Archaeopteryx: oviraptorosaur or archaeopterygid/deinonychosaur?

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Abstract

It has recently been argued that, based on a maximum parsimony analysis of a broad set of oviraptorosaur, archaeopterygid, and basal deinonychosaur morphological data, Archaeopteryx is not on the main line of avian evolution, and instead is more similar in general morphology to the oviraptorosaurs than to the archaeopterygids and basal deinonychosaurs. A new, variable-character-coding-based Bayesian phylogenetic analysis does not sustain this view.

Keywords: Archaeopteryx, maximum parsimony Bayesian phylogenetic, paleo-ornithology

1.0 Introduction

Archaeopteryx is widely accepted as the most basal bird discovered to date, and thus has been central to our understanding of avialan origins ([8], [9]). It has recently been argued ([4]) that, based on a maximum parsimony phylogenetic assessment ([6]) of oviraptorosaur, archaeopterygid, and basal deinonychosaur morphological data, together with the discovery of a new *Archaeopteryx*-like theropod, *Xiaotingia zhengi*, *Archaeopteryx* is *not* on the main line of avian evolution, and instead is more similar in general morphology to the oviraptorosaurs than to the archaeopterygids and basal deinonychosaurs. These relationships are depicted in Figure 1.

A previous Bayesian/Monte Carlo analysis ([13]) of the data for [4] assumed a 32-bit model and fixed coding of morphological characteristics (requiring ~500 separate executions of the phylogenetic software). The present work uses a 64-bit upgrade of the software used in [13] and variable coding.

2.0 Method

The taxon descriptors in [5] were converted from PDF to MS-DOS text format using the *deskUNPDF Standard Version 3.1* software ([7]). The resulting text file was reformatted under Microsoft *Notebook* to be compatible with the variable-character coding requirements of [1]. The resulting script was then executed under a 64-bit Bayesian phylogenetic ([2]) software package (*MRBAYES*, [1]). The software was run on a Dell Inspiron 545 with an Intel Core2 Quad CPU Q8200 clocked at 2.33 GHz, with 8.00 GB RAM, under *Windows Vista Home Premium/SP2.* The above experiment was repeated

with *X. zhengi* removed from the taxon set in [5], and the phylogenetic trees generated by [1] with, and without (not shown), *X. zhengi* were compared. In addition, the results of the work reported here were compared with the results reported in [3] and [13].

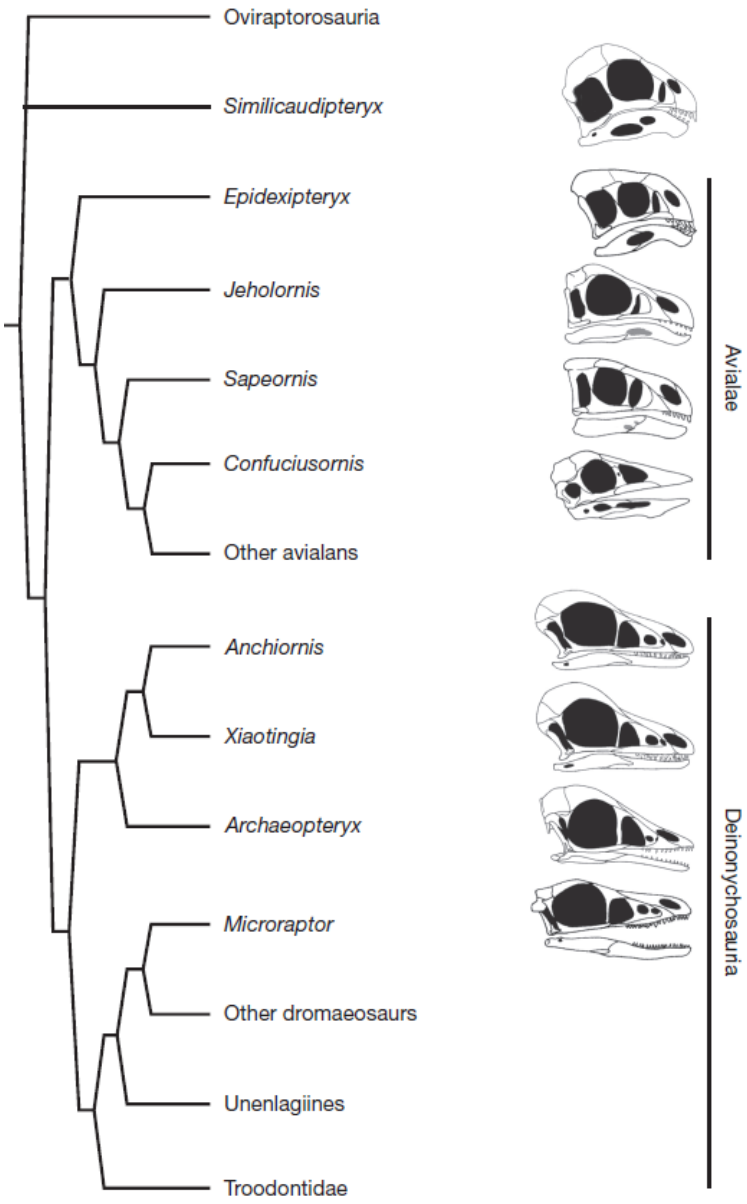


Figure 1. Simplified cladogram from [4] (p. 469) showing the systematic position of *Xiaotingia* and *Archaeopteryx*.

```
begin data;
     dimensions ntax=89 nchar=374;
     format datatype=Standard gap=- missing=?;

     matrix

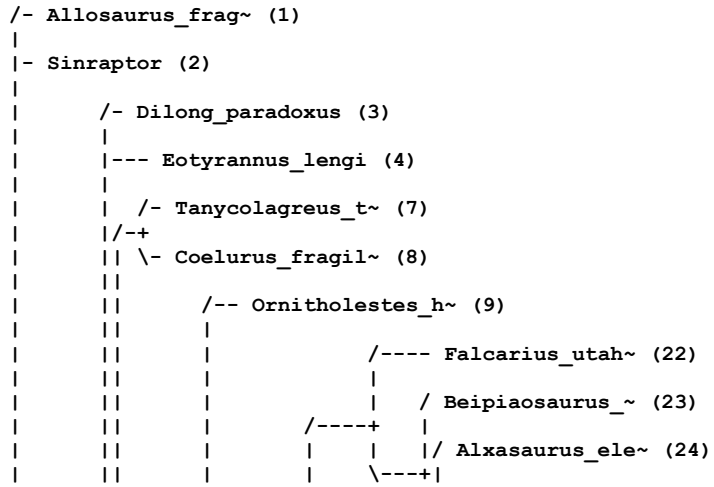
[data matrix adapted from Appendix goes here]
;
end;

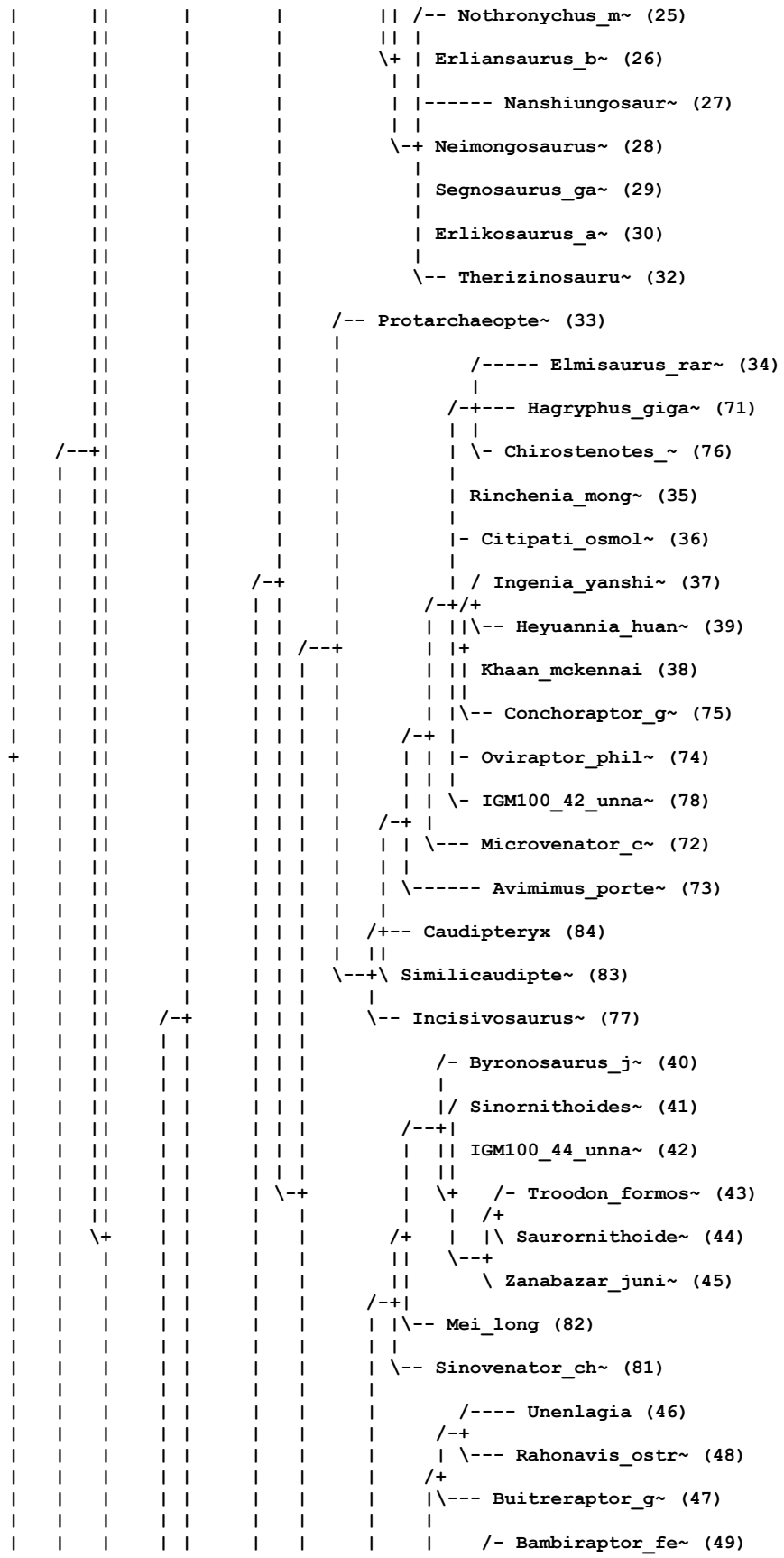
begin mrbayes;
   log start filename=archae4_log.log replace;
   set autoclose=yes;
   mcmcp nruns=2 ngen=3000000 printfreq=100
       samplefreq=100 nchains=4 savebrlens=yes
       filename=archae;
   mcmc;
   plot filename=archae.run1.p;
   plot filename=archae.run2.p;
   sumt filename=archae burnin=10000 contype=halfcompat;
   log stop;
end;
```

