Avialan status for Oviraptorosauria

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Oviraptorosauria is a clade of Cretaceous theropod dinosaurs of uncertain affinities within Maniraptoriformes. All previous phylogenetic analyses placed oviraptorosaurs outside a close relationship to birds (Avialae), recognizing Dromaeosauridae or Troodontidae, or a clade containing these two taxa (Deinonychosauria), as sister taxon to birds. Here we present the results of a phylogenetic analysis using 195 characters scored for four outgroup and 13 maniraptoriform (ingroup) terminal taxa, including new data on oviraptorids. This analysis places Oviraptorosauria within Avialae, in a sister-group relationship with *Confuciusornis*. *Archaeopteryx*, Therizinosauria, Dromaeosauridae, and Ornithomimosauria are successively more distant outgroups to the *Confuciusornis*-oviraptorosaur clade. *Avimimus* and *Caudipteryx* are successively more closely related to Oviraptoroidea, which contains the sister taxa Caenagnathidae and Oviraptoridae. Within Oviraptoridae, "*Oviraptor*" *mongoliensis* and *Oviraptor philoceratops* are successively more closely related to the *Conchoraptor-Ingenia* clade. Oviraptorosaurs are hypothesized to be secondarily flightless. Emended phylogenetic definitions are provided for Oviraptoridae, Caenagnathidae, Oviraptoroidea, Oviraptorosauria, Avialae, Eumaniraptora, Maniraptora, and Maniraptoriformes.

Key words: Dinosauria, Theropoda, Avialae, Oviraptorosauria, birds, phylogenetic analysis, phylogenetic nomenclature.

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Introduction

Oviraptorosauria is a clade comprising small- to medium-sized Cretaceous theropod dinosaurs generally characterized by a highly modified and extensively pneumatized skull, toothless jaws, and a rather standard theropod postcranium (Barsbold et al. 1990). Oviraptorosaurs are known from Laurasia, although a few supposedly oviraptorosaur fossils have also been reported from Gondwana (Frey and Martil 1995; Currie et al. 1996; Frankfurt and Chiappe 1999). In the adequately known advanced oviraptorosaurs, assigned to the family Oviraptoridae, the preorbital part of the skull is strongly shortened and deep, and sometimes there is a median crest along the skull roof. The oviraptorosaurian family Caenagnathidae is less well known, being represented only by scarce and incomplete specimens. Judging from the shape of the maxilla and mandible in some caenagnathids (R.M. Sternberg 1940; Cracraft 1971; Currie et al. 1994; Sues 1997), the snout was probably moderately elongate. The caenagnathid metatarsus has a proximally pinched metatarsal III, and, as far as known, it was more slender than in any of the oviraptorids.

Oviraptoridae is represented by six Asian species: *Oviraptor philoceratops* Osborn, 1924, "*Oviraptor*" *mongoliensis* Barsbold, 1986, *Ingenia yanshini* Barsbold, 1981, *Conchoraptor gracilis* Barsbold, 1986, *Citipati osmolskae* Clark et al., 2001, and *Khaan mckennai* Clark et al., 2001. Four named species were recently included in Caenagnathidae by Sues (1997). These are: the North American *Chirostenotes pergracilis* Gilmore, 1924 and *Chirostenotes elegans* (Parks, 1933), as well as the Asian *Caenagnathasia martinsoni* Currie et al., 1994 and *Elmisaurus rarus* Osmólska, 1981. The caenagnathid status of the first three species has not been questioned. However, no convincing evidence has been presented to justify the placement of *Elmisaurus rarus* in this family. The holotype of this species consists of the incomplete manus and pes. The manus characteristics are not exclusive of *Elmisaurus* and Caenagnathidae but are shared by most maniraptoran theropods. The metatarsus of *Elmisaurus rarus* does not resemble those in Caenagnathidae. It differs from the caenagnathid metatarsus in having a proximal slit between metatarsals III and IV, a proximal protuberance on the extensor surfaces of metatarsals II–IV, and a deeply concave flexor side (Osmólska 1981). The slit evidently corresponds to the lateral proximal vascular foramen in *Confuciusornis sanctus* Hou et al., 1995 and modern birds. The proximal protuberance may be a homologue of the proximal tubercle that has been found on metatarsal II in *Confuciusornis sanctus* and Enantiornithes

(Chiappe et al. 1999). This tubercle was interpreted by Chiappe et al. (1999) as the insertion site for the tibialis cranialis muscle. Moreover, *Elmisaurus rarus* shows a proximally extended "spur" on the fourth tarsal, unknown in Caenagnathidae but very much like that in *Avimimus portentosus* Kurzanov, 1981.

Two unusual Asian theropods have recently been recognized as oviraptorosaurs of indeterminate familial status (Sereno 1999a; Barsbold et al. 2000). One is the feathered *Caudipteryx zoui* Ji et al., 1998, in which the preorbital part of the skull is still moderately elongate and the premaxilla bears four recumbent teeth. The other is *Nomingia gobiensis* Barsbold et al., 2000, in which the tail ended with a pygostyle. The former species was originally described as the closest relative of birds (Ji et al. 1998).

The North American *Microvenator celer* Ostrom, 1970 appears to be also an oviraptorosaur (Currie and Russell 1988; Makovicky and Sues 1998; Holtz 2000; this paper). In addition, our phylogenetic analysis (this paper) recognizes the Asian *Avimimus portentosus* as a basal oviraptorosaur. This species has been considered to be a close relative of birds, or a bird (Kurzanov 1983, 1987; Thulborn 1984; Paul 1988; Chatterjee 1991). It has been suggested that the hypodigm of *Avimimus portentosus* might be a chimera composed of the remains of several different theropods (Holtz 1996; Padian et al. 1999); this is not the case, as evidenced by a new find in Mongolia (Watabe et al. 2000).

The phylogenetic relationships of Oviraptorosauria have been ambiguous since its first known species, *Chirostenotes pergracilis* and *Oviraptor philoceratops*, were named. *Chirostenotes pergracilis* was originally referred to the family Coeluridae (Gilmore 1924), and recently Sues (1997) assigned it to Caenagnathidae. *Oviraptor philoceratops* was originally referred to the family Ornithomimidae (Osborn 1924). Romer (1956, 1966) and Steel (1970) followed this placement of *Oviraptor*, although Russell (1972) questioned it. Based on the morphological resemblance between the mandible of *Oviraptor philoceratops* and those of some caenagnathids, Osmólska (1976) relegated *Oviraptor* to Caenagnathidae. This family was originally placed among birds (R.M. Sternberg 1940) and was so treated by Cracraft (1971). However, Wetmore (1960) listed several characters to support a "reptilian" relationship of Caenagnathidae. Romer (1956) and Steel (1970) regarded caenagnathids as coelurosaurian theropods, removed from a close relationship to birds; this view later became generally accepted. Barsbold (1976a) erected a new family, Oviraptoridae, for *Oviraptor*, which he subsequently (1976b) referred to the new infraorder Oviraptorosauria, later (1981) also including Caenagnathidae.

Since Oviraptorosauria was named, it has generally been placed outside a close relationship to birds, and there has been a prevailing consensus that Dromaeosauridae or Troodontidae, or a clade containing the two taxa (Deinonychosauria), is the closest relative of birds. Gauthier (1986) was first to point out that Oviraptorosauria (his Caenagnathidae) shares a number of derived features with birds (his new taxon Avialae) and Deinonychosauria. He named the corresponding clade Maniraptora. His hypothesis nested Caenagnathidae in an unresolved polytomy with a clade containing Avialae and Deinonychosauria, as well as several other coelurosaurian genera. Russell and Dong (1994a) grouped oviraptorosaurs, together with Troodontidae, Therizinosauria, and Ornithomimidae, in a clade that they referred to as Oviraptorosauria; this clade excluded Dromaeosauridae. Holtz (1994) recognized oviraptorosaurs as an outgroup to a clade comprising Tyrannosauridae, Ornithomimosauria, and Troodontidae; later (1995, 1996), he combined them with Therizinosauroidea within his new taxon Maniraptoriformes. His oviraptorosaur-therizinosauroid clade was nested in an unresolved polytomy with a dromaeosaurid-avialan clade and a clade including Tyrannosauridae, Ornithomimosauria, and Troodontidae. Sues (1997) and Makovicky and Sues (1998) proposed a sister-group relationship between the oviraptorosaur-therizinosauroid clade and a clade encompassing Deinonychosauria and Avialae. A close relationship between Oviraptorosauria and Therizinosauroidea was also postulated by Xu, Tang, and Wang (1999) and Holtz (2000), but it was not accepted by other authors (Sereno 1997, 1998, 1999a, b; Clark et al. 2001). Sereno (1997, 1998, 1999a, b) hypothesized Oviraptorosauria as the sister taxon to a clade containing deinonychosaurs and birds. Forster et al. (1998) and Padian et al. (1999) also advocated this relationship, although the former recognized Troodontidae as the closest relative of birds.

Only few recent authors have considered oviraptorosaurs as close relatives of birds, or birds. Paul (1988) hypothesized oviraptorosaurs as secondarily flightless theropods more closely related to modern birds than is *Archaeopteryx*. Olshevsky (1991: 94) envisioned oviraptorosaurs as "descended from a group of volant theropods more derived than the archaeopterygids". Elżanowski (1995), based primarily on his study of the palate in *Conchoraptor gracilis* (his *Ingenia yanshini*) and *Archaeopteryx*, suggested a close relationship between oviraptorosaurs and birds. Recently (1999), he placed Oviraptorosauria in an unresolved tetrachotomy with ornithomimosaurs, therizinosauroids, and a clade containing *Archaeopteryx*, *Gobipteryx,* and *Hesperornis*. He hypothesized that oviraptorosaurs might be the earliest known flightless birds. The same opinion was expressed by Lü (2000).

Our investigation of the numerous well-preserved oviraptorid specimens housed in the Paleontological Center of the Mongolian Academy of Sciences, the Institute of Paleobiology of the Polish Academy of Sciences, and the Paleontological Institute of the Russian Academy of Sciences yielded new data for assessing the phylogenetic relationships of Oviraptorosauria. Here we present the results of a phylogenetic analysis using these data to examine the oviraptorosaurian affinities within Maniraptoriformes. These results provide evidence supporting the avialan status of Oviraptorosauria, suggesting that oviraptorosaurs were secondarily unable to fly.

Material and methods

The database for this study consists of 195 characters of skull (numbered 1–69), mandible (70–94), dentition (95–97), axial skeleton (98–124), and appendicular skeleton (125–195), defined in Appendix 1, scored for 37 species of Theropoda (Table 1). Species-level taxa (as recently advocated by Yeates 1995, Kron and Judd 1997, Wiens 1998, and Prendini 2001) were used in the cladistic analysis for all oviraptorosaur and four non-oviraptorosaur terminals. After corroborating (as postulated by Bininda-Emonds et al. 1998) monophyletic status for each of seven groups of the remaining species (through our preliminary analyses and evidence from the literature—e.g., Holtz 1994; Pérez-Moreno et al. 1994; Currie 1995; Chiappe et al. 1998; Padian et al. 1999; Xu, Tang, and Wang 1999; Norell et al. 2000), the corresponding supraspecific taxa were used as terminals by combining complementary information from the included species, in order to reduce the impact of missing data on the analysis and to decrease the number of terminals to obtain results in a reasonable length of time. The resulting taxon-character matrix (Appendix 2) was constructed using MacClade version 3.05 (Maddison and Maddison 1992).

Whereas all terminal taxa were used in the preliminary cladistic analysis, three terminals were excluded from the final cladistic analysis. These were: *Microvenator celer*, Alvarezsauridae, and Troodontidae. They were excluded because of a large amount of missing data (Appendix 2); a further reason for excluding Alvarezsauridae is that new material from Mongolia indicates that some of the earlier published anatomical interpretations of Mongolian alvarezsaurids may be incorrect (V.R. Alifanov and E.N. Kurochkin, personal communication 2001).

The maximum-parsimony branch-and-bound searches were conducted using PAUP* version 4.0b8 for Macintosh PPC (Swofford 1998). As recommended by Barriel and Tassy (1998, and references therein), more than one outgroup taxon was used. Trees were rooted such that the collective outgroup (composed of *Herrerasaurus ischigualastensis*, *Coelophysis bauri*, Allosauroidea, and Tyrannosauridae) was forced to be paraphyletic with respect to the maniraptoriforms (which were forced to be monophyletic), in accordance with the current views on theropod phylogeny (see Padian et al. 1999 for review). Choosing the alternative methods for rooting trees (rooting at an internal node with basal polytomy or making the collective outgroup a monophyletic sister group to the monophyletic ingroup) did not alter the ingroup topology of the shortest tree.

All characters were assumed to be of equal weight, and multistate characters were treated as unordered, to minimize assumptions of evolutionary process in the cladistic analysis (Lee 1999, and references therein). Some characters proved to be parsimony-uninformative and therefore were excluded from the cladistic analysis. These were: characters 7, 99, 116, and 161 for the preliminary analysis; and characters 7, 51, 99, 116, 161, and 193 for the final analysis. The distribution of character states on the most-parsimonious cladogram was mapped using the accelerated (ACCTRAN) and delayed (DELTRAN) transformation optimizations (Swofford and Maddison 1987, 1992). Character variability within terminal taxa was interpreted as polymorphism. Inapplicable conditions were assigned to discrete states, as advocated by Maddison and Maddison (1992) and Maddison (1993). Treating the character variability as uncertainty about ancestral state of the terminal taxon, or the inapplicable codings as missing (unknown) data, or both simultaneously, did not change the topology of the shortest tree.

Bootstrap proportions (Felsenstein 1985) were obtained by generating 2000 maximum-parsimony branch-and-bound replicates within PAUP. The decay index (Bremer 1988, 1994) was calculated using TreeRot version 2b (Sorenson 1999).

The phrasing of the emended phylogenetic definitions follows recommendations in the draft *PhyloCode* (Cantino and de Queiroz 2000). To minimize ambiguity in the clade to which the defined name applies, the phrases "least-inclusive clade" and "most-inclusive clade" are used in the node-based and stem-based definitions, respectively (Schander and Thollesson 1995; Cantino et al. 1997; Lee 1998). The meaning of a defined name depends on the meanings of taxon names listed in the definition, so that any ambiguity in their meaning will result in ambiguity in the meaning of the name that is being defined. For this reason, only species-level taxa are included in the emended definitions (Bryant 1996; Cantino et al. 1997). To preserve consistency with the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature 1999), the type species of the genus name is included in each of the emended definitions of the names that are derived from the stem of the genus name (Caenagnathidae, Oviraptoridae, Oviraptoroidea). Consequently, the generic and familial names cited in the original definitions are replaced in the emended definitions by the respective type species.

Results

The final cladistic analysis yielded one shortest tree (length, 548 steps; consistency index, 0.58; retention index, 0.67) shown in Fig. 1. A single shortest tree (length, 629 steps; consistency index, 0.52; retention index, 0.63) also resulted from our preliminary analysis that additionally included Troodontidae, Alvarezsauridae, and *Microvenator celer*. The topology of this tree was identical to that presented in Fig. 1, excepting the presence of the three extra terminals. Troodontidae was nested as the sister taxon to Dromaeosauridae, Alvarezsauridae was the most-basal terminal taxon of Avialae, and *Microvenator celer* was placed within Ovirap-

Table 1. Specimens and literature used to score characters for the phylogenetic analysis. Institutional abbreviations: GIN, Paleontological Center, Mongolian Academy of Sciences, Ulaanbaatar; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Taxon	Sources
Herrerasaurus ischigualastensis Reig, 1963	Novas 1994; Sereno 1994; Sereno and Novas 1994
Coelophysis bauri (Cope, 1889)	Colbert 1989
Allosauroidea:	
Allosaurus fragilis Marsh, 1877	Madsen 1976
Sinraptor dongi Currie and Zhao, 1994b	Currie and Zhao 1994b
Tyrannosauridae:	
Daspletosaurus torosus Russell, 1970	Russell 1970
Tarbosaurus bataar (Maleev, 1955)	Maleev 1955, 1974; K. Sabath, personal communication 2001
Tyrannosaurus rex Osborn, 1905	Osborn 1906, 1912; Molnar 1991
Ornithomimosauria:	
Gallimimus bullatus Osmólska et al., 1972	Osmólska et al. 1972; Hurum 2001
Pelecanimimus polyodon Pérez-Moreno et al., 1994	Pérez-Moreno et al. 1994
Struthiomimus altus (Lambe, 1902)	Russell 1972
Dromaeosauridae:	
Deinonychus antirrhopus Ostrom, 1969a	Ostrom 1969a, b
Velociraptor mongoliensis Osborn, 1924	Norell and Makovicky 1997, 1999; Barsbold and Osmólska 1999
Troodontidae:	
Borogovia gracilicrus Osmólska, 1987	Osmólska 1987
Byronosaurus jaffei Norell et al., 2000	Norell et al. 2000
Saurornithoides junior Barsbold, 1974	Barsbold 1974; Osmólska and Barsbold 1990
Saurornithoides mongoliensis Osborn, 1924	Osborn 1924; Russell 1969; Currie and Peng 1994
Sinornithoides youngi Russel and Dong, 1994b	Russell and Dong 1994b
Troodon formosus Leidy, 1856	Russell 1969; Currie 1987; Currie and Zhao 1994a
Alvarezsauridae:	
Mononykus olecranus Perle et al., 1993	Perle et al. 1993, 1994; Chiappe et al. 1996; Novas 1996
Shuvuuia deserti Chiappe et al., 1998	Chiappe et al. 1998
Therizinosauria:	
Alxasaurus elesitaiensis Russell and Dong, 1994a	Russell and Dong 1994a
Beipiaosaurus inexpectus Xu, Tang, and Wang, 1999	Xu, Tang, and Wang 1999
Erlikosaurus andrewsi Perle in Barsbold and Perle, 1980	Barsbold and Perle 1980; Clark et al. 1994
Nanshiungosaurus brevispinus Dong, 1979	Dong 1979
Segnosaurus galbinensis Perle, 1979	Perle 1979; Barsbold and Perle 1980
Therizinosaurus cheloniformis Maleev, 1954	Maleev 1954; Barsbold 1976c
Archaeopteryx lithographica Meyer, 1861	Wellnhofer 1974; Elżanowski and Wellnhofer 1996; Elżanowski 2001, in press
Confuciusornis sanctus Hou et al., 1995	Chiappe et al. 1999
Avimimus portentosus Kurzanov, 1981	GIN unnumbered (specimen referred to by Watabe et al. 2000); PIN 3906-1, 3907-1, 3907-3–3907-6; Kurzanov 1987
Caudipteryx zoui Ji et al., 1998	Ji et al. 1998; Zhou and Wang 2000; Zhou et al. 2000
Chirostenotes pergracilis Gilmore, 1924 (including *Caenagnathus collinsi* R.M. Sternberg, 1940 and *Macrophalangia canadensis* C.M. Sternberg, 1932)*	C.M. Sternberg 1932; R.M. Sternberg 1940; Currie and Russel 1988; Currie et al. 1994; Sues 1997
Nomingia gobiensis Barsbold et al., 2000	GIN 100/119
Microvenator celer Ostrom, 1970	Ostrom 1970; Makovicky and Sues 1998
"*Oviraptor*" *mongoliensis* Barsbold, 1986	GIN 100/32a
Oviraptor philoceratops Osborn, 1924	GIN 100/42**
Conchoraptor gracilis Barsbold, 1986	GIN 100/21, 100/36, 100/38, 100/39, 100/46, 100/47, unnumbered specimens; PIN unnumbered specimen; ZPAL MgD-I/95, MgD-I/100, MgD-I/106
Ingenia yanshini Barsbold, 1981	GIN 100/30–100/35

* The synonymy is after Sues (1997).

** We follow Barsbold (1981, 1983) in referring this specimen to *Oviraptor philoceratops*, pending the preparation and redescription of the holotype of this species (which is currently going on in the American Museum of Natural History; Clark et al. 2000) is finished. Some differences between the holotype (Smith 1992) and GIN 100/42 suggest that the two specimens may represent different species (see also Clark et al. 2001).

torosauria, in a sister-group relationship with "*Oviraptor*" *mongoliensis*.

Based on the final cladistic analysis (Fig. 1) we recognize the ingroup internal clades presented below. In their diagnoses, only synapomorphies considered here as unambiguous are included. A full list of synapomorphies postulated for these clades by the present analysis is given in the explanation to Fig. 1.

Maniraptoriformes Holtz, 1995

Emended definition.—The least-inclusive clade containing *Passer domesticus* (Linnaeus, 1758) and *Ornithomimus velox* Marsh, 1890.

Diagnosis.—Ten unambiguous synapomorphies (under both ACCTRAN and DELTRAN) diagnose Maniraptoriformes: palatal shelves of the maxillae in contact for most of their

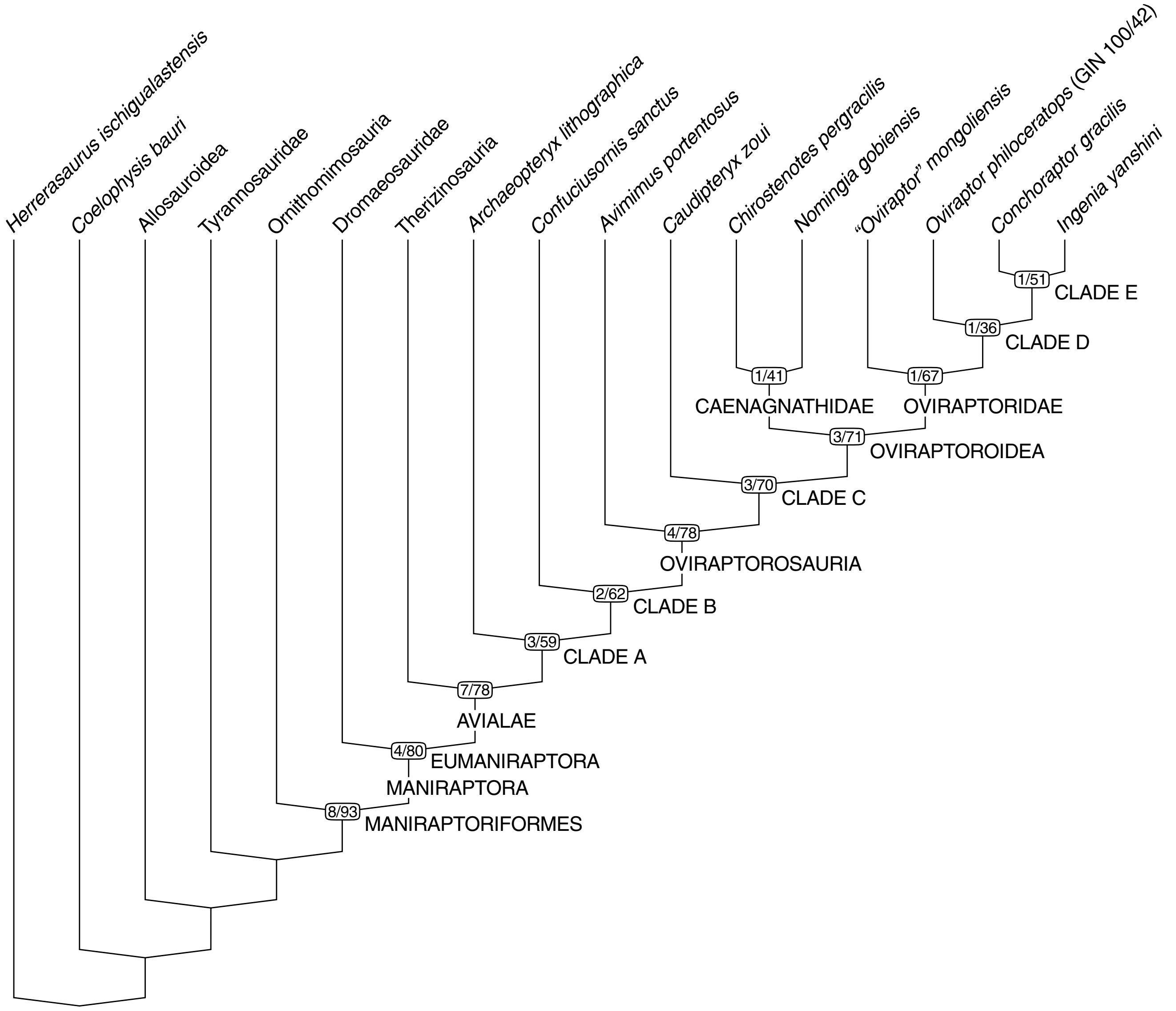

Fig. 1. Most-parsimonious cladogram inferred from the final cladistic analysis, based on the data matrix presented in Appendix 2. Cladogram statistics: length, 548 steps; consistency index, 0.58; retention index, 0.67. Numbers at the ingroup nodes are indices of support for the respective clades: the decay indices are to the left of the slash, and the bootstrap proportions are to the right. The synapomorphies of the ingroup internal clades, as revealed by the cladistic analysis, are listed below. They are invariant under the ACCTRAN and DELTRAN criteria unless preceded by superscript A (ACCTRAN only) or superscript D (DELTRAN only). The synapomorphies that are free from parallelism are italicized. The reversals are preceded by a minus sign. In bold are shown the unambiguous synapomorphies; i.e., the synapomorphies that are absent (except polymorphic occurrence in a single terminal) outside of the clade, and that could be scored for its sister and most-basal terminal taxa and for at least 50% of its terminals. MANIRAPTORIFORMES: ^{A}*5.1*, ***11.1***, ^{D}17.1, 24.0, ^{A}*29.1*, ^{D}31.1, ***37.1***, ^{A}*38.1*, ^{D}43.2, ^{A}*49.1*, ^{A}*53.1*, ***55.1***, ^{D}*69.1*, ^{A}*94.1*, ***100.1***, ^{A}-103.0, ^{A}104.0, ***106.1***, ^{A}*109.1*, ^{D}*111.1*, ***114.1***, ^{A}*117.1*, ^{A}-125.0, ***127.2***, ^{D}132.0, ^{A}*134.1*, ^{A}*136.1*, ^{D}*139.1*, ***149.2***, ***154.1***, **168.1**, ^{A}*178.1*, ^{A}*185.1*, 187.1, 194.1, ^{A}*195.2*. MANIRAPTORA, EUMANIRAPTORA: ***23.1***, ^{A}-40.0, ^{A}***101.1***, ^{A}105.1, ***108.1***, ^{D}109.1, ^{D}117.1, ***124.1***, ^{A}*126.2*, ***128.1***, ^{A}130.2, 133.2, ***137.3***, ^{A}***141.1***, ^{D}144.1, ***145.1***, 146.1, ^{D}148.1, ^{A}-150.0, ^{A}-153.0, ^{D}157.1, **159.1**, ^{A}-162.0, ***165.2***, ^{A}*167.1*, ***170.1***, ^{A}***172.1***, ^{A}***174.1***, -175.0, 179.0, 182.0, ^{A}-189.0. AVIALAE: ^{A}3.1, 6.1, ***16.1***, 19.1, ^{A}-22.0, ***24.2***, ^{D}29.1, ***33.1***, ^{A}37.2, ^{D}38.1, ^{A}*50.1*, ^{D}53.1, *54.1*, *57.1*, *64.1*, *65.1*, *67.1*, *68.1*, ^{A}77.1, ^{A}79.0, 87.1, ^{D}94.1, ^{D}104.0, ***119.1***, 121.0, ^{A}-125.1, ^{A}*131.1*, *152.1*, ^{D}-162.0, 173.1, ^{D}174.1. CLADE A: ^{A}4.1, ***20.1***, ***35.1***, ^{A}*39.1*, ^{A}*45.2*, ^{A}*52.1*, ^{D}66.1, ^{A}-69.0, 71.1, ^{A}76.1, ^{A}***85.1***, ^{A}*125.2*, ^{A}135.1, 140.1, ^{A}-142.1, 143.1, -155.0, 156.1, ^{D}172.1, *188.1*, ^{A}-192.0. CLADE B: ^{D}4.1, ^{A}18.1, 21.1, ^{A}-22.1, ^{A}***26.1***, ***42.1***, ^{A}43.1, ^{A}44.1, ^{A}*60.1*, ^{A}*62.1*, ^{A}*64.2*, ***72.1***, ^{A}*73.1*, ^{A}*80.1*, -83.0, 84.0, ^{D}85.1, ^{A}*91.1*, ^{A}*92.1*, ^{A}*93.1*, **96.2**, **97.1**, ^{A}-105.0, ^{A}113.0, ^{A}122.1, ^{A}*126.1*, ^{A}129.1, *136.2*, -139.0, -163.0, ^{A}180.1. OVIRAPTOROSAURIA: ^{A}*1.1*, ^{A}-6.0, ^{A}*9.1*, ^{A}*14.1*, 17.0, ^{D}*26.1*, 28.1, ^{A}***30.2***, ^{D}43.1, ^{D}*45.2*, **47.1**, ^{D}50.1, ^{A}*59.1*, ^{A}*63.1*, ^{A}74.1, 75.1, ^{D}76.1, ^{A}-77.0, ^{A}*79.2*, ^{A}*81.1*, ***86.1***, ^{D}87.1, ^{A}98.1, ^{A}107.0, ^{A}-114.0, ***122.2***, ^{A}-125.0, ^{D}*126.1*, -128.0, ***133.1***, ^{D}134.1, ^{D}135.1, -149.0, -152.0, ^{A}-165.0, ^{D}167.1, ^{D}180.1, ^{D}185.1, ^{D}-193.0. CLADE C: ^{D}*1.1*, ^{D}*9.1*, ^{A}*12.1*, ^{D}*14.1*, ^{D}37.2, ^{A}-40.1, ^{A}*41.1*, ^{A}*70.1*, ^{D}*79.2*, ^{A}*88.1*, ^{A}*89.1*, ^{A}*90.1*, ^{D}*92.1*, ^{A}102.1, ^{D}129.1, ^{A}-131.0, 136.1, ^{D}142.1, ^{A}-150.1, 153.1, 155.1, ^{A}165.1, ***169.1***, -187.0, -188.0. OVIRAPTOROIDEA: ^{A}*2.1*, ^{A}4.2, ^{A}*8.1*, ^{D}*12.1*, ^{A}*19.2*, ^{A}*27.1*, ^{A}*61.1*, ^{D}*70.1*, ^{D}*73.1*, ^{D}*81.1*, ***82.1***, ^{D}*88.1*, ^{D}*89.1*, ^{D}*90.1*, ^{D}*91.1*, ^{D}*93.1*, ^{A}*95.1*, ^{A}-107.1, ^{D}113.0, ^{D}-114.0, ***115.1***, ^{A}-125.1, ^{D}150.1, ^{A}151.1, -159.0, ^{D}165.1, 176.1, ^{D}178.1, ^{A}-195.0. CAENAGNATHIDAE: ^{A}-15.0, ^{A}-48.0, ^{A}72.2, ^{A}-74.0, ^{A}-108.0, ^{A}120.1, ^{A}-121.1, ^{A}-127.1, ^{D}151.1, -152.1, ^{A}-189.1. OVIRAPTORIDAE: ^{D}3.1, ^{D}4.2, ^{D}-6.0, ^{D}*8.1*, *10.1*, ^{D}-17.0, ^{D}18.1, ^{D}*19.2*, ^{D}*27.1*, ^{D}*30.2*, ^{D}32.1, ^{D}39.1, ^{D}40.1, ^{D}*41.1*, ^{D}48.1, ^{D}49.1, *50.2*, ^{D}*52.1*, *58.1*, ^{D}*59.1*, ^{D}*60.1*, ^{D}*61.1*, ^{D}*62.1*, ^{D}*63.1*, ^{D}*64.2*, ^{D}-69.0, ^{D}74.1, *77.2*, *78.1*, ^{A}-80.0, ^{D}95.1, ^{D}98.1, ^{D}101.1, ^{D}102.1, -117.0, ^{D}130.2, ^{A}**166.1**, ^{D}-179.1, ^{A}183.1. CLADE D: ^{D}5.1, ^{D}44.1, ^{A}-105.1, ^{D}141.1, ^{A}-151.0, 154.2, -158.0, ^{D}166.1. CLADE E: ^{A}-2.0, 122.1, ^{D}125.1, -132.1, -140.0, -156.0.

lengths (11.1); ascending (squamosal) process of the quadratojugal slender, bordering not more than the ventral half of the infraorbital fenestra (37.1); three tympanic recesses present (55.1); cranial articular facets of the centra in the anterior postaxial cervicals wider than deep (100.1); shafts of the cervical ribs not longer than the respective centra (106.1); transverse processes present on 14 or less caudals (114.1); caudoventral process of the coracoid long, extending caudoventrally beyond the glenoid (127.2); humerus length to femur length ratio being at least 0.7 (149.2); cuppedicus fossa or wide shelf present on the ventral margin of the preacetabular process of the ilium (154.1); pubic apron not longer dorsoventrally than a half of the total length of the pubis (168.1).

Comments.—Holtz and Padian (1995) and Holtz (1996) were first to define phylogenetically the name Maniraptoriformes. The former defined it as "The node connecting Arctometatarsalia with Maniraptora", and the latter (p. 538) as "the most recent common ancestor of *Ornithomimus* and birds (i.e., the most recent common ancestor of Arctometatarsalia and Maniraptora), and all descendants of that common ancestor". Holtz and Padian's (1995) Arctometatarsalia consisted of "all coelurosaurs closer to *Ornithomimus* than to birds", and their Maniraptora was "all descendants of the common ancestor of *Dromaeosaurus* and birds". Holtz's (1996: 536) Arctometatarsalia was "the clade composed of *Ornithomimus* and all theropods sharing a more recent common ancestor with *Ornithomimus* than with birds", and his (p. 537) Maniraptora was "all theropods closer to birds than to ornithomimids". Accordingly, our emendation of the two definitions of Maniraptoriformes uses, as reference taxa, *Passer domesticus* (a species of birds) and *Ornithomimus velox* (the type species of the genus *Ornithomimus*, the type genus of the family Ornithomimidae). We do not include the type species of the genus *Dromaeosaurus* as a reference taxon because the genus is not mentioned in Holtz's (1996) definition and Dromeosauridae has consistently been recognized (e.g., Forster et al. 1998; Makovicky and Sues 1998; Padian et al. 1999) as part of a less inclusive clade than that containing *Ornithomimus*.

Maniraptora Gauthier, 1986

Emended definition.—The most-inclusive clade containing *Passer domesticus* (Linnaeus, 1758) but not *Ornithomimus velox* Marsh, 1890.

Diagnosis.—Same as for Eumaniraptora (see below).

Comments.—The first phylogenetic definition of the name Maniraptora was published by Gauthier (1986). He (p. 35) worded it as "the group of theropods including birds and all coelurosaurs that are closer to birds than they are to Ornithomimidae". Consequently, our emendation of this definition employs, as reference taxa, *Passer domesticus* (a species of birds) and *Ornithomimus velox* (the type species of the type genus of the family Ornithomimidae).

Eumaniraptora Padian et al., 1997

Emended definition.—The least-inclusive clade containing *Passer domesticus* (Linnaeus, 1758) and *Deinonychus antirrhopus* Ostrom, 1969a.

Diagnosis.—Thirteen unambiguous synapomorphies diagnose Eumaniraptora. These postulated under ACCTRAN and DELTRAN are: frontal process of the postorbital upturned at about 90 degrees (23.1); postzygapophyses on the dorsals markedly extending beyond the respective centra (108.1); sternum ossified, large (124.1); pectoral girdle with the laterally oriented glenoid (128.1); carpals I and II fused, forming a half-moon-shaped element covering metacarpals I and II, with the trochlea carpalis present on its proximal surface (137.3); lip or nubbin present on the proximodorsal edge of the manual unguals (145.1); pubic peduncle of the ilium deeper dorsoventrally than the ischiadic peduncle (159.1); pelvis opisthopubic (165.2); obturator process placed at about mid-length of the ischium (170.1). The unambiguous synapomorphies under ACCTRAN only are: cranial articular facets of centra in the anterior postaxial cervicals strongly inclined ventrocaudad, almost continuous with the ventral surfaces of the centra (101.1); proximal margin of metacarpal I angled in dorsal view, due to the medial extent of the carpal trochlea (141.1); ischium length to pubis length ratio being 0.70 or less (172.1); posterior (greater) trochanter on the femur extended craniocaudally (174.1).

Comments.—The first explicit phylogenetic definition of the name Eumaniraptora was provided by Padian et al. (1999). They (p. 69) phrased it as "the most recent common ancestor of *Deinonychus* and Neornithes and all descendants of that ancestor". Accordingly, our emendation of this definition includes *Passer domesticus* (a species of Neornithes) and *Deinonychus antirrhopus* (the type species of the genus *Deinonychus*).

Avialae Gauthier, 1986

Emended definition.—The most-inclusive clade containing *Passer domesticus* (Linnaeus, 1758) but not *Dromaeosaurus albertensis* Matthew and Brown, 1922 or *Troodon formosus* Leidy, 1856.

Diagnosis.—Four unambiguous synapomorphies (under both ACCTRAN and DELTRAN) diagnose Avialae: nasal as long as or shorter than the frontal (16.1); orbit length to antorbital fossa's length ratio being at least 1.2 (24.2); suborbital part of the jugal shallow dorsoventrally or rod-shaped (33.1); tail including not more than 30 caudals (119.1).

Comments.—Following Gauthier (1986), Avialae is equated in this paper with the vernacular name "birds". The name Avialae was originally defined phylogenetically by Gauthier (1986: 36) as "Ornithurae plus all extinct maniraptorans that are closer to Ornithurae than they are to Deinonychosauria". He (p. 12) referred the name Ornithurae to a clade "encompassing all extant birds, as well as all other birds that are closer phylogenetically to extant birds than is *Archaeopteryx*". His

Deinonychosauria included Dromaeosauridae and Troodontidae. Accordingly, our emendation of his definition of Avialae uses, as reference taxa, *Passer domesticus* (a species of extant birds), *Dromaeosaurus albertensis* (the type species of the type genus of the family Dromaeosauridae), and *Troodon formosus* (the type species of the type genus of the family Troodontidae).

Clade A

Diagnosis.—According to our analysis, three unambiguous synapomorphies diagnose this clade. Two (ventral margin of the external naris situated dorsal to the maxilla, 20.1; quadratojugal process of the jugal tapering caudad, 35.1) were postulated under ACCTRAN and DELTRAN. One (caudoventral process of the dentary long and shallow, extending caudad at least to the caudal margin of the external mandibular fenestra, 85.1) was recognized under ACCTRAN only.

Comments.—*Archaeopteryx lithographica* has traditionally been regarded as a species of Aves. The first phylogenetic definition of Aves that accomodated the traditional usage of this name was proposed by Chiappe (1992: 348) "to include the common ancestor of *Archaeopteryx* and modern birds plus all its descendants". This definition corresponds to the clade here referred to as Clade A. Although the definition has been adopted by many authors (e.g., Padian and Chiappe 1998; Sereno 1998, 1999a, b, c; Padian et al. 1999), others (e.g., Wagner and Gauthier 1999; Sumida and Brochu 2000; Norell and Clarke 2001) have followed Gauthier (1986), who first defined phylogenetically Aves, restricting its meaning and content to the crown-group birds, and thus excluding *Archaeopteryx*. His purpose in doing so was (p. 12) "to maximize stability and phylogenetic informativeness" of the name Aves. However, the opinion that crown-clade phylogenetic definitions are more stable in meaning and content than traditional, more-inclusive definitions, and that crown clades are more highly corroborated than traditional, more-inclusive clades (e.g., Gauthier 1986; Gauthier, Estes, and de Queiroz 1988; Gauthier, Kluge, and Rowe 1988; Gauthier et al. 1989), is not justified as shown by Lee (1996), Lee and Spencer (1997), and Sereno (1998, 1999c). There is therefore no compelling reason to abandon the traditional usage of the familiar name Aves to apply it to a crown clade. Although priority is a heuristic principle with long-standing usage in taxonomy, we agree with Sereno (1999b) that utility should carry more weight than priority in phylogenetic nomenclature. Nevertheless, taking account of the current controversy over the meaning of the name Aves, we refrain from using it in this paper.

Clade B

Diagnosis.—We consider five character states as the unambiguous synapomorphies of this clade. As postulated under ACCTRAN and DELTRAN, these are: quadrate with the lateral cotyla for the quadratojugal (42.1); mandibular symphysis tightly sutured (72.1); maxillary teeth lost (96.2); dentary teeth lost (97.1). The fifth synapomorphy, a large parietal comparable in size to or longer than the frontal (26.1), was recognized under ACCTRAN only.

Comments.—Loss of the maxillary and dentary teeth (96.2, 97.1) in Clade B and in the derived ornithomimosaurs (Appendix 2) is an evident parallelism because the teeth are still present in *Pelecanimimus polyodon* Pérez-Moreno et al., 1994, a basal species of Ornithomimosauria (Makovicky and Sues 1998).

According to a new reconstruction of the skull in *Confuciusornis sanctus* (Chiappe et al. 1999: fig. 20A), the parietal is about as large as the frontal, contrary to Martin et al.'s (1998) interpretation (illustrated by Chiappe et al. 1999: fig. 20B). Taking account of this controversy, we coded the involved character 26 as unknown in *Confuciusornis sanctus* (Appendix 2). However, if Chiappe et al.'s (1999: fig. 20A) reconstruction is correct, then character state 26.1 will be a synapomorphy of Clade B under both the ACCTRAN and DELTRAN criteria.

Oviraptorosauria Barsbold, 1976b

Emended definition.—The most-inclusive clade containing *Oviraptor philoceratops* Osborn, 1924 but not *Passer domesticus* (Linnaeus, 1758).

Diagnosis.—Five unambiguous synapomorphies characterize this clade. Those postulated under ACCTRAN and DELTRAN are: foramen magnum larger than the occipital condyle (47.1); coronoid eminence of the mandible present (86.1); hypapophyses prominent in the cervicodorsal vertebral region (122.2); ectepicondyle of the humerus more prominent than the entepicondyle (133.1). The fifth synapomorphy, a large, square infratemporal fenestra (30.2), was recognized under ACCTRAN only.

Comments.—Padian et al. (1997) and Currie and Padian in Barsbold (1997) were first to define phylogenetically the name Oviraptorosauria. Padian et al. referred this name to "all taxa closer to *Oviraptor* than to Aves", regarding Aves as "a node uniting *Archaeopteryx* and extant birds plus descendants of their most recent common ancestor". Currie and Padian defined Oviraptorosauria "to include Oviraptoridae and all taxa closer to *Oviraptor* than to birds". Because the so-defined name refers to non-existing clade according to our phylogenetic analysis (Fig. 1), we consider the chronologically third definition, by Sereno (1998: 65), which ties the name Oviraptorosauria with 'all maniraptorans closer to *Oviraptor* than to Neornithes'. This definition appears to be consistent with the original intent of both Padian et al. (1997) and Currie and Padian in Barsbold (1997). Our emendation of Sereno's (1998) definition includes *Oviraptor philoceratops* (the type species of the genus *Oviraptor*) and *Passer domesticus* (a species of Neornithes).

Concerning synapomorphy 30.2, here postulated under ACCTRAN only, the infratemporal fenestra is not separated from the orbit (character state 30.3) in *Avimimus portentosus*, a basal oviraptorosaur, because the postorbital bar is reduced in this species. However, due to the unique, far caudal position of the quadratojugal and the shape of its unreduced ventral portion, the ventrally angular caudal border of the fenestra in *Avimimus portentosus* is identical to those in all other oviraptorosaurs. This construction evidences that the condition found in *Avimimus portentosus* is advanced in relation to state 30.2. This speaks in favor of the reliability of this synapomorphy for Oviraptorosauria.

Clade C

Diagnosis.—One character state, a strongly concave caudal margin of the ischiadic shaft (169.1), is considered here the unambiguous synapomorphy (ACCTRAN and DELTRAN) of Clade C.

Comments.—A weak character support for this clade is due to the lack of information concerning the relevant characters in the basal species *Caudipteryx zoui*, as well as to the inadequate knowledge of *Avimimus portentosus*, which constitutes the sister taxon to the clade. Among character states postulated by our analysis as synapomorphies for Clade C (Fig. 1), states 1.1, 9.1, 14.1, 79.2, and 92.1 are potentially diagnostic of the more inclusive clade Oviraptorosauria.

Oviraptoroidea Barsbold, 1976a

Emended definition.—The least-inclusive clade containing *Oviraptor philoceratops* Osborn, 1924 and *Caenagnathus collinsi* R.M. Sternberg, 1940.

Diagnosis.—Two unambiguous synapomorphies (ACCTRAN and DELTRAN) characterize this clade: rostrodorsal margin of the dentary deeply concave (82.1); pleurocoels present at least in the centra of the proximal tail vertebrae (115.1).

Comments.—The name Oviraptoroidea was defined phylogenetically by Sereno (1999a: 2147) as "*Oviraptor*, *Caenagnathus*, their most recent common ancestor, and all descendants". Consequently, we emend this definition, using, as reference taxa, the type species of the two genera.

Character support for this clade is weak, mainly due to the inadequate knowledge of its caenagnathid terminals *Chirostenotes pergracilis* and *Nomingia gobiensis* (Appendix 2).

Caenagnathidae R.M. Sternberg, 1940

Emended definition.—The most-inclusive clade containing *Caenagnathus collinsi* R.M. Sternberg, 1940 but not *Oviraptor philoceratops* Osborn, 1924.

Comments.—Sues (1997: 699) was first to define phylogenetically the name Caenagnathidae. However, in addition to species whose caenagnatid status has not been questioned, his definition also included *Elmisaurus rarus* as an internal reference taxon. Because we do not accept the caenagnathid status of this species (see Introduction), we consider here the chronologically second definition of Caenagnathidae, which is consistent with the traditional usage of this name. Sereno (1998: 65) worded this definition as "All oviraptorosaurs closer to *Caenagnathus* than to *Oviraptor*". Accordingly, its emendation includes the type species of the two genera.

None of the character states postulated by the cladistic analysis as synapomorphies for Caenagnathidae (Fig. 1) appears to be reliable. This clade is poorly differentiated and very incompletely preserved. For the latter reason, only *Chirostenotes pergracilis* (*sensu* Sues 1997) was scored for characters, in addition to the incompletely documented oviraptorosaur *Nomingia gobiensis*, recognized as a caenagnathid by the present analysis. Most of the hypothetical synapomorphies of Caenagnathidae (Fig. 1) are known in either *Chirostenotes pergracilis* or *Nomingia gobiensis*. For both species, only two synapomorphies could be recorded: dorsal margin of the ilium arched along the central portion of the blade (151.1); preacetabular process of the ilium longer than the postacetabular process (152.1). The two character states, however, are not exclusive of Caenagnathidae. State 151.1 also occurs in *Archaeopteryx lithographica* and "*Oviraptor*" *mongoliensis*, and state 152.1 is also present in Therizinosauria, *Archaeopteryx lithographica*, and *Confuciusornis sanctus*. The decay index and bootstrap supports are low for Caenagnathidae (Fig. 1). Thus, this clade is poorly supported by our analysis, and the assignment of *Nomingia gobiensis* in Caenagnathidae should be considered tentative (*faut de mieux*).

Recently, Sues (1997) published a revised diagnosis of Caenagnathidae, including the following features: antorbital fossa with a pronounced rim; manual digit III longer than digit I, and with very slender phalanges; synsacrum composed of six vertebrae. These features are also characteristic of most oviraptorids, and therefore cannot be considered caenagnathid synapomorphies.

Oviraptoridae Barsbold, 1976a

Emended definition.—The most-inclusive clade containing *Oviraptor philoceratops* Osborn, 1924 but not *Caenagnathus collinsi* R.M. Sternberg, 1940.

Diagnosis.—Oviraptoridae can presently be diagnosed only by one unambiguous synapomorphy, the pubic shaft concave cranially (166.1), which was recognized under ACCTRAN only.

Comments.—The first phylogenetic definition of the name Oviraptoridae was proposed by Sereno (1998). He (p. 65) worded it as "All oviraptorosaurs closer to *Oviraptor* than to *Caenagnathus*". Consequently, our emendation of this definition includes the type species of the two genera.

Most characters providing oviraptorid synapomorphies in the present analysis (Fig. 1) could not be scored for *Caudipteryx zoui* (Appendix 2), so that any one of the involved hypothetical synapomorphies is potentially diagnostic of the more inclusive Clade C. For this reason, we do not regard them here as unambiguous.

Four of the synapomorphies hypothesized for Oviraptoridae are only known in this clade. These are: premaxilla main-body ventral length to subnarial height ratio being 0.7 or less (4.2); premaxilla pneumatized (8.1); caudal part of the naris overlapping most of the antorbital fossa (19.2); skull-roof bones pneumatized (27.1). However, it is uncertain whether these synapomorphies are indeed exclusive of Oviraptoridae because none of the concerned characters could be scored for either *Chirostenotes pergracilis* or *Nomingia gobiensis*, resulting in the unknown status of these characters in the sister taxon Caenagnathidae.

Clade D

Comments.—This clade is weakly supported. The values of the decay index and bootstrap are low (Fig. 1), and almost all of its hypothetical synapomorphies also occur in any other maniraptoriform taxa. The only exception could be the cranially concave pubic shaft (166.1). However, character 166 could not be scored for "*Oviraptor*" *mongoliensis*, the sister taxon to Clade D, so that state 166.1 was recognized, under ACCTRAN, as a synapomorphy of the more inclusive clade Oviraptoridae.

Clade E

Comments.—All hypothetical synapomorphies of Clade E also occur outside of this clade, and the values of the decay index and bootstrap are low (Fig. 1), so there is a weak support for the clade. Clade E is equivalent to the subfamily Ingeniinae erected by Barsbold (1981) to include *Ingenia yanshini* and *Conchoraptor gracilis*.

Summary and conclusions

As traditionally understood, the infraorder Oviraptorosauria Barsbold, 1976b included the family Oviraptoridae Barsbold, 1976a and the family Caenagnathidae R.M. Sternberg, 1940. A recent cladistic analysis of Theropoda by Sereno (1999a) added *Caudipteryx* Ji et al., 1998 as a basal oviraptorosaur. Since description of the first species of Oviraptorosauria, *Chirostenotes pergracilis* Gilmore, 1924 and *Oviraptor philoceratops* Osborn, 1924, the phylogenetic relationships of the clade have been unclear. The present paper is an attempt to elucidate the phylogenetic position of Oviraptorosauria within Maniraptoriformes. In the ingroup, most of the known oviraptorids and caenagnathids, *Caudipteryx zoui*, and two species of uncertain relationships within Maniraptoriformes (*Avimimus portentosus*, *Nomingia gobiensis*) were included, as well as two basal birds (*Archaeopteryx lithographica*, *Confuciusornis sanctus*) and three maniraptoriform clades (Ornithomimosauria, Dromaeosauridae, Therizinosauria). According to our analysis (Fig. 1):

- oviraptorosaurs are avialans (birds), with *Confuciusornis sanctus*, *Archaeopteryx lithographica*, and Therizinosauria as successively more remote avialan outgroups to Oviraptorosauria;
- *Avimimus* and *Caudipteryx* are basal oviraptorosaurs;
- oviraptorosaurs are secondarily flightless;
- monophyly of caenagnathids is weakly supported at the present state of knowledge;
- phylogenetic position of Dromaeosauridae as a basal taxon of Eumaniraptora is supported.

Some skull features observed in oviraptorids (skulls of other oviraptorosaurs are not sufficiently known to confirm the presence of these features) support our hypothesis about the avialan status of Oviraptorosauria. These features include: extensive pneumatization; enlargement of the parietal portion of the skull roof; double-headed otic process of the quadrate (Maryańska and Osmólska 1997); lateral cotyla on the quadrate for articulation with the quadratojugal (Maryańska and Osmólska 1997); functional loss of contact between the palate and jugal; shallow or rod-like jugal (Elżanowski 1999). This set of traits is absent in non-avialan theropods but is present in advanced birds. The majority of these traits also occur in *Confuciusornis*. In modern birds, the presence of the last four features is connected with cranial kinesis. However, they appear to be secondarily adapted to play the opposite roles in the akinetic skulls of oviraptorids because both otic heads of the oviraptorid quadrate are immovably attached to the squamosal and braincase, effectively restraining any swing or rotation of the quadrate. The oviraptorid palate, although functionally disengaged from the jugal, became rigid due to the development of a pair of longitudinally oriented pterygoid-ectopterygoid bars. We hypothesize that these traits, which in ancestors of modern birds developed to permit independent protraction and retraction of the rostrum relative to the braincase, in oviraptorids (and probably in other oviraptorosaurs) became secondarily adapted to make the skull a rigid unit.

Some features characteristic of birds also occur in the oviraptorid postcranium. The oviraptorid neck is long, including 12 or 13 vertebrae (instead of 10, present in non-avialan theropods) without any change in the total number (23) of presacrals. This results in the shortening of the thoracic section of the vertebral column, which in oviraptorosaurs includes less than 12 vertebrae, as in advanced birds (Chiappe et al. 1999). In oviraptorids, the deep ventral processes (hypapophyses) occur on vertebrae at the root of the neck. In addition, there is a massive furcula, well stabilized on the acromion, similar in shape to those in *Archaeopteryx* and *Confuciusornis*. Moreover, in all known oviraptorosaurs, the tail is shorter than in any of non-avialan theropods. In spite of these similarities to volant birds, oviraptorosaurs do not show any evident flight adaptations in their postcrania.

The basal species of Oviraptorosauria, *Avimimus portentosus* and *Caudipteryx zoui*, were smaller and lighter built than the more-derived species of the clade. As estimated by Jones et al. (2000), the limb proportions and placement of the mass centre in *Caudipteryx zoui* were very much like those of extant cursorial birds. A similar pattern of postcranial structure is present in *Avimimus portentosus*; both species may have used the same running mechanism. Their forelimbs were short in relation to the hindlimbs, and these basal oviraptorosaurs were evidently unable to fly. The advanced oviraptorosaurs, Oviraptoroidea, had relatively longer forelimbs of a rather standard proportion among non-avialan theropods, but nothing in their anatomy implies that they could function as wings. As postulated by our phylogenetic analysis, the volant *Confuciusornis sanctus* and *Archaeopteryx lithographica* are successively more remote outgroups to the flightless Oviraptorosauria. If this pattern of relationship is feasible, oviraptorosaurs were most parsimoniously secondarily unable to fly. Consequently, some postcranial character states of oviraptorosaurs are recognized by the analysis as reversals. Examples of such reversals are: caudoventral orientation of the pectoral glenoid; humerus about half as long as the femur; about equally long metatarsals II and IV. These reversions apparently accompanied the change from the flying to ground-dwelling mode of life.

Although no evidence of feathers has been found with oviraptoroid remains, the presence of feathers has been documented in one basal oviraptorosaur (*Caudipteryx zoui*; Ji et al. 1998), and it was implied for the other (*Avimimus portentosus*; Kurzanov 1987). The feathers of *Caudipteryx zoui* are similar to those in *Archaeopteryx* and *Confuciusornis*, and in this respect they differ from the "integumentary" structures in therizinosaurs (Xu, Tang, and Wang 1999) or "filamentous" structures in dromaeosaurids (Xu, Wang, and Wu 1999). The recent discoveries of several oviraptorid skeletons overlying eggs in nests (Norell et al. 1995; Dong and Currie 1996; Clark et al. 1999) indicate that oviraptorids brooded their eggs. This specialized form of parental care has thus far been known only in modern birds. Both the brooding behavior and the feather structure of *Caudipteryx zoui* additionally support our phylogenetic hypothesis placing oviraptorosaurs among birds more derived than *Archaeopteryx*.

The status of oviraptorosaurs as secondarily flightless birds, more advanced than is *Archaeopteryx*, has already been suggested (Paul 1988; Olshevsky 1991; Elżanowski 1999; Lü 2000). At the moment, it is difficult to propose a scenario depicting the successive stages of evolution from volant birds to flightless oviraptorosaurs. Nevertheless, character evidence accumulated indicates that such a radical change of adaptation—from the flying to ground-dwelling mode of life—may have occurred for the first time early in avialan evolution.

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Appendix 1

List of characters used in this study. The definitions are either derived from the literature (Gauthier 1986; Clark et al. 1994; Holtz 1994; Russell and Dong 1994a; Chiappe et al. 1996; Novas 1996; Sues 1997; Ji et al. 1998; Makovicky and Sues 1998; Elżanowski 1999; Sereno 1999a; Xu, Tang, and Wang 1999; Norell et al. 2000), and modified where appropriate, or are new.

1. Preorbital skull length to basal skull length ratio: 0.6 or more (0); 0.5 or less (1).
2. Longitudinal pneumatized crest-like prominence on the skull roof: absent (0); present (1).
3. Snout width (across the premaxilla-maxilla suture) to snout length ratio: less than 0.3 (0); 0.3–0.4 (1); 0.5 or more (2).
4. Premaxilla main-body length (ventral) to height (below the naris) ratio: 1.0–1.4 (0); more than 1.7 (1); 0.7 or less (2).
5. Share of the premaxilla ventral length in the basal skull length: 0.10 or less (0); 0.15 or more (1).
6. Subnarial (maxillary) process of the premaxilla: contacts the nasal, the maxilla excluded from the narial border (0); does not contact the nasal, the maxilla participates in formation of the narial border (1).
7. Palatal processes of the premaxillae: contacting each other medially (0); absent (1).
8. Pneumatization of the premaxilla: absent (0); present (1).
9. Maxilla length (in lateral view) to basal skull length ratio: 0.4–0.7 (0); about 0.3 (1).
10. Subantorbital portion of the maxilla: not inset medially (0); inset medially (1).
11. Palatal shelves of the maxillae: completely separated by the vomer (0); in contact for most of their lengths (1).
12. Palatal shelf of the maxilla with two longitudinal ridges and a tooth-like process: absent (0); present (1).
13. Rim around the antorbital fossa: well pronounced (0); poorly delimited (1).
14. Antorbital fossa: not bordered rostrally by the premaxilla (0); bordered rostrally by the premaxilla (1).
15. Accessory maxillary fenestrae: absent (0); at least one accessory fenestra present (1).
16. Nasal: longer than the frontal (0); shorter than or as long as the frontal (1).
17. Subnarial process of the nasal: long (0); absent or negligible (1).
18. Nasal recesses: absent (0); present (1).
19. Caudal margin of the naris: rostral to the rostral border of the antorbital fossa (0); nearly reaching or overlapping the rostral part of the antorbital fossa (1); overlapping most of the antorbital fossa (2).
20. Ventral margin of the external naris: at the level of the maxilla (0); dorsal to the maxilla (1).
21. Prefrontal: present (0); absent or fused with the lacrimal (1).
22. Lacrimal recess: absent (0); present (1).
23. Postorbital: T-like (0); with the frontal process upturned at about 90 degrees (1).
24. Orbit length to antorbital fossa length ratio: 0.7–0.9 (0); 0.6 or less (1); 1.2 or more (2).
25. Elongate rostromedial process on the frontal: absent (0); present (1).
26. Parietal length to frontal length ratio: 0.6 or less (0); 1.0 or more (1).
27. Pneumatization of skull-roof bones: absent (0); present (1).
28. Sagittal crest on the parietals: absent (0); present (1).
29. Supratemporal fossa: invading the frontals (0); not invading the frontals (1).
30. Infratemporal fenestra: ventrally nearly as long as rostrally high (0); shorter ventrally than high (1); large, square (2); not separated from the orbit (3).
31. Descending (prequadratic) process of the squamosal: constricting the dorsal part of the infratemporal fenestra (0); not constricting the infratemporal fenestra (1).
32. Pneumatization of the squamosal: absent (0); present (1).
33. Suborbital part of the jugal: deep dorsoventrally and flattened lateromedially (0); shallow dorsoventrally or rod-shaped (1).
34. Jugal-postorbital contact: present (0); absent (1).
35. Quadratojugal process of the jugal in lateral view: forked (0); tapering (1); fused with the quadratojugal (2).
36. Quadratojugal-squamosal contact: tips of the bones closely approaching but not contacting each other (0); the bones widely separated (1); the contact present (2).
37. Ascending (squamosal) process of the quadratojugal: massive, bordering about the ventral half of the infratemporal fenestra (0); slender, bordering the ventral half or less of the infratemporal fenestra (1); slender, bordering the ventral two thirds or more of the infratemporal fenestra (2); absent (3).
38. Dorsal part of the quadrate: erect (0); directed backwards (1).
39. Otic process of the quadrate: articulating only with the squamosal (0); articulating with the squamosal and the lateral wall of the braincase (1).
40. Pneumatization of the quadrate: absent (0); present (1).
41. Accessory process for a contact with the quadratojugal on the distal end of the quadrate: absent (0); present (1).
42. Lateral cotyla for the quadratojugal on the quadrate: absent (0); present (1).
43. Mandibular condyles of the quadrate situated: caudal to the occipital condyle (0); in the same vertical plane as the occipital condyle (1); rostral to the occipital condyle (2).
44. Nuchal transverse crest: pronounced (0); not pronounced (1).
45. Paroccipital process directed: laterad (0); lateroventrad (1); ventrad (2).
46. Proximal portion of the paroccipital process: solid (0); hollow (1).
47. Foramen magnum: smaller than or equal to the occipital condyle (0); larger than the occipital condyle (1).
48. Basal tubera: modestly pronounced (0); well pronounced, widely separated (1).
49. Pneumatization of the basisphenoid: weak or absent (0); extensive (1).
50. Basipterygoid processes: well developed (0); strongly reduced (1); absent (2).
51. Bulbous parasphenoid: absent (0); present (1).
52. Parasphenoid rostrum: horizontal or directed rostrodorsad (0); slanting rostroventrad (1).
53. Depression in the periotic region: absent (0); present (1).
54. Pneumatization of the periotic region: absent or weak (0); extensive (1).
55. Three tympanic recesses: absent (0); present (1).
56. Medially extended pterygoids meeting each other along the midline and underlying ventrally the basisphenoid and parasphenoid: absent (0); present (1).
57. Quadrate wing of the pterygoid: distant from the braincase wall (0); overlapping the braincase (1).
58. Pterygoid basal process for a contact with the basisphenoid: absent (0); present (1).
59. Ectopterygoid situated: lateral to the pterygoid (0); rostral to the pterygoid (1).
60. Ectopterygoid contacts with the maxilla and lacrimal: absent (0); present (1).
61. Hook-like jugal process on the ectopterygoid: present (0); absent (1).

62. Massive pterygoid-ectopterygoid longitudinal bar: absent (0); present (1).
63. Palate extending below the cheek margin: absent (0); present (1).
64. Palatine: tetraradiate or trapezoid (0); triradiate, without a jugal process (1); developed in three planes perpendicular to each other (2).
65. Pterygoid wing of the palatine situated: dorsal to the pterygoid (0); ventral to the pterygoid (1).
66. Maxillary process of the palatine: shorter than the vomeral process (0); longer than the vomeral process (1).
67. Vomer: distant from the parasphenoid rostrum (0); approaching or in contact with the rostrum (1).
68. Suborbital (ectopterygoid-palatine) fenestra: well developed (0); closed or reduced (1).
69. Pterygopalatine fenestra: absent (0); present (1).
70. Jaw joint: distant from the skull midline (0); close to the skull midline (1).
71. Movable intramandibular joint: present (0); absent (1).
72. Mandibular symphysis: loose (0); tightly sutured (1); fused (2).
73. Extended symphyseal shelf at the mandibular symphysis: absent (0); present (1).
74. Downturned symphyseal portion of the dentary: absent (0); present (1).
75. U-shaped mandibular symphysis: absent (0); present (1).
76. Retroarticular process' length to total mandibular length ratio: less than 0.05 or the process absent (0); about 0.10 (1).
77. Mandible maximum height to length ratio: about 0.2 (0); about 0.1 (1); 0.3–0.4 (2).
78. External mandibular fenestra's height to length ratio: 0.2–0.5 (0); 0.7–1.0 (1); the fenestra absent (2).
79. External mandibular fenestra's length to total mandibular length ratio: 0.15–0.20 (0); 0.10 or less (1); 0.25 or more (2); the fenestra absent (3).
80. Coossification of the articular with the surangular: absent (0); present (1).
81. Mandibular rami in dorsal view: straight (0); bowed laterad at the mid-length (1).
82. Rostrodorsal margin of the dentary: straight or weakly concave (0); deeply concave (1).
83. Caudal margin of the dentary: incised, producing two caudal processes (0); oblique (1).
84. Long and shallow caudodorsal process of the dentary: present (0); absent (1).
85. Long and shallow caudoventral process of the dentary, extending caudad at least to the caudal border of the external mandibular fenestra: absent (0); present (1).
86. Coronoid eminence: absent (0); present (1).
87. Surangular foramen: present (0); absent (1).
88. Mandibular articular facet for the quadrate: formed of the surangular and articular (0); formed exclusively of the articular (1).
89. Mandibular articular facet for the quadrate: with one or two cotylae (0); convex in lateral view, transversely wide (1).
90. Articular facet for the mandibular joint positioned: below the dorsal margin of the caudal part of the mandibular ