital_region
starting_close_or_at_the_anterior_portion_of_the_skull_and_extended_over_the_occipital_region start-
ing_at_the_posterior_half_of_the_nasoantorbital_fenestra
starting_at_the_middle_part_of_the_nasoantorbital_fenestra_and_extended_over_the_occipital_region_;

{36 Premaxillary_sagittal_crest,_shape striated,_low_with_a_nearly_straight_dorsal_margin stri-
ated,_high_with_a_nearly_straight_dorsal_margin round_dorsal_margin,_bladeshaped smooth,_expand-
ed_anteriorly_and_forming_a_low_rod-like_extension_posteriorly
smooth,_starting_low_anteriorly_and_very_expanded_posteriorly striated,_low,_convex_dorsal_margin;

{37 Premaxillary_crest,_elongated_dorsal_premaxillary_spike-like_projection_ absent_ present_;

{38 Premaxillary_crest,_distinct_expansion_on_the_anterior_part_ absent present;

{39 Premaxillary_crest,_concentric_striae_on_the_anterior_region absent present;

{40 Premaxillary_crest,_anterior_expansion_of_the_anterior_margin absent present;

{41 Maxilla,_posterior_ventral_expansion_ absent_ present_;

{42 Maxilla-nasal_contact absent present;

{43 Maxilla-nasal_contact,_broadness broad narrow;

{44 Nasal_descending_process absent present;

{45 Nasal_descending_process,_position_ placed_laterally placed_medially absent;

{46 Nasal_descending_process,_length_ long_(almost_reaching_the__ventral_margin_of_the_skull)_OR-
DERED short knob-like_(extremely_reduced) absent;

{47 Nasal_descending_process,_orientation_ inclined_anteriorly subvertical;

{48 Nasal_descending_process,_lateral_foramen_ absent_ present_;

{49 Lacrimal,_extensive_fenestration absent_ present_;

{50 Lacrimal,_orbital_process_ absent_ present_;

{51 Jugal,_lacrimal_process_base,_width_ broad narrow;

{52 Jugal,_lacrimal_process,_inclination_ORDERED inclined_anteriorly subvertical inclined_posteriorly;

{53 Jugal,_presence_of_pronounced_ridge_on_the_lateral_side absent present;

{54 Jugal,_posterior_process,_orbital_process absent present;

{55 Quadrate,_inclination_relative_to_ventral_margin_of_skull_ORDERED anteriorly subvertical inclined_about_120°_posteriorlyned_about_120°_backwards_ inclined_about_150°_posteriorly;

{56 Cranio-mandibular_articulation,_position_relative_to_orbit_ORDERED _posterior_to_posterior_margin_of_orbit under_center_of_orbit_ under_anterior_margin_of_the_orbit anterior_to_anterior_margin_of_orbit;

{57 Helical_jaw_joint absent_ present_;

{58 Frontal,_anterior_portion_rugose absent present;

{59 Frontal,_ossified_crest absent present;

{60 Frontal,_ossified_crest,_position_ORDERED confined_to_posterior_end_of_skull starting_above_orbit starting_on__posterior_half_of_nasoantorbital_fenestra;

{61 Frontal,_ossified_crest,_shape_ low,_blunt short._spike-like,_dorsally_deflected spikelike,_directed_posteriorly narrow,_broad,_directed_posteriorly low,_broad_base,_fans-shaped high,_broad_base,_crown-shaped high,_broad_base,_casqued-shaped high,_broad,_directed_posteriorly,_at_least_doubling_shight_of_skull_above_orbit absent;

{62 Parietal,_ossified_crest absent present;

{63 Parietal,_ossified_crest,_shape_ blunt_ constituting_the_base_of_the_posterior_portion_of_the_cranial_crest expanded,_with_rounded_margin;

{64 Posterior_region_of_the_skull_rounded_with_the_squamosal_displaced_ventrally absent_ present_;

{65 Supraoccipital does_not_extend_backwards_ extends_backwards_;

{66 Supraoccipital,_foramen_ absent_ present_;

{67 Paroccipital_processes,_expanded_distal_ends_ absent_ present_;

{68 Foraminae_piercing_the_anterior_portion_of_the_palate,_numerous absent present;

{69 Palatal_occlusal_surface_ORDERED smooth discrete_palatal_ridge,_tapering_anteriorly_ strong_palatal_ridge,_tapering_anteriorly strong_palatal_ridge,_confined_to_the_posterior_portion_of_the_palate;

{70 Palate,_dorsal_deflection absent present;

{71 Palate,_slight_expansion_close_to_the_anterior_margin_of_the_nasoantorbital_(or_naris_+_antorbital)_fenestra absent present;

{72 Maxilla_and_internal_naris,_contact_ absent_ present_;

{73 Palatines,_shape_ broad thin_bars;

{74 Basisphenoid_body,_length_ shorter_than_wide longer_than_wide;

{75 Mandibular_rostral_end,_extension_of_the_contact_surface_of_opposing_dentaries_ORDERED short,_limited_to_the_tip short,_extended_posteriorly_less_than_30%_of_mandible_length long,_up_to_55%_the_mandible_length long,_extended_over_55%_of_mandible_length;

{76 Mandibular_rostral_end,_odontoid_process absent present;

{77 Mandibular_rostral_end,_opposing_dentaries_ unfused fused;

{78 Mandibular_rostral_end,_shape_ rounded pointed sharp_tip;

{79 Dentary,_dorsal_margin,_distinct_posterior_eminence_close_to_the_separation_of_mandibular_rami absent present;

{80 Tip_of_the_dentary_projected_anteriorly absent_ present_;

{81 Dentary_ossified_sagittal_crest absent present;

{82 Dentary_ossified_sagittal_crest,_position_ confined_to_the_anterior_third_of_the_lower_jaw extinding_close_to_the_middle_portion_of_the_lower_jaw;

{83 Dentary_ossified_sagittal_crest,_shape_ shallow blade-like deep,_broad_in_lateral_view elongated_ridge;

{84 Dentary,_posteroventral_fossa absent present;

{85 Teeth,_position_and_presence present,_evenly_distributed_along_the_jaws_ teeth_absent_-from_the_anterior_portion_of_the_jaws_ confined_to_the_anterior_part_of_the_jaws jaw_toothless;

{86 Teeth,_confined_to_the_anterior_part_of_the_jaws confined_to_the_anterior_half_of_the_jaws confined_to_the_anterior_quarter_of_the_jaws;

{87 Maxillary_teeth,_largest_positioned_posteriorly_ absent_ present_;

{88 Teeth,_shape_variation isodont heterodont;

{89 Teeth,_anterior,_height_versus_width_proportion more_than_twice_their_width less_than_twice_their_width;

{90 Teeth,_anterior,_marked_variation_in_size absent present;

{91 Teeth,_upper_-jaw,_variation_in_the_size_of_the_anterior_teeth_with_the_5th_and_6th_smaller_than_the_4th absent_ present_;

{92 Teeth,_base_broad_and_oval absent_ present_;

{93 Teeth,_serrated present absent;

{94 Teeth,_cingulum absent present;

{95 Teeth,_peg-like_(cone-shaped) absent_ present;

{96 Teeth,_small_needle-shaped absent present;

{97 Teeth,_labiolingually_compressed_crowns absent present;

{98 Teeth,_labiolingually_compressed_crowns,_compression_ORDERED not_compressed slightly_compressed strongly_compressed;

{99 Teeth,_sharp_carinae absent present;

{100 Teeth,_elongated absent present;

{101 Teeth,_striated absent present;

{102 Teeth,_curvature_of_the_toothline absent present;

{103 Teeth,_first_pair_above_second_pair absent present;

{104 Alveoli,_lateral_platform absent present;

{105 Atlas_and_axis unfused_ fused_;

{106 Cervical_vertebrae,_postexapophyses_ absent_ present_;

{107 Mid-cervical_vertebrae,_centrum,_lateral_foramen_ absent_ present_;

{108 Mid-cervical_vertebrae,_length_ORDERED short,_sub-equal_in_length_ longer_than_wide,_with_length_less_than_3_times_width elongated,_with_length_more_than_3_-times_width extremely_elongate;

{109 Mid-cervical_vertebrae,_ribs present_ absent_;

{110 Mid-cervical_vertebrae,_neural_spines,_height_ORDERED tall low extremely_reduced_or_absent;

{111 Mid-cervical_vertebrae,_neural_spines,_shape_ blade-shaped spike-shaped_ ridge;

{112 Notarium absent_ present_;

{113 Caudal_vertebrae,_quantity_ more_than_15_ 15_or_less_;

{114 Caudal_vertebrae,_zygapophyses_forming_rod-like_ossified_processes_ absent present;

{115 Proximal_caudal_vertebrae_centrum,_centrum_shape_ single douplex;

{116 Scapula,_length_relative_to_coracoid_length_ORDERED subequal_or_longer_than_coracoid_ scapula_shorter_than_coracoid_(1_>_sca/cor_>_0.80)_ substantially_shorter_than_coracoid_(sca/cor_<_0.80);

{117 Scapula,_proximal_end_ elongated_ sub-oval_;

{118 Scapula,_shape_ elongated_ stout,_with_constructed_shaft_;

{119 Coracoid,_proximal_end,_shape flattened oval;

{120 Coracoid,_sternal_articulation_ORDERED no_developed_articulation articulation_surface_straight_or_slightly_concave articulation_surface_strongly_concave;

{121 Coracoid,_sternal_articulation,_posterior_expansion_ absent present;

{122 Coracoid,_ventral_margin,_deep_flange absent present;

{123 Coracoid,_broad_tubercle_on_ventroposterior_margin absent present;

{124 Cristospine,_shape_ absent_ shallow_and_elongated_ deep_and_short;

{125 Humerus,_proportional_length_relative_to_the_metacarpal_IV_(hu/mcIV)_ORDERED hu/mcIV_>_2.50_ 1.50_<_hu/mcIV_<_2.50_ 0.40_<_hu/mcIV_<_1.50 hu/mcIV_<_0.40;

{126 Humerus,_proportional_length_relative_to_the_femur_(hu/fe)_ORDERED hu/fe_<0.80_ 1.4_>_hu/fe>___0.80_ hu/fe_>_1.40;

{127 Humerus_plus_ulna,_proportional_lengths_relative_to_the_femur_plus_tibia_(hu+ul/fe+ti)_ORDERED humerus_plus_ulna_about_0.80%_or_less_of_femur_plus_tibia_length_(hu+ul/fe+ti_<_0.80)_ humerus_plus_ulna_larger_than_0.80%_of_femur_plus_tibia_length_(hu+ul/fe+ti_>_0.80)_;

{128 Humerus,_proximal_end,_small_foramen_on_dorsal_surface_distal_to_proximal_articulation absent present;

{129 Humerus,_proximal_end,_foramen_on_ventral_surface_close_to_proximal_margin_ absent_ present_;

{130 Humerus,_deltopectoral_crest,_shape_ reduced,_positioned_close_to_the_humerus_shaft enlarged,_proximally_placed,_with_almost_straight_proximal_margin_ enlarged,_hatchet_shaped,_proximally_placed enlarged,_hatched_shaped,_positioned_further_down_the_humerus_shaft enlarged,_warped long,_proximally_placed,_curving_ventrally;

{131 Humerus,_medial_(=_ulnar)_crest_ reduced_ directed_posteriorly_ massive,_with_a_developed_proximal_ridge;

{132 Humerus,_distal_articulation,_shape_ oval_or_D-shaped_ subtriangular_;

{133 Humerus,_between_distal_condyles,_pneumatic_foramen absent present;

{134 Ulna_and_radius,_diameter_at_midshaft_ORDERED subequal_ diameter_of_radius_about_half_that_of_ulna diameter_of_radius_less_than_half_that_of_ulna;

{135 Proximal_syncarpal,_large_posterodistal_process absent present;

{136 Proximal_syncarpal,_shape_(proximal_view) quadrangular_or_irregular pentagonal;

{137 Distal_syncarpals,_shape_(distal_view)_ irregular form_rectangular_unit_ form_triangular_unit;

{138 Pteroid_ORDERED absent_ shorter_than_half_the_length_of_the_ulna_ longer_that_half_the_length_of_the_ulna;

{139 Pteroid,_proximal_articulation,_expanded_in_right_angle_with_shaft absent present;

{140 Metacarpals_I_-_III,_relation_with_carpus_ORDERED articulating_with_carpus_ metacarpal_I_articulates_with_carpus,_metacarpals_II_and_III_reduced_ not_articulating_with_carpus;

{141 Manual_digit_IV_first_phalanx,_proportional_length_relative_to_metacarpal_IV_(ph1d4/mcIV)_ORDERED both_small_and_reduced_ ph1d4/mcIV>4.0 4.0>ph1d4/mcIV>2.0 '2.0>_ph1d4/mcIV>1.0' 'ph1d4/mcIV<_1.0';

{142 Manual_digit_IV_first_phalanx,_proportional_length_relative_to_tibiotarsus_(ph1d4/ti)_ORDERED ph1d4_reduced_ ph1d4_elongated_and_less_than_twice_the_length_of_ti_(ph1d4/ti_smaller_than_2.00) ph1d4_elongated_about_or_longer_than_twice_the_length_of_ti_(ph1d4/ti_subequal/larger_than_2.00);

{143 Manual_digit_IV_second_phalanx,_proportional_length_relative_to_first_phalanx_(ph2d4/ph1d4)__ORDERED both_short_or_absent_ elongated_with_second_phalanx_about_the_same_size_or_longer_than_first_(ph2d4/ph1d4_larger_than_1.00)_ elongated_with_second_phalanx_up_to_30%_shorter_than_first_(ph2d4/ph1d4_between_0.70_-_1.00) elongated_with_second_phalanx_more_than_30%_shorter_than_first_(ph2d4/ph1d4_smaller_than_0.70);

{144 Manual_digit_IV_third_phalanx,_proportional_length_relative_to_first_phalanx_(ph3d4/ph1d4)__ORDERED both_short_or_absent_ ph3d4_about_the_same_length_or_larger_than_ph1d4_ ph3d4_shorter_than_ph1d4;

{145 Proportional_length_of_the_forth_phalanx_of_manual_digit_IV_relative_to_the_first_phalanx_of_manual_digit_IV_(ph4d4/ph1d4)_ORDERED both_short_or_absent both_elongated,_with_the_forth_phalanx_longer_than_the_first_(ph4/d4>1.00) both_elongated,_with_the_forth_phalanx_the_same_length_or_shorter,_but_longer_than_35%_the_length_of_the_first both_elongated,_with_the_forth_phalanx_less_than_35%_the_length_of_the_first;

{146 Femur,_length_relative_to_metacarpal_IV_length_(fe/mcIV)__ORDERED femur_at_least_twice_the_metacarpal_IV_length_(fe_?_mcIV_>_2.00) femur_longer_but_less_than_twice_the_length_of_metacarpal_IV_(1.00_<_fe/mcIV_<_2.00)_ femur_about_the_same_length_or_shorter_than_metacarpal_IV_(fe/mcIV_<_1.00);

{147 Metatarsal_III,_proportional_length_relative_to_tibia_length_ more_than_30%_of_tibia_length_ less_than_30%_of_tibia_length_;

{148 Pedal_digit_V,_number_of_phalanges__ORDERED with_four_phalanges_ with_2_phalanges_ with_1_or_no_phalanx_(extremely_reduced);

{149 Pes,_second_phalanx_of_digit_V,_shape__ reduced_or_absent_ elongated,_straight_ elongated,_curved elongated,_very_curved_(boomerang_shape);

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ccode + 16 22 46 52 55 56 60 75 98 108 110 116 120 125 126 127 134 140 141 142 143 144 145 146 148*;

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