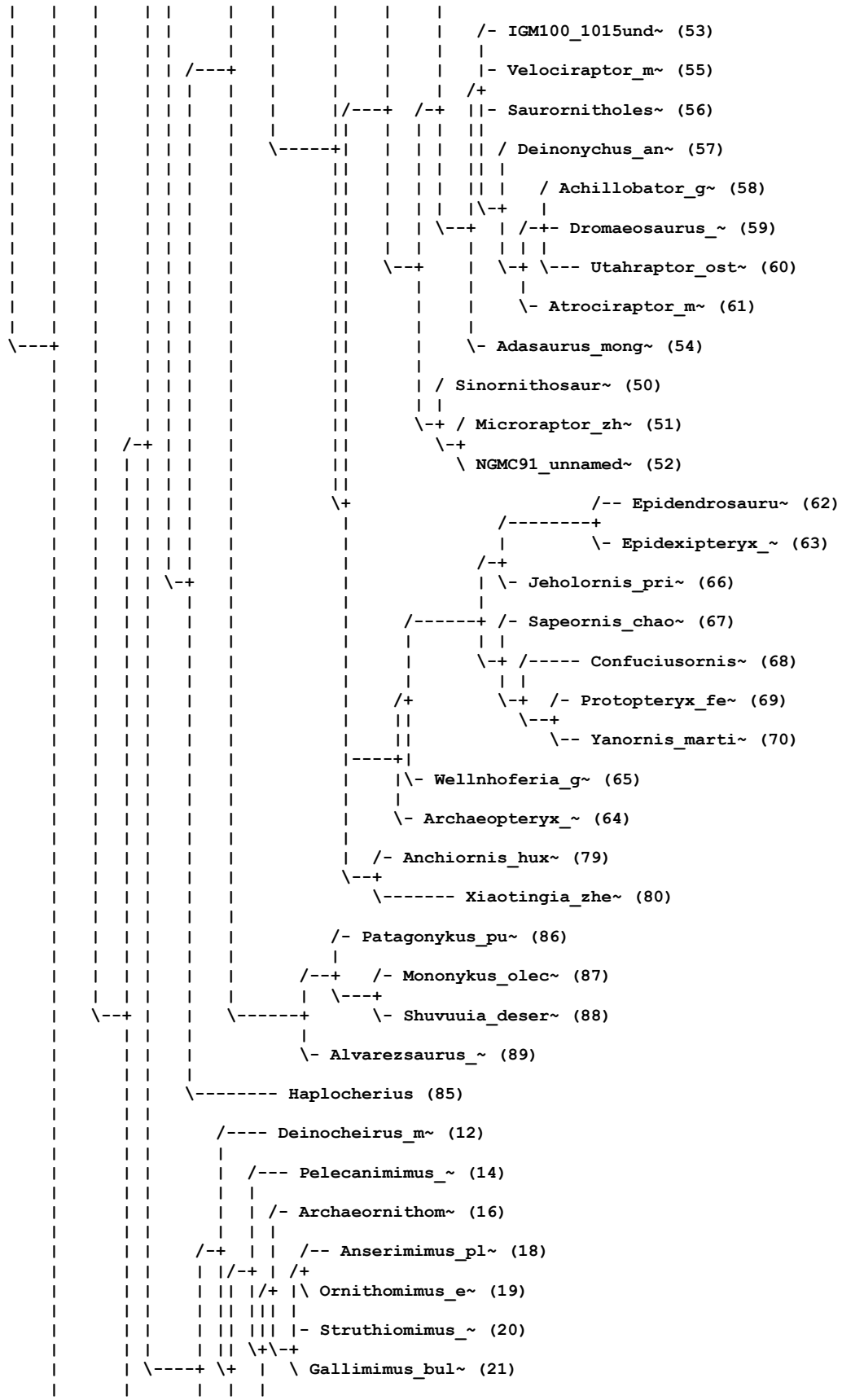
Figure 2. Template of the *MRBAYES* script [1]) used in this study. The script creates 3000000 (*ngen*) Markov Chain ([10]) generations, (Monte Carlo, [11]) sampling every 100 (*samplefreq*) generations. The first 10000 (*burnin*) trees are discarded. Partial tree consensus (*contype*) is allowed. For definitions of other parameters used in this script, see [1].

3.0 Results

Figure 3 (which includes *X. zhengi*) is the tree output by the script shown in Figure 2. The time to solution on the platform described in Section 2.0 was 4 hours 51 minutes. (Some taxon names are shortened in Figure 3; the full names can be found in [5])




Nothronychus_m~ (25)
Erliansaurus_b~ (26)
Nanshiungosaur~ (27)
Neimongosaurus~ (28)
Segnosaurus_ga~ (29)
Erlikosaurus_a~ (30)
Therizinosauru~ (32)
Protarchaeopte~ (33)
Elmisaurus_rar~ (34)
Hagryphus_giga~ (71)
Chirostenotes_~ (76)
Rinchenia_mong~ (35)
Citipati_osmol~ (36)
Ingenia_yanshi~ (37)
Heyuannia_huan~ (39)
Khaan_mckennai (38)
Conchoraptor_g~ (75)
Oviraptor_phil~ (74)
IGM100_42_unna~ (78)
Microvenator_c~ (72)
Avimimus_porte~ (73)
Caudipteryx (84)
Similicaudipte~ (83)
Incisivosaurus~ (77)
Byronosaurus_j~ (40)
Sinornithoides~ (41)
IGM100_44_unna~ (42)
Troodon_formos~ (43)
Saurornithoide~ (44)
Zanabazar_juni~ (45)
Mei_long (82)
Sinovenator_ch~ (81)
Unenlagia (46)
Rahonavis_ostr~ (48)
Buitreraptor_g~ (47)
Bambiraptor_fe~ (49)


/- IGM100_1015und~ (53)
|- Velociraptor_m~ (55)
|- Saurornitholes~ (56)
/ Deinonychus_an~ (57)
/ Achillobator_g~ (58)
/-+- Dromaeosaurus_~ (59)
\--- Utahraptor_ost~ (60)
\- Atrociraptor_m~ (61)
\- Adasaurus_mong~ (54)
/ Sinornithosaur~ (50)
\-+ / Microraptor_zh~ (51)
\ NGMC91_unnamed~ (52)
/-- Epidendrosauru~ (62)
\- Epidexipteryx_~ (63)
\- Jeholornis_pri~ (66)
/- Sapeornis_chao~ (67)
\-+ /----- Confuciusornis~ (68)
/- Protopteryx_fe~ (69)
\-- Yanornis_marti~ (70)
|\- Wellnhoferia_g~ (65)
\- Archaeopteryx_~ (64)
/- Anchiornis_hux~ (79)
\------- Xiaotingia_zhe~ (80)
/- Patagonykus_pu~ (86)
/- Mononykus_olec~ (87)
\- Shuvuuia_deser~ (88)
\- Alvarezsaurus_~ (89)
\-------- Haplocherius (85)
/---- Deinocheirus_m~ (12)
/--- Pelecanimimus_~ (14)
/- Archaeornithom~ (16)
/-- Anserimimus_pl~ (18)
Ornithomimus_e~ (19)
|- Struthiomimus_~ (20)
\ Gallimimus_bul~ (21)

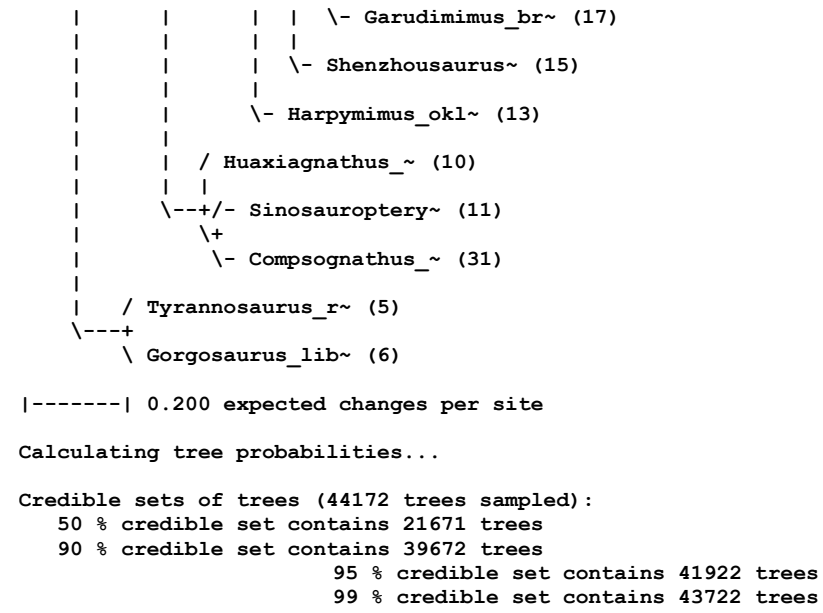


Figure 3. Phylogenetic tree produced by the script shown in Figure 2, with *X. zhengi*, showing that *Archaeopteryx* (in red) is more similar archaeopterygids and basal deinonychosaurs than to the oviraptorosaurs. *X. zhengi* is shown in blue. The relative phylogenetic position of *Archaeopteryx* does not change if *X. zhengi* is removed from the dataset (tree not shown).

Based on the system monitor of the platform described in Section 2.0, two of the four cores on the system performed 99% of the computational work for the MRBAYES script. Utilization of these two cores ranged from about 25% to 50%. The computation required approximately 1.5 GB memory.

4.0 Conclusions and discussion

The results in Section 3.0 motivate several observations:

1. Figure 3 demonstrates that *Archaeopteryx* is more similar to the archaeopterygids and basal deinonychosaurs than to the oviraptorosaurs, even when *X. zhengi* is included in the dataset.

2. The results of this study agree with those of [3] and [13].

3. It is not unusual for different phylogenetic methods to produce somewhat different results when applied to the same data set. Except on data sets containing no more than a few tens of taxa, today's practical phylogenetic algorithms must use some approximations and heuristics in order to execute in tolerable time. The MP algorithm used in [5], for example, restricts its combinatorial tree searches to a relatively localized region of tree space; the Bayesian algorithm used in the present study samples less than

the full population of generations produced. Bayesian methods have the distinct theoretical advantage, however, that if the sample selected is large enough, the Central Limit Theorem ([12], Chap. 7) guarantees the solution based on the sample will converge to the population distribution of trees; heuristic MP cannot be guaranteed to satisfy this criterion.

5.0 Acknowledgements

This work benefited from discussions with Tony Pawlicki and Mike Lee, with Town Peterson and Kris Krishtalka of the University of Kansas Biodiversity Institute, and with Joan Hunt of the University of Kansas Medical Center. For any problems that remain, I am solely responsible.

APPENDIX. Data matrix used in the MRBAYES script shown in Figure 2.

```
#NEXUS

[
     File:     bay_archae_nexus4.txt

     Purpose:  this file implements a MrBayes (Ref. 1) script for
               the morphological data in the Supplementary Data,
               Ref. 2, edited to 374 characters.


     Notes:

       none


     History:

       1.  30 July 2011.  Adapted from Supplementary Information for Ref. 2.  J. Horner.


     References:


         1.  Ronquist F and Huelsenbeck JP.  MRBAYES 3: Bayesian
             phylogenetic inference under mixed models.  Bioinformatics
             19 (2003),  1572-1574.

        2.  Xu X, You H, Du K, and Han F.  An Archaeopteryx-like
             theropod from China and the origin of Avialae.
             Nature 475 (28 July 2011), 465-470. Supplementary
             information, including the morphological descriptors,
             can be found at www.nature.com.


     Language/format:

         MrBayes NEXUS (Ref. 1)

]


[   Character list (Characters 1-363 are from Hu et al. (2009), whereas 364-374 are newly
added in Ref. 1).

1.  Vaned feathers on forelimb symmetric (0) or asymmetric (1). The barbs on opposite
sides of the rachis differ in length; in extant birds, the barbs on the leading edge of
flight feathers are shorter than those on the trailing edge.

2.  Orbit round in lateral or dorsolateral view (0) or dorsoventrally elongate (1). It is
unclear that the eye occupied the entire orbit of those taxa in which it is keyhole
shaped.

3.  Anterior process of postorbital projects into orbit (0) or does not project into
orbit (1).
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4. Postorbital in lateral view with subhorizontal anterior (frontal) process (0) or frontal process diagonal (anterior tip of process higher than base of process) (1). (Formerly: postorbital in lateral view with straight anterior (frontal) process (0) or frontal process curves anterodorsally and dorsal border of temporal bar is dorsally concave (1))

5. Postorbital bar parallels quadrate, lower temporal fenestra rectangular in shape (0) or jugal and postorbital approach or contact quadratojugal to constrict lower temporal fenestra (1).

6. Otosphenoidal crest vertical on basisphenoid and prootic, and does not border an enlarged pneumatic recess (0) or well developed, crescent shaped, thin crest forms anterior edge of enlarged pneumatic recess (1). This structure forms the anterior, and most distinct, border of the ?lateral depression? of the middle ear region (see Currie, 1985; Currie and Zhao, 1992) of troodontids and some extant avians.

7. Crista interfenestralis confluent with lateral surface of prootic and opisthotic (0) or distinctly depressed within middle ear opening (1).

8. Subotic recess (pneumatic fossa ventral to fenestra ovalis) absent (0) or present (1)

9. Basisphenoid recess present between basisphenoid and basioccipital (0) or entirely within basisphenoid (1) or absent (2).

10. Posterior opening of basisphenoid recess single (0) or divided into two small, circular foramina by a thin bar of bone (1).

11. Base of cultriform process not highly pneumatized (0) or base of cultriform process (parasphenoid rostrum) expanded and pneumatic (parasphenoid bulla) (1).

12. Basipterygoid processes ventral or anteroventrally projecting (0) or lateroventrally projecting (1).

13. Basipterygoid processes well developed, extending as a distinct process from the base of the basisphenoid (0) or processes abbreviated or absent (1).

14. Basipterygoid processes solid (0) or processes hollow (1).

15. Basipterygoid recesses on dorsolateral surfaces of basipterygoid processes absent (0) or present (1).

16. Depression for pneumatic recess on prootic absent (0) or present as dorsally open fossa on prootic/opisthotic (1) or present as deep, posterolaterally directed concavity (2). The
Wdorsal tympanic recess referred to here is the depression anterodorsal to the middle ear on the opisthotic, not the recess dorsal to the crista interfenestralis within the middle ear as seen in Archaeopteryx lithographica, Shuuvuia deserti and Aves.

17. Accessory tympanic recess dorsal to crista interfenestralis absent (0) small pocket present (1) or extensive with indirect pneumatization (2). According to Witmer (1990), this structure may be an extension from the caudal tympanic recess, although it has been interpreted as the main part of the caudal tympanic recess by some authors (e.g., Walker, 1985).

18. Caudal (posterior) tympanic recess absent (0) present as opening on anterior surface of paroccipital process (1) or extends into opisthotic posterodorsal to fenestra ovalis, confluent with this fenestra (2).

19. Exits of C. N. X-XII flush with surface of exoccipital (0) or cranial nerve exits located together in a bowl-like basisphenoid depression (1).

20. Maxillary process of premaxilla contacts nasal to form posterior border of nares (0) or maxillary process reduced so that maxilla participates broadly in external naris (1) or maxillary process of premaxilla extends posteriorly to separate maxilla from nasal posterior to nares (2).

21. Internarial bar rounded (0) or flat (1).

22. Crenulate margin on buccal edge of premaxilla absent (0) or present (1).

23. Caudal margin of naris farther rostral than (0), or nearly reaching or overlapping (1), the rostral border of the antorbital fossa (Chiappe et al. 1998).

24. Premaxillary symphysis acute, V-shaped (0) or rounded, U-shaped (1).

25. Secondary palate short (0) or long, with extensive palatal shelves on maxilla (1).

26. Palatal shelf of maxilla flat (0) or with midline ventral ?tooth-like? projection (1)

27. Pronounced, round accessory antorbital fenestra absent (0) or present (1). A small fenestra, variously termed the accessory antorbital fenestra or maxillary fenestra, penetrates the medial wall of the antorbital fossa anterior to the antorbital fenestra in a variety of coelurosaurs and other theropods.

28. Accessory antorbital fossa situated at rostral border of antorbital fossa (0) or situated posterior to rostral border of fossa (1).

29. Tertiary antorbital fenestra (fenestra promaxillaris) absent (0) or present (1).

30. Antorbital fossa without distinct rim ventrally and anteriorly (0) or with distinct rim composed of a thin wall of bone (1). A rim is most strongly developed in the therizinosauroid Erlikosaurus andrewsi (Clark et al., 1994) but is nearly absent in ornithomimosaurs.

31. Narial region apneumatic or poorly pneumatized (0) or with extensive pneumatic fossae, especially along posterodorsal rim of fossa (1).

32. Jugal and postorbital contribute equally to postorbital bar (0) or ascending process of jugal reduced and descending process of postorbital ventrally elongate (1).

33. Jugal quadratojugal process tall beneath lower temporal fenestra, twice or more as tall dorsoventrally as it is wide transversely (0) or rod-like (1) or concealed by quadratojugal (2).

34. Jugal pneumatic recess in posteroventral corner of antorbital fossa present (0) or absent (1).

35. Medial jugal foramen present on medial surface ventral to postorbital bar (0) or absent (1).

6. Quadratojugal without horizontal process posterior to ascending process (reversed ?L? shape) (0) or with process (i.e., inverted ?T? or ?Y? shape) (1).

37. Jugal and quadratojugal separate (0) or quadratojugal and jugal fused and not distinguishable from one another (1).

38. Supraorbital crests on lacrimal in adult individuals absent (0) or dorsal crest above orbit (1) or lateral expansion anterior and dorsal to orbit (2).

39. Enlarged foramen or foramina opening laterally at the angle of the lacrimal, absent (0) or present (1).

40. Lacrimal posterodorsal process absent (0) or present (1)

41. Prefrontal large, dorsal exposure similar to that of lacrimal (0) or greatly reduced in exposure (1) or without exposure (2).

42. Frontals narrow anteriorly as a wedge between nasals (0) or end abruptly anteriorly, suture with nasal transversely orientated (1) or suture with nasals W-shaped (2).

43. Anterior emargination of supratemporal fossa on frontal straight or slightly curved (0) or strongly sinusoidal and reaching onto postorbital process (1).

44. Frontal postorbital process (dorsal view): smooth transition from orbital margin (0) or sharply demarcated from orbital margin (1)?

45. Frontal edge smooth in region of lacrimal suture (0) or edge notched (1).

46. Dorsal surface of parietals flat, lateral ridge borders supratemporal fenestra (0) or parietals dorsally convex with very low sagittal crest along midline (1) or dorsally convex with well developed sagittal crest (2).

47. Parietals separate (0) or fused (1).

48. Descending process of squamosal parallels quadrate shaft (0) or nearly perpendicular to quadrate shaft (1).

49. Descending process of squamosal contacts quadratojugal (0) or does not contact quadratojugal (1).

50. Posterolateral shelf on squamosal overhanging quadrate head absent (0) or present (1).

51. Dorsal process of quadrate single headed (0) or with two distinct heads, a lateral one contacting the squamosal and a medial head contacting the braincase (1).

52. Quadrate vertical (0) or strongly inclined anteroventrally so that distal end lies far forward of proximal end (1).

53. Quadrate solid (0) or hollow, with depression on posterior surface (1).

54. Lateral border of quadrate shaft straight (0) or with lateral tab that touches squamosal and quadratojugal above an enlarged quadrate foramen (1)

55. Foramen magnum subcircular, slightly wider than tall (0) or oval, taller than wide (1).

56. Occipital condyle without constricted neck (0) or subspherical with constricted neck (1).

57. Paroccipital process elongate and slender, with dorsal and ventral edges nearly parallel (0) or process short, deep with convex distal end (1).

58. Paroccipital process straight, projects laterally or posterolaterally (0) or distal end curves ventrally, pendant (1).

59. Paroccipital process with straight dorsal edge (0) or with dorsal edge twisted rostrolaterally at distal end (1).

60. Ectopterygoid with constricted opening into fossa (0) or with open ventral fossa in the main body of the element (1).

61. Dorsal recess on ectopterygoid absent (0) or present (1).

62. Flange of pterygoid well developed (0) or reduced in size or absent (1).

63. Palatine and ectopterygoid separated by pterygoid (0) or contact (1).

64. Palatine tetraradiate, with jugal process (0) or palatine triradiate, jugal process absent (1).

65. Suborbital fenestra similar in length to orbit (0) or about half or less than half orbital length (1) or absent (2).

66. Symphyseal region of dentary broad and straight, paralleling lateral margin (0) or medially recurved slightly (1) or strongly recurved medially (2).

67. Dentary symphyseal region in line with main part of buccal edge (0) or downturned at rostral end (1)

68. Mandible without coronoid prominence (0) or with coronoid prominence (1).

69. Posterior end of dentary without posterodorsal process dorsal to mandibular fenestra (0) or with dorsal process above anterior end of mandibular fenestra (1) or with elongate, strongly arched dorsal process extending over most of fenestra (2).

70.Labial face of dentary flat (0) or with lateral ridge and inset tooth row (1).

71.Dentary subtriangular in lateral view (0) or with subparallel dorsal and ventral edges (1).

72.Nutrient foramina on external surface of dentary superficial (0) or lie within a deep groove that widens posteriorly (1).

73.External mandibular fenestra oval (0) or subdivided by a spinous rostral process of the surangular (1).

74.Internal mandibular fenestra small and slit-like (0) or large and rounded (1).

75.Foramen in lateral surface of surangular rostral to mandibular articulation, absent (0) or present (1).

76.Splenial not widely exposed on lateral surface of mandible (0) or exposed as a broad triangle between dentary and angular on lateral surface of mandible (1).

77.Coronoid ossification large (0) or only a thin splint (1) or absent (2).

78.Articular without elongate, slender medial, posteromedial, or mediodorsal process from retroarticular process (0) or with process (1).

79.Retroarticular process short, stout (0) or elongate and slender (1).

80.Mandibular articulation surface as long as distal end of quadrate (0) or twice or more as long as quadrate surface, allowing anteroposterior movement of mandible (1).

81.Premaxilla toothed (0) or edentulous (1).

82.Second premaxillary tooth approximately equivalent in size to other premaxillary teeth (0) or second tooth markedly larger than third and fourth premaxillary teeth (1) or first premaxillary tooth considerably larger than the posterior ones (2) modified.

83.Maxilla toothed (0) or edentulous (1).

84.Maxillary and dentary teeth serrated (0) or some without serrations anteriorly (except at base in S. mongoliensis) (1) or all without serrations (2).

85.Dentary and maxillary teeth large, less than 25 in dentary (0) or large number of small teeth (25 or more in dentary) (1) or small number of dentary teeth (=11) (2) or dentary without teeth (3).

86.Serration denticles large (0) or small (1).

87.Serrations simple, denticles convex (0) or distal and often mesial edges of teeth with large, hooked denticles that point toward the tip of the crown (1).

88.Teeth constricted between root and crown (0) or root and crown confluent (1).

89.Dentary teeth evenly spaced (0) or anterior dentary teeth smaller, more numerous, and more closely appressed than those in middle of tooth row (1).

90.Dentaries lack distinct interdental plates (0) or with interdental plates medially between teeth (1).

91.In cross section, premaxillary tooth crowns sub-oval to sub-circular (0) or asymmetrical (D-shaped in cross section) with flat lingual surface (1) or first premaxillary tooth with flat lingual surface, other premaxillary teeth without flat lingual surfaces (2).

92.Number of cervical vertebrae: 10 (0) or 12 or more (1).

93.Axial epipophyses absent or poorly developed, not extending past posterior rim of postzygopophyses (0) or large and posteriorly directed, extend beyond postzygapophyses (1).

94.Axial neural spine flared transversely (0) or compressed mediolaterally (1).

95.Epipophyses of cervical vertebrae placed distally on postzygapophyses, above postzygopophyseal facets (0) or placed proximally, proximal to postzygapophyseal facets (1).

96.Anterior cervical centra level with or shorter than posterior extent of neural arch (0) or centra extending beyond posterior limit of neural arch (1).

97.Carotid process on posterior cervical vertebrae absent (0) or present (1).

98.Anterior cervical centra subcircular or square in anterior view (0) or distinctly wider than high, kidney shaped (1).

99.Cervical neural spines anteroposteriorly long and dorsoventrally tall (0) or anteroposteriorly short, dorsoventrally low and centred on neural arch, giving arch an ?X? shape in dorsal view (1) or anteroposteriorly short and dorsoventrally tall (2) or anteroposteriorly long and dorsoventrally short (3).

100.Cervical centra with one pair of pneumatic openings (0) or with two pairs of pneumatic openings (1).

101.Cervical and anterior trunk vertebrae amphiplatyan (0) or opisthocoelous (1).

102.Anterior trunk vertebrae without prominent hypapophyses (0) or with large hypapophyses (1).

103.Parapophyses of posterior trunk vertebrae flush with neural arch (0) or distinctly projected on pedicels (1).

104.Hyposphene -hypantrum articulations in trunk vertebrae absent (0) or present (1).

105.Zygapophyses of trunk vertebrae abutting one another above neural canal, opposite hyposphenes meet to form lamina (0), or zygapohyses placed lateral to neural canal and separated by groove for interspinuous ligaments, hyposphens separated (1).

106.Middle and posterior dorsal vertebrae not pneumatic (0) or pneumatic (1).

107.Transverse processes of anterior dorsal vertebrae long and thin (0) or short, wide, and only slightly inclined (1).

108.Neural spines of dorsal vertebrae not expanded distally (0) or expanded to form ?spine table? (1).

109.Scars for interspinous ligaments terminate at apex of neural spine in dorsal vertebrae (0) or terminate below apex of neural spine (1).

110.Number of sacral vertebrae: 5 (0) or 6 (1) or 7 or more (2).

111.Sacral vertebrae with unfused zygapophyses (0) or with fused zygapophyses forming a sinuous ridge in dorsal view (1).

112.Ventral surface of posterior sacral centra gently rounded, convex (0) or ventrally flattened, sometimes with shallow sulcus (1) or centrum strongly constricted transversely, ventral surface keeled (2).

113.Pleurocoels absent on sacral vertebrae (0) or present on anterior sacrals only (1) or present on all sacrals (2).

114.Last sacral centrum with flat posterior articulation surface (0) or convex articulation surface (1).

115.Caudal vertebrae with distinct transition point (0) or without transition point (1).

116.Transition point in caudal series begins distal to the 10th caudal (0) or between 7th and 10th caudal vertebra (1) or proximal to the 7th caudal vertebra (2).

117.Anterior caudal centra tall, oval in cross section (0) or with box-like centra in caudals I-V (1) or anterior caudal centra laterally compressed with ventral keel (2).

118.Neural spines of caudal vertebrae simple, undivided (0) or separated into anterior and posterior alae throughout much of caudal sequence (1).

119.Neural spines on distal caudals form a low ridge (0) or spine absent (1) or midline sulcus in center of neural arch (2).

120.Prezygapophyses of distal caudal vertebrae between 1/3 and whole centrum length (0) or with extremely long extensions of the prezygapophyses (up to 10 vertebral segments long in some taxa) (1) or strongly reduced as in Archaeopteryx lithographica (2).

121.More than 30 caudal vertebrae (0) or 21?30 caudal vertebrae (1) or < 10 caudal vertebrae, followed by pygostyle (2) or 11?20 vertebrae (3).

122.Proximal end of chevrons of proximal caudals short anteroposteriorly, shaft proximodistally elongate (0) or proximal end elongate anteroposteriorly, flattened and plate-like (1).

123.Distal caudal chevrons are simple (0) or anteriorly bifurcate (1) or bifurcate at both ends (2).

124.Shaft of cervical ribs slender and longer than vertebra to which they articulate (0) or broad and shorter than vertebra (1).

125.Ossified uncinate processes absent (0) or present (1).

126.Ossified ventral rib segments absent (0) or present (1).

127.Lateral gastral segment shorter than medial one in each arch (0) or distal segment longer than proximal segment (1).

128.Ossified sternal plates separate in adults (0) or fused (1).

129.Sternum without distinct lateral xiphoid process posterior to costal margin (0) or with lateral xiphoid process (1).
130.Anterior edge of sternum grooved for reception of coracoids (0) or sternum without grooves (1).

131.Articular facet of coracoid on sternum (conditions may be determined by the articular facet on coracoid in taxa without ossified sternum): anterolateral or more lateral than anterior (0); almost anterior (1).

132.Hypocleidium on furcula absent (0) or present (1). The hypocleidium is a process extending from the ventral midline of the furcula, and is attached to the sternum by a ligament in extant birds.

133.Acromion margin of scapula continuous with blade (0) or anterior edge laterally everted (1).

134.Anterior surface of coracoid ventral to glenoid fossa unexpanded (0) or anterior edge of coracoid expanded, forms triangular subglenoid fossa bounded laterally by coracoid tuber (1).

135.Scapula and coracoid separate (0) or fused into scapulacoracoid (1).

136.Coracoid in lateral view subcircular, with shallow ventral blade (0) or subquadrangular with extensive ventral blade (1) or shallow ventral blade with elongate posteroventral process (2) or subtriangular (proximal end constricted, distal end wide) (3).

137.Scapula and coracoid form a continuous arc in posterior and anterior views (0) or coracoid inflected medially, scapulocoracoid ?L? shaped in lateral view (1).

138.Glenoid fossa without (0) or with extension of glenoid floor onto external surface of scapula (the surface opposite the costal surface) (1).

139.Scapula longer than humerus (0) or humerus longer than scapula (1).

140.Deltopectoral crest large and distinct, proximal end of humerus quadrangular in anterior view (0) or deltopectoral crest less pronounced, forming an arc rather than being quadrangular (1) or deltopectoral crest very weakly developed, proximal end of humerus with rounded edges (2) or deltopectoral crest extremely long (3) or proximal end of humerus extremely broad, triangular in anterior view (4).

141.Anterior surface of deltopectoral crest smooth (0) or with distinct groove or ridge near lateral edge along distal end of crest (1).

142.Olecranon process weakly developed (0) or distinct and large but not hypertrophied (1) or hypertrophied (2).

143.Distal articular surface of ulna flat (0) or convex, semilunate surface (1).

144.Proximal surface of ulna a single continuous articular facet (0) or divided into two distinct fossae separated by a median ridge (1).

145.Lateral proximal carpal (ulnare?) quadrangular (0) or triangular in proximal view (1).

146.Two distal carpals in contact with metacarpals, one covering the base of metacarpal I (and perhaps contacting metacarpal II) the other covering the base of metacarpal II (distal carpals 1 and 2 unfused) (0) or a single distal carpal capping metacarpals I and II (distal carpals 1 and 2 fused) (1).

147.Distal carpals not fused to metacarpals (0) or fused to metacarpals, forming carpometacarpus (1).

148.Distal carpals 1+2 well developed, covering all of proximal ends of metacarpals I and II (0) or small, cover about half of base of metacarpals I and II (1) or cover bases of allmetacarpals (2).

149.Metacarpal I half or less than half the length of metacarpal II, and longer proximodistally than wide transversely (0) or subequal in length to metacarpal II (1) or very short and wider transversely than long proximodistally (2).

150.Third manual digit present, phalanges present (0) or reduced to no more than metacarpal splint (1).

151.Flexor tubercles of manual unguals proximal (0) or displaced distally from articular end (1) or proximodistally elongated with proximal end close to articular facet (2).

152.Unguals on all digits generally similar in size (0) or digit I bearing large ungual and unguals of other digits distinctly smaller (1).

153.Proximodorsal ?lip? on first manual ungual ? a transverse ridge immediately dorsal to the articulating surface ? absent (0) or present (1).

154.Ventral edge of anterior ala of ilium straight or gently curved (0) or ventral edge hooked anteriorly (1) or very strongly hooked (2).

155.Preacetabular part of ilium roughly as long as postacetabular part of ilium (0) or preacetabular portion of ilium markedly longer (more than 2/3 of total ilium length) than postacetabular part (1).

156.Anterior end of ilium gently rounded or straight (0) or anterior end strongly curved (1) or pointed at anterodorsal corner (2).

157.Supraacetabular crest on ilium as a separate process from antitrochanter, forms ?hood? over femoral head present (0) reduced, not forming hood (1) or absent (2).

158.Postacetabular ala of ilium in lateral view squared (0) or acuminate (1).

159.Postacetabular blades of ilia in dorsal view parallel (0) or diverge posteriorly (1).

160.Tuber along dorsal edge of ilium, dorsal or slightly posterior to acetabulum absent (0) or present (1).

161.Brevis fossa shelf-like (0) or deeply concave with lateral overhang (1).

162.Antitrochanter posterior to acetabulum absent or poorly developed (0) or prominent (1).

163.Ridge bordering cuppedicus fossa extends far posteriorly and is confluent or almost confluent with acetabular rim (0) or ridge terminates rostral to acetabulum or curves ventrally onto anterior end of pubic peduncle (1).

164.Cuppedicus fossa deep, ventrally concave (0) or fossa shallow or flat, with no lateral overhang (1) or absent (2).

165.Posterior edge of ischium without (0) or with prominent proximodorsal prong (1).

166.Shaft of ischium straight in lateral view (0) or ventrodistal end curved anteriorly (1) or curved dorsally (posterodorsally concave) (2) (Marya?nska et al. 2002).

167.Obturator process of ischium absent (0) or proximal in position (1) or distally displaced (2).

168.Obturator process does not contact pubis (0) or contacts pubis (1).

169.Length of pubic boot=30% length of pubis (0) or=40% (1).

170.Semicircular scar on posterior part of the proximal end of the ischium, absent (0) or present (1).

171.Ischium, ischium length as measured by ischial length/pubic length ratio: between 70%-100% (0), or between 50%- 70% (1) or below 50% (2) or above 100% (3).

172.Distal ends of ischia form symphysis (0) or approach one another but do not form symphysis (1) or widely separated (2).

173.Ischial boot (expanded distal end) present (0) or absent (1).

174.Tubercle on anterior edge of ischium absent (0) or present (1).

175.Pubis propubic (0) or pubis vertical (1) or pubis moderately posteriorly oriented (2) or pubis fully posteriorly oriented (opisthopubic) (3).

176.Pubic boot projects anteriorly and posteriorly (0) or with little or no anterior process (1) or no anteroposterior projections (2).

177.Shelf on pubic shaft proximal to symphysis (?pubic apron?) extends medially from middle of cylindrical pubic shaft (0) or shelf extends medially from anterior edge of anteroposteriorly flattened shaft (1).

178.Pubic shaft straight (0) or distal end curves anteriorly, anterior surface of shaft concave in lateral view (1) or anterior surface of shaft convex in lateral view (2).

179.Pubic apron about half of pubic shaft length (0) or less than 1/3 of shaft length (1).

180.Femoral head without fovea capitalis (for attachment of capital ligament) (0) or circular fovea present in center of medial surface of head (1).

181.Lesser and greater trochanters unfused (0) or fused (1).

182.Lesser trochanter of femur alariform (0) or cylindrical in cross section (1).
183.Posterior trochanter absent or represented only by rugose area (0) or posterior trochanter distinctly raised from shaft, mound-like (1).

184.Fourth trochanter on femur present (0) or absent (1).

185.Accessory trochanteric crest distal to lesser trochanter absent (0) or present (1).

186.Anterior surface of femur proximal to medial distal condyle without longitudinal crest (0) or crest present extending proximally from medial condyle on anterior surface of shaft (1).

187.Popliteal fossa on distal end of femur open distally (0) or closed off distally by contact betweeen distal condyles (1).

188.Fibula reaches proximal tarsals (0) or short, tapering distally, and not in contact with proximal tarsals (1).

189.Medial surface of proximal end of fibula concave along long axis (0) or flat (1).

190.Deep oval fossa on medial surface of fibula near proximal end absent (0) or present (1).

191.Distal end of tibia and astragalus without distinct condyles (0) or with distinct condyles separated by prominent tendinal groove on anterior surface (1).

192.Medial cnemial crest absent (0) or present on proximal end of tibia (1).

193.Ascending process of the astragalus tall and broad, covering most of anterior surface of distal end of tibia (0) or process short and slender, covering only lateral half of anterior surface of tibia (1) or ascending process tall with medial notch that restricts it to lateral side of anterior face of distal tibia (2).

194.Ascending process of astragalus confluent with condylar portion (0) or separated by transverse groove or fossa across base (1).

195.Astragalus and calcaneum separate from tibia (0) or fused to each other and to the tibia in late ontogeny (1).

196.Distal tarsals separate, not fused to metatarsals (0) or form metatarsal cap with intercondylar prominence that fuses to metatarsal early in postnatal ontogeny (1).

197.Metatarsals not co-ossified (0) or co-ossification of metatarsals begins proximally (1) or distally (2).

198.Distal end of metatarsal II smooth, not ginglymoid (0) or with developed ginglymus (1).

199.Distal end of metatarsal III smooth, not ginglymoid (0) or with developed ginglymus (1).

200.Metatarsal III, proximal end: not pinched (0) or pinched, but visible in anterior view (1) or pinched, and invisible in anterior view (2).

201.Ungual of pedal digit II similar in size to that of III (0) or pedal ungual II about 50% larger than pedal ungual III (1).

202.Metatarsal I articulates at middle of metatarsal II (0) or metatarsal I attaches to distal quarter of metatarsal II (1) or metatarsal I articulates with metatarsal II near its proximal end (2) or metatarsal I absent (3).

203.Metatarsal I attenuates proximally (0) or proximal end of metatarsal I similar to that of metatarsals II?IV (1).

204.Shaft of MT IV round or thicker dorsoventrally than wide in cross section (0) or shaft of MT IV mediolaterally widened and flat in cross section (1).

205.Foot symmetrical (0) or asymmetrical with slender MTII and very robust MT IV (1).

206.Neural spines on posterior dorsal vertebrae in lateral view rectangular or square (0) or anteroposteriorly expanded distally, fanshaped (1).

207.Shaft diameter of phalanx I-1 less (0) or greater (1) than shaft diameter of radius.

208.Angular exposed almost to end of mandible in lateral view, reaches or almost reaches articular (0) or excluded from posterior end angular suture turns ventrally and meets ventral border of mandible rostral to glenoid (1).

209.Laterally inclined flange along dorsal edge of surangular for articulation with lateral process of lateral quadrate condyle absent (0) or present (1).

210.Distal articular ends of metacarpals I + II ginglymoid (0) or rounded, smooth (1).

211.Radius and ulna well separated (0) or with distinct adherence or syndesmosis distally (1).

212.Kink and downward deflection in dentary buccal margin at rostral end of dentary: absent (0) or present (1).

213.Quadrate head covered by squamosal in lateral view (0) or quadrate cotyle of squamosal open laterally exposing quadrate head (1).

214.Brevis fossa poorly developed adjacent to ischial peduncle and without lateral overhang, medial edge of brevis fossa visible in lateral view (0), or fossa well developed along full length of postacetabular blade, lateral overhang extends along full length of fossa, medial edge completely covered in lateral view (1).

215.Vertical ridge on lesser trochanter present (0) or absent (1).

216.Supratemporal fenestra bounded laterally and posteriorly by the squamosal (0) or supratemporal fenestra extended as a fossa on to the dorsal surface of the squamosal (1).

217.Dentary fully toothed (0) or only with teeth rostrally (1) or edentulous (2).

218.Posterior edge of coracoid not or shallowly indented below glenoid (0), or posterior edge of coracoid deely notched just ventral to glenoid, glenoid lip everted (1).

219.Retroarticular process points caudally (0) or curves gently dorsocaudally (1) (Kobayashi, 2001).

220.Flange on supraglenoid buttress on scapula (see Nicholls and Russell, 1985) absent (0) or present (1).

221.Depression (possibly pneumatic) on ventral surface of postorbital process of laterosphenoid absent (0) or present (1).

222.Basal tubera set far apart, level with or beyond lateral edge of occipital condyle and/or foramen magnum (may connected by a web of bone or separated by a large notch) (0) or tubera small, directly below condyle and foramen magnum, and separated by a narrow notch (1).

223.Basioccipital without pneumatization on occipital surface (0) or with subcondylar recess (1).

224.Ventral surface of dentary straight or nearly straight (0) or descends strongly posteriorly (1).

225.Distal humerus with small or no medial epicondyle (0) or with large medial epicondyle, medial condyle centered on distal end (1).

226.Distal humeral condyles on distal end (0) or on anterior surface (1).

227.Ilium and ischium articulation flat or slightly concavo-convex (0) or ilium with process projecting into socket in ischium (1).

228.Roots of dentary and maxillary teeth mediolaterally compressed (0) or circular in cross-section (1).

229.Preacetabular portion of ilium parasagital (0) moderately laterally flaring (1) strongly laterally flaring (2).

230.Maxillary and dentary teeth labiolingually flattened and recurved, with crowns in middle of tooth row more than twice as high as the basal mesiolateral width (0) or lanceolate and subsymmetrical (1) or conical (2) or labiolingually flattened and recurved, with crowns in middle of tooth row less than twice as high as the basal mesiolateral width (fore?aft basal length) (3).

231.Dentary teeth do not (0) or do increase in size anteriorly, becoming more conical in shape (1).

232.Length of skull more than 90% femoral length (0) or less than 80% (1).

233.Height of skull (minus mandible) at middle of naris more than half the height of skull at middle of orbit (0) or less than half (1).

234.Dorsal margin of naris below level of dorsal margin of orbit (0) or above (1).

235.Snout does not (0) or does taper to an anterior point (1).

236.Area of antorbital fenestra greater than that of orbit (0) or less than that of orbit (1).

237.Body of premaxilla dorsoventrally deep (0) or dorsoventrally shallow (1).

238.Antorbital fossa anteriorly bounded by maxilla (0) or by premaxilla (1).

239.Maxillary antorbital fossa: small, from 10% to less than 40% of the rostrocaudal length of the antorbital cavity (0), large, greater than 40% of the rostrocaudal length of the antorbital cavity (1).

240.Maxillary fenestra large and round (0), a large, craniocaudally elongate oblong (1), a small, craniocaudally elongate slit, not dorsally displaced (2), or a small, dorsally displaced opening (3).

241.Nasal fusion: absent, nasals separate (0) or present, nasals fused together (1).

242.Nasal surface: smooth (0) or rugose (1).

243.Suborbital process of jugal short and dorsoventrally stout (0) or elongate and dorsoventrally narrow (1).

244.Nasals at least as long as frontals (0) or shorter than frontals (1).

245.Anterior upturning of nasals absent (0) or present (1).

246.Jugo-maxillary bar at ventral end of antorbital fenestra dorsoventrally deep (0) or dorsoventrally narrow (1).

247.Anteroventral corner of premaxilla does not (0) or does form an acute, ventrally orientated point in lateral view (1).

248.Length of preorbital region of cranium>height at anterior edge of preorbital bar (exclusive of midline sagittal ridge, if any) (0) or=height at anterior edge of preorbital bar (1).

249.Frontals without supraorbital rim (0) or with supraorbital rim (1).

250.Parietals shorter than frontals (0) or longer (1).

251.Length of ventral border of infratemporal fenestra comparable to that of orbit (0) or much shorter (1).

252.Foramen magnum smaller than or subequal to size of occipital condyle (0) or larger than occipital condyle (1).

253.Dentary not bowed (0) or bowed (concave dorsally) (1).

254.Meckelian groove of dentary deep (0) or shallow (1).

255.Dentary without posteroventral process extending to posterior end of external mandibular fenestra (0) or with such a process (1).

256.Horizontal shelf on the lateral surface of the surangular, rostral and ventral to the mandibular condyle: absent or faint ridge (0), prominent and extending laterally (1).

257.Premaxillary teeth subequal in size to (0) or much smaller than (1) the maxillary teeth.

258.Approximately the same number of denticles per 5 mm on mesial keels of teeth as on distal keels (0) or markedly more denticles per 5 mm on mesial keels (1).

259.Maxillary teeth subperpendicular to ventral margin of maxilla (0) or strongly inclined (1).

260.Dentary tooth implantation: in sockets (0), in paradental groove (1).

261.Dentary dentition continues cranially to tip of dentary (0) or terminates before reaching dentary tip (1).

262.Length of mid-cervical centra approximately the same as dorsal centra (0) or markedly longer than dorsal centra (1).

263.Cervical prezygapophyses unflexed (0) or flexed (1).

264.Dorsal centra=1.2?taller than long (0) or height=length (1).

265.Posterior dorsal neural spines=1.5xtaller than long (0) or height<1.5?length (1).

266.Postzygapophyses of middle and posterior dorsal vertebrae do not extend posterior to centrum (0) or do (1).

267.Anteriormost haemal arches=1.5xlonger than associated centra (0) or<1.5?as long as centra (1).

268.Angle between furcular arms>80? (0) or<60? (1).

269.Acromion process contacts coracoid (0), or reduced and does not contact coracoid (1).

270.Acromion process does not match any of the following descriptions: (0) rectangular with its dorsal edge forming a 90? angle with the dorsal edge of the scapular blade (1) or a quarter-circle in shape (2) or triangular, with apex pointing away from and subparallel to scapular blade (3).

271.Scapulocoracoid dorsal margin: pronounced notch between the acromion process and the coracoid (0) or margin smooth (1).

272.Wide distal expansion of scapula absent (0) or present (1).

273.Acrocoracoid process absent (0) or present (1).

274.Humeral length is half femoral length or less (0) or shorter than femur but more than half femoral length (1) or longer than femur (2).

275.Length of humeral shaft between deltopectoral crest and distal condyles<4.5xshaft diameter (0) or>4.5?shaft diameter (1).

276.Ulna not bowed away from humerus (0), or bowed away from humerus (1).

277.Length of radius<1/3 femoral length (0) or between 1/3 and 2/3 femoral length (1) or between 2/3 and 1?femoral length (2) or>femoral length (3).

278.Radial diameter>0.5?ulnar diameter (0) or=0.5? (1).

279.Distal carpals 1+2 flattish (0) or semilunate in shape (1).

280.Length of manual digit II (including metacarpal) less than 1.25?femoral length (0) or=1.25?femoral length (1).

281.Distal end of metacarpal I medially (0) or laterally rotated (1).

282.Medial side of metacarpal II: expanded proximally (0), not expanded (1).

283.Metacarpal III>0.8?length of metacarpal II (0) or<0.8?(1).

284.Manual phalanx I-1 longer than metacarpal II (0) or shorter (1).

285.Length of metacarpal II<length of metacarpal I + phalanx I-1 (0) or=(1).

286.Metacarpals II and III are not (0) or are appressed for their entire lengths (1).

287.Proximal end of metacarpal III is not (0) or is mainly palmar to that of metacarpal II (1).

288.Length of manual phalanx II-2<1.2?length of phalanx II-1 (0) or>1.2?(1).

289.Medial ligament pits of manual phalanges deep (0) or shallow (1).

290.Posterior flange on manual phalanx II-1 absent (0) or present (1).

291.Combined lengths of manual phalanges II-1 and II- 2>length of metacarpal II + carpus (0) or=length of metacarpal II +carpus (1).

292.Length of manual phalanx II-1<2?length of III-1 (0) or=2?length of III-1 (1).

293.Length of manual phalanx II-2<2?length of II-1 (0) or=2?(1).

294.Length of manual phalanx III-1, sub-equal to III-2 (0) or considerably longer (1) or considerably shorter (2). Modified.

295.Manual phalanx I-1 straight (0) or bowed (palmar surface concave) (1).

296.With proximal articular surface of ungual orientated vertically, dorsal surface of manual ungual I does not (0) or does arch higher than level of dorsal extremity of proximal articular surface (1).

297.With proximal articular surface of ungual orientated vertically, dorsal surface of manual ungual II does not (0) or does arch higher than level of dorsal extremity of proximal articular surface.

298.Manual ungual I strongly curved (0), weakly curved (1), or straight (2).

299.Manual unguals II and III strongly curved (0), weakly curved, (1), or straight (2).

300.Proximodorsal ?lip? on manual unguals II and III absent (0) or present (1).

301.Manual digit III with four phalanges (0) or less than four phalanges (1).

302.Manual phalanx III-3 markedly shorter than combined lengths of phalanges III-1 and III-2 (0), subequal in length to their combined lengths (1), or markedly longer (2).

303.Arching of preacetabular iliac blade above height of postacetabular blade absent or small (0) or extreme (1).

304.Shaft of ischium subequal in thickness to the pubis (0), slenderer than the pubic shaft (1), thicker than the pubic shaft (2).

305.Obturator process does not (0) or does form a strongly acute angle in lateral view (1).

306.Obturator process does not (0) or does reach tip of ischium (1).

307.Ventral notch between the distal portion of the obturator process and the shaft of the ischium: present (0), absent (1).

308.Strong kink of pubis at midshaft absent (0) or present, displacing distal half of pubis caudally (1).

309.In adult, femur longer than tibia (0) or shorter (1)

310.Tip of lesser trochanter below level of femoral head (0) or level with femoral head (1).

311.Proximolateral (fibular) condyle of the tibia, development in proximal view: bulge from the main surface of the tibia (0), conspicuous narrowing between the body of the condyle and the main body of the tibia (1).

312.Metatarsus less than half length of femur (0) or more than half femoral length (1) or longer than femur (2).

313.Metatarsal cross-sectional proportions: subequal or wider mediolaterally than craniocaudally at midshaft (0), deeper craniocaudally than mediolaterally at midshaft (1).

314.Shafts of metatarsals not appressed (0) or appressed (1).

315.Length of metatarsal V=0.5?length of metatarsal IV (0) or<0.5?(1).

316.Marked decrease in transverse width of metatarsus distally, absent (0) or present (1).

317.Plantar surface of hallux faces posteriorly (0) or hallux reorientated so that plantar surface faces medially or anteriorly (1).

318.Hallucal ungual reduced in size relative to other pedal unguals (0) or not reduced (1).

319.Hallucal ungual weakly curved (0) or strongly curved (1).

320.Length of pedal phalanx II-2 between 0.6?and 1?length of phalanx II-1 (0),=0.6 ?, or (1)=1?(2).

321.Total length of pedal phalanx II-2 (not counting posteroventral lip, if any)>2?length of distal condylar eminence (0) or=2?(1).

322.Pedal phalanx II-2 without posteroventral lip or keel (0) with transversely wide posteroventral lip (1) with transversely narrow posteroventral keel (2).

323.Pedal phalanx II-1 without dorsal extension of distal condyles (0) or with extension (1).

324.Pedal unguals III and IV straight or weakly curved (0), or strongly curved (1).

325.With fingers extended, tip of ungual III extends no further distally than flexor tubercle of ungual II (0) or extends further (1).

326.Manual ungual III smaller than ungual II (0) or approximately the same size (1).

327.Diameter of non-ungual phalanges of manual digit III>0.5?diameter of non-ungual phalanges of digit II (0) or < 0.5?(1).

328.Manual phalanx II-1 shorter than I-1 (0) or longer (1).

329.Ischial shaft rodlike (0) or flat, platelike (1).

330.Lateral face of ischial shaft flat (or round in rodlike ischia) (0) or laterally concave (1) or with longitudinal ridge dividing lateral surface into anterior and posterior parts (2).

331.Contact between pubic apron contributions of both pubes meet extensively (0) or contact interrupted by a slit (1) or no contact (2).

332.Dorsal margin of postacetabular iliac blade straight or convex (0) or concave (1).

333.Large, longitudinal flange along caudal or lateral face of metatarsal IV absent (0) or present (1).

334.Distally placed dorsal process along caudal edge of ischial shaft absent (0) or present (1).

335.Length of metatarsus<3.5?transverse midshaft diameter (0) or 3.5?8?midshaft diameter (1) or>8?midshaft diameter (2).

336.Lengths of mid-caudal centra subequal to or less than those of proximal caudal centra (0) or=twice as long as proximal caudal centra (1).

337.Pubic peduncle of ilium craniocaudally longer (0) or shorter (1) than ischial peduncle of ilium.

338.Phalanges of pedal digit III not blocky (proximal phalanx length=2?diameter) (0) or blocky (proximal phalanx length<2?diameter) (1).

339.Width of distal humeral expansion<1/3 humeral length (0) or=1/3 humeral length (1).

340.Lateral epicondyle of humerus not expanded laterally (0) or expanded laterally (1).

341.Distal end of metatarsal I reduced in size relative to distal ends of other metatarsals (0) or comparable in size to distal ends of other metatarsals (1).

342.Pedal phalanx II-1 longer (0) or shorter (1) than pedal phalanx IV-1.

343.Dentary ramus elongate (0) or shortened, not much longer than tall (1).

344.Metacarpal II=1/3 humeral length (0) or<1/3 humeral length (1).

345.With fingers extended, tip of ungual I does not extend past flexor tubercle of ungual II (0) or extends past flexor tubercle of ungual II but does not extend past tip of ungual II (1) or extends past tip of ungual II (2).

346.Premaxillary teeth serrated (0) or unserrated (1).

347.Sublacrimal process of jugal dorsoventrally expanded (taller than suborbital bar of jugal) (0) or not dorsoventrally expanded (1).

348.Flexor tubercles of manual unguals=1/3?height of articular facet (0) or<1/3 (1).

349.Distal chevrons straight or L-shaped in lateral view (0) or upside-down T-shaped (1).

350.Metacarpal III distally not ginglymoid (0) or ginglymoid (1).

351.Breadth of acromion process perpendicular to long axis of scapular blade: deep (0) or shallow (1).

352.Proximal end of metatarsal IV curls around plantar side of proximal end of metatarsal III (0) or does not (1).

353.Midsagittal ridge formed by dorsal displacement of midline of frontals, nasals and premaxillae, absent (0) or present (1).

354.Ectopterygoid lateral to pterygoid (0) or rostral to pterygoid (1).

355.Palatine-pterygoid-ectopterygoid bar does not (0) or does (1) arch below ventral cheek margin.

356.Co-ossification of angular and surangular absent (0) or present (1).

357.Cervical ribs unfused to cervical vertebrae (0) or fused to cervical vertebrae (1).

358.Anterior caudal vertebrae without pneumatopores (0) or with pneumatopores (1).

359.External mandibular fenestra not rostrally displaced (sits beneath orbit) (0) or rostrally displaced (sits largely anterior to orbit) (1).

360.Ilium, pubic peduncle: substantially larger than (0) or subequal to (1) ischial peduncle.

361.Ischium, shape: distally narrower (0) or distally wider (1) (excluding obturator process).

362.Humerus, thickness relative to femur: much thinner (0) or subequal (1).

363.Promaxillary fenestra, exposure in lateral view: minimal (0) or significant (1).

364.Antorbital fossa, shape: anteroposterior diameter greater (0) or less (1) than dorsoventral diameter.

365.Antorbital fenestra, size relative to external naris: larger (0) or smaller (1).

366.Jugal, postorbital process, location: considerably anterior to the posterior end of the jugal (0) or nearly at the posterior end so that the quadratojugal process is minimal (1).

367.External mandibular fenestra, size: small (0) or large (1).

368.Dentary, dorsal margin: straight or concave (0) or convex (1) in lateral view.

369.Furcula, cross-section of lateral end: elliptical (0) or L-shaped (1).

370.Ilium, preacetabular process: deep (0) or shallow (1).

371.Dentary, ventral margin: straight or convex (0) or concave (1).

372.Lacrimal, posterodorsal process, orientation: subvertical (0) or posteriorly inclined (1)

373.Anterior caudal vertebrae, transverse processes, distal tapering: absent (0) or present (1).

374.Lacrimal, anterior process, extending anteriorly to interfenestral bar: absent (0) or present (1).

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0001?0?00?01???00000011?1?1?0?0001000???010?0?00?0000001?1??0?01?0????1?000???
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Byronosaurus_jaffei
?????101???101?1100110101011?00??????20120??
??????????1?100??????0000001??11????00021??01?0?0???????010110????????0??02??????
??1????0?0??0????????1????????
??0????0????100???0?20?100?101100??0100???10?00110?????????????????????????????
????????????????????????????????11?????????????????????0??11?????0??????????00?00??0
1?1

Sinornithoides_youngi
?0??0?????????????1?000??1???0????0020?2????
???1?0??????????????00??0010??????000110101??????11?1001???????????0011?2210210
1??????01?11??0?00??10000000???????????0?200?????1?1???11110?????1????0001?11001
?0??010????0000???00????30110011011??1?0100??1?000?1?0?011???0?00??011110100101
000100000000000000???0???11?11111000111110000010????2100000000001?010110???00?000
?0?0?0?00?1?

IGM100_44_unnamedtroodontid
??????012?????????????????????????????????????
???????1??0??????????????1??11????????1?0??????0?????????????????????????????????????
??????????????????10000000???01?1?001???00??
????0?0??1????????3?????????????????????1???0?????????????????????1?0101000?000???
?00000?????????????1???0?1111????0?????????0???0?????0?0?????????000????????????

Troodon_formosus
???1?1112?1101000001???0?010100??????20120
000210?00?1?01100????0?10??001?????????0110101010???111110010110111?1000?1020?
?11??????????????010????0??????????1?????????????????1??0?011?100??????01000012l0?
01????0?0????0??01000???0?30??????0?1????????10?000???1?10??111?????????1?01?0???
??????????????????????????????11?10101111?????0?101??0??000??0?????10???0??0001??
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Saurornithoides_mongoliensis
?01??1?1??1101???0?110001?10?00????????1??????
?????????????1?010?100?0010??1????000110101?????????1???0??0?????100??1????0?????
??????????????????????????????????????002000?0101?10??11110??????????00??211?01????
??0??1?0?????00??00?30?000110110010000??1?0???1?010??1??0??????????????????????
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111

Zanabazar_junior
?01101?12?110100?001?000??10??000????201200
0?21??0????11100??????100?001???1????000110101010????????????????????1?1000?1020???
??01?????????????
????00??00???1100???0?30?1001101?0010000010100007110?0?????0??????????????????????
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0111

Unenlagia
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??1111?01????0???????0???????
???0?0??1?01???????????0122111O?111020102???1112011?01??0????????????1?????0????
???11???????????0?0?????????????????????????????????????101??0??0?11?????????????????
??1?0????02???011????????????1?????1221?1??0?00??????????1????????00????????0????

Buitreraptor_gonzalezorum
?0110?????????????????00001011??00??????????100
?10??0011?0??????????00??001?????????021??100?00101111001l1?010???100011012?021
???????01101111010?1?100?0??????11?101??122??1?111?110???11?0??0??1?011?01111000
0?????????1??00?0????000??2?0???????1001001?0?01?0??????0?0?111?00?10011120????
??????????????????????0?101?1????1?0???0?2??????12011021??000?0??1??1?1?0??0?00001?
0?0?0??0?0?

Rahonavis_ostromi
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??011111?0?1?11?011012?02??????
???0????11??000?????????011211001111102?002?101??00111?10000??1??10001101000???
?????1?????0??????0?0?????????????????????????????????????1111??3?0???130?????????????
???????????0211?011?101?01?10021?????11?1111100??01??????1?11?????0?00????????0??
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Bambiraptor_feinbergi
?0110?????0?0?1??1??0000?01110000??10?01??10
?1????0?01?0??????????00??010??1??0000?0101-100?????0?120011??10??0???0011??110??
???00110010111l0?001?101000010?21?001110020001?1021100?1?110000??10010001111
?0?000?00?0?1??0000????000?0000000?1013001??100101?10?0111000110110000?0011120
10110100010000010110010102011011O1?10000100110O?0012001011000001000010111l0?
??0000001001?0000100

Sinornithosaurus_millenii

?011?????0?????????0?01???11100????10001?1100?
1???0?01???????????00?00100??1????0101010000????????1??1???????0???00?1??1??
?????0111?01031110?00???0?0000010?211?0??10?2?0?21102?0????1???????1?010001111
10?0?000?1001??0000???0??00?000100110130 0?0?100101?1?00110?0??????000100111
21?00101100001000111100001?211111??1?10000120110000012??112?00000100011010 1?0
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Microraptor_zhaoianus
1?1?????????????????0?01?????1?????????????????????????1????????????0??010?0?1????0?0
100000????001?1??01?1000?01???0110?11?2111?01?100?131?10100?11010000110121
10?011002?0?21102210 0?11111??00?1001?10111110??00??010?11?000????0??00?20?10
0?1??????????00??1?1?0???0??0?111100010011121 10??011000010001111001000211111 0?1?
1000012011100000 20?11210000010001?0101?0???00?001?00100000?0?

NGMC91_unnameddromaeosaurid
?011?????????????????00????111?00?????001??
?0?????????????????????????0000100??1??0?0?010??00??0?????????????????????01???1?
???1?????10??031?10?00??1?100001?????????????????????????????1???0????????????11?
???0???10????000????10?????0010011013?01?1100??1?1?0?1?0?00?????0?0?00111211 0??0
11000?1000110100100??????1??1?1??0012011100 00??????21?0000100011010??0?????000
1?00100000?0?

IGM100_1015undescribeddromaeosaurid
?011001001000012011200001010100001?1000121
10110001000??00001?0???00000100?111100010101010000????0??2?????????????????????
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??0??00??00?0?0000???0?0??0001001 3?0001000001?1???0?0?0?????????????????????????
??0???1?????0?????????1???????
0???

Adasaurus_mongoliensis
??1100?????????????????????????????0?????001?????
??????0????0?????????????????0?????0?0?0????????01???0?2?01?1?????011000????1???????
?????0??1?1?????????????????00221100111 0???0????021?0??1???00?????????001100?0010??
???0?1??000????????0?000?????????????0????????1????0?????01111??00?0?????????????????
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Velociraptor_mongoliensis
?011001001000012011200001011100001110001211
1?1000100010000111010100000100111100001010101000011000120011111101111100011 01
11021110011100111111010011100000010022110011100200011112110011110000000100101
011010010000 00?0011000000000000000000010013000010000010100101000011010000 1
00111101001010001000001011001020200101 1?0011000001110000012001011000000100001
010110000?000001000 00?00100

Saurornitholestes_langstoni
??????????????????????????01110????????????111????
??????????11????0???010?????00???010101000?11000120011111101101110 0?1011??11?????
?????01?1???????10??000100221?0?11???0???00?
0????00?000?0???0000??????013?????0??00??10?1?1000011????00100?????1????????????
????11001??0?????????????????????1??00?1??010??0?????0??0?0?01?0???0????01??????????
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Deinonychus_antirrhopus
?0110????1???????11?0000?011100001110001 2???
???0?1????0?00?11010?000?0100111?1000?010101000?1100012001?111011???00110110?
21?10???1?0101111010011100000010022110011100200011 10?0100111110000001001000 11
01000000?00?00110000 0?0?000?0000??00?0013000?000????000?1?110001001??????01111
0100101000010000010110010200001011000110001011110000012?0000100000100001010110
0000000001000 00?00100

Achillobator_giganticus
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??0101?????????????00?010220?0111100100?011010?00?11110?0????00?000?101????0???
????1???0????????0?000??????013?????????????????10??00000??00??0???1???????????0??
???01?0????0000010010 0?1??????11??????1000000?0??????????0??1?????0??0?01?????????
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Dromaeosaurus_albertensis

?0??001000000000010??0?0?0???0??01110????111
1????10001?1001100???0000010011111000?000101000?????????????????????????????????
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0??????00?0?0000???0?00?000?00????0??00?001001010000?????????????????????????
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Utahraptor_ostrommaysi
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??????????????????????????????????????01???101??0????00??1011111?0??????0?1011????????
??????01?????????????????????2?????11001??0???0??????1???000????00?0??????????????
???????0????????0???????0?0?????????????????????0?????000?????????????????????????
??????????001?00?????????????????????10???0???????????0??????????0?????????????????

Atrociraptor_marshalli
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0??????0???0?00??00?00?3??????0?????010?0110?????????????????????????????????????
??1???????????

Epidendrosaurus_ningchengensis
?0?????????????????????????????????????10001?1?00??
?????????0????????2??00000?002000????2?????????????????00?010?00???01?0?011????1?
??????011?10?00??10100000011?1???1??020?0?3?1?02?0??1?0100?0???0?????000010?000
?0110?1??100????00?0?0??0??????????1??????01???10????00?1111????00210201O??01000
1000000000000000????011?1?1?01102000011O0???000110000000102?11101?0??1?01111???
?11???0?0

Epidexipteryx_ningchengensis
-0?????????????????????????0?00???000?100?0011????000?????????????010?0?0????0000
2022?-10020?????????0???0?0?1???102???23?-100-1????0?01?01000???????00??011?10???
??020-0?311?02?0?????????0????01111??0?10??00???10??1?1?0?1??000???210??01?1?????
??????01?0????0-1?00?111???0?0021120?????1?0????????000000??00---01??10110????????
????10?000110?000?0??1?1??11???10?1111?11011?11???

Archaeopteryx_lithographica
101?0010??000??112011010??11100?011?000121000l0?0000?0??100111?10000001100002
?0000020??00000?1?1??100?0??010?0???00210121110000?????00103111000?11000000101
121?0001?1020002210111O1?111100000?10010010?1010?0000001001100000?0?00001020
0101110100010010010l?0??00?0001?11110?3?012113011O?0100010001010010010202010
011?1011011120010000010000121000000000110101?000000000110010010O100

Wellnhoferia_grandis　　?0??????????????????110?0????????????????????????
??????????????????00??01?????????00020?-0020?????????????????0????02?0?231??00???
???01031110?0????0?0000001??1????1??0??0?2?1?11?01?1?0100?0????01001??1010?000?
?010????00?0???1000?0200101?1???????0?00????0???0?0?0??11?1?0310?21130?10?01100
1000101001001020 2???011?1?1101112001000001??00121000000000l?0101??????0?00110
0100?00???

Jeholornis_prima
10?????????????????1?????0??????????0??????0??????????????????????100?010??00200???
022??00??0?????????????1???1????02???211?1????1?1?0003?110?00??1100000001221??0?
??10??0?????21?0?????1?000??1?01011??0010?000?0010????1000???00?0102?0?0?1????0
?10?1???01?0110????01?1111?031012113011??011000?1100110000000002???01??1?1?0111
200?100101??0??1100000000011010l?0??1?01001?1?011011???

Sapeornis_chaoyangensis
?011?????????????????11011?????00001?000012??0
011???00?????????????000?000??00?00002?20??????0????????0?00?010?2???0??????21?1
001????100011110?00??1120000?011?1??01??100?0?1?1021101???010000???0??1110000??
?000?0010?1???000???1010?02?0?0?1111?00100?0??01?0??0?????1?111?003101211311?1
011100?1110011100?1?02???011?1?110111????1??101?00?01?0000000001l0?0110??1?010
01?110?10110?0

Confuciusornis_sanctus
10110?????????????11010?0???00001???0??2??0?01??0?0???01???????0000010000?10?000
1?1-3??????0???1??1????01110?2???0??????2??111?11010001311140001111100001011210
1????100?0012103210111??10??11?1121111010010?0000001001l0?000???001??0??0011??
???00100000?01?0?10?????11111?0001012112111010100000101020110010002???011?1?11
01112000101101??0001?000000000?10?01?0??10?1001?110110?0???

Protopteryx_fengningensis

10?????????????????110?????????????????0????????????01?????????????000??1???????0?0??
2???0??0??????????0?????1??2??????????2??111?11?11??031?10000??1120000001?????????
????0?1?1??????????1???1????????1110010?0?0??0101????00?????0????2?01?111???00?10
?00?01?0???????01?????1?3?012113111??011000?1100-0110001???????11?1?1?0111200?0?
?10??????1??000000000110?01?0??????001???0?0?00???

Yanornis_martini

?01?????????????????111?0??????0??????0????????
???0?1?0???????????000?010??00????00021??0000????11??????????0?2?????????????111?
1???0?0031?10?00??1120?00?????????????00???121?32?01???0100?1??11??112?00010?00
0??010????00?????101?1?200001?1???00110?00??1?00?00?0001111??1???0121131111??011
0?0011?0-1111101??????01??1?1101??20000???0???????1??000000000110?0??0??10??001?11
-00?-0???

Hagryphus_giganteus

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00100?????????????????????????0?11?????????????????0??0?0?????????????????????????

Microvenator_celer

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????0000??01000??????0??1002???0111????0?????10110?0101100?0010010???????0??0???
0???11??0?0????00??0?????????????????????????00????????0?111??????011110??0??????????
?????0?0???0????011?????????????????????0????00000?1????0????????0?1????????11?01?0
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Avimimus_portentosus

?01?0???10001?00??0??1?1????????1???1?????00
?11??0?00100110??????2?1???00?0??0110???3???????011011110101?0?00??100??????????
?????????01?000100???110?????00?211?01??022000???0101000011100?0???10011110020??
?00??0???01?0??00000?00??0?????0???????1?????1011???0?????001?????????111??1?????
?0?????????????????00??011?101?0???00000????1000002?0000?0?????????10??01??000??
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Oviraptor_philoceratops

?0110??????????1??00?????111?0?011???0112??0?1
?0???0?100?????1????1120?01100?01?1?1?3??????0??1???1??????1?0?????????????????1?
????11?1?0?000001?110?0001???21?00???0010
0100?????00?0000???????01?1?010??1??1?00?010?10?????0?111?010?00?11?01??1010000
000000000100?????????????????????????1000??????????00??100?10?01?0?10??1?00-11011
?010?0

Conchoraptor_gracilis

?0110??????????1???00111?1100?1011?100112100
0110?000?????1?0????221120?010?0?0111?1?3?????????????????010??1?012?110??1???0?01
11???1?11?1100001?????????011?00210001?102???0???01001??11010?0????0??000000??0
?0???00??0110??0?000000??0???0101011?10100111010?????????????0?????1?1????010
?0???0?00?0000111000??????1???110???????0?0001000000?????0???0?10?0??011011?00?-
11011??1000

Chirostenotes_pergracilis

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??????01110????0?????????????????????1?????????????????1101?11????1?12?????????????????
??001?????????????000110021?0001?0220001110?00?0?????0?????10?100?00100000????0
???1???0?0?00?????????????????????????????1?????????1?1????????0??????00??????00001
0?0?1001000?001?1??101?0000000?0001110000?1?000000??0??0????????01?????????????
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Incisivosaurus_gauthieri

?0110???1??01?????10001010100010010?0?011??000
11000?0101011010111120010000100l?1?02022??0002?????????????????????????????????
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??00??00?0??000???0020?00010110?0100100101100l0??001?????????????????????????
??0??11?????0110??1???----11??10?
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IGM100_42_unnamedoviraptorid
?0110?????????????00111111?01011?10011210
0?11??000???01100?11122112?01100??111?1?3??????10??0??1??1?1?1???1???01??00?10?
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000000100?001?0??00?0?0?00?0??1010101101010011101?1?10????00101001?001011?
100?010001?000000000010000001011?10110???00000110010?000100010001?10101111
10111???????????1???

Anchiornis_huxleyi
0011?0????????????????101???111?00?????0?1?000??1????1?1?????????-000??01??1?????0
0022?-01??0?101??-00?0??010?01???01101210??011----011111110000??100000010?21?10
01102200?2?112112???1?1?000??1?01?000110100010?0000?1??00?0???0????02011O?1101
000100100?01?0?0?0-0?011111101?000111201001010001010100011001010201?0011?10110
00?20?1100001000?021000?00000110101?0??000000110010000011O

Xiaotingia_zhengi ?01?????????????????1?1???1111000????0?1?????
?????01?1?????-----?001001??1???00??022?-01??0?-0???1?0????000?01?????1???---10?1--
--01?03101?10???102000001011?1110?12012?????103?12??????????10????????1?01000101
0000?0??0?10???0???102?110111?1??0110100?01?1100?-0?0?1111?013?1?1112110010100O
1??000101100102020l????0??1??001000111000l2?0?1??000?00000??0??1????00?000110?
10010011?

Sinovenator_changii
?0???1002?000011120010101?11100???1????1?00
0011???011?10100??????000?001??????000001111101??????1?111000110100001000110l???
1?????????010111?0???????????000?0?21??011100200021101110O?11110000???0010001011
??000?????0?1??000011?0??0??301100?10?000??010?1?1100??0?000?1111??00100???????
????0???0????0000000???2011011?101?1???0011??0??1000112?00??000??1?0??110???0??
000100100000111

Mei_long
?0?????????????????1010?????00?01?0000121
00001?10?010??100?????00010010??1?0000?021??01?001101111001O?1010?01???011022
??11011????101?11?10?0?1?10000000?0?2111?1???020??2110111O?0111100?0101101?000
1111011?0?0000???00000????0????3?110011???001?0100101??????????1111??0001001111
0?0??0?0???0??????00000?????1??1??1?11100?0?11?000?10??1121?000000?01?010110???
000000???10000011?

Similicaudipteryx
00110??????????????00010??1000000??000112100011O0??0?????????????20010000?10??1
002022??00?20?????10010??1?0?0???01??00210?111010??00001000l?001?100000001002
1??????02200?111?1?????1??0??00????0??00001000?00000010???00?0????0????02110001
0110001?01001?1?0?10??1?000111001O?001111010??010000??0100000001010000101l?10
1100000000000101000001000000000011010l?????0?1000-11011?01000

Caudipteryx
00110??????????????0?110?01000011?000112100O1?00?00?????????????20010?00?????10
021?3?????00????0?100????????0???01????210?111000??000010001?00??1000000010020?
??11?02200?111?10?10?11?01??0????0100000100000000010?110?000???0?00?0??100010
1100011010011l?0010?????001110?10?0001110100?0100000010?0001101?00001011?101
1000000000???0100000100000000011010l?0??0001000-11011?010?0

Haplocherius
?0110??000010?????0110100?11110101?0000101
100210000011?0000?0100100010100110100O0?0-11010?00?100??0-0111101??0?1000000?
??0?0001???0?0?0102000??210?0010021O?000???10?200100?111001100?00000?00?0?00?000
?000???00110010O?100100001100?0010010000001001001000O1?0001??00000???1??2?100
10101000100101000100000010O1?000101101011O???000000000000?00100000?0000111?1
00000000000000000?00??0

Patagonykus_puertai
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??111????????1??2?????????????
??0020??30210?110??110?????????1??????0?????10?00?11?1?00???10011?0??0?????01??0?
??1???0??????010????????????????????????????????????1?1???????????00?0???????0?????
00?1???????????11??1????0?????????????????????1???????1?????????0???0??????????0?

Mononykus_olecranus
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?1000?000200030210?1122?1100??1????1??000???????3??0?0110100111011211000020?00

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001??00???1??0?0????01??010??????0??????????????????????0?111??00?00000000?01000
1000?????00?1??????????111??1??00000000????0??00???001100?1???1?00?????00?000?00
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Alvarezsaurus_calvoi
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end;
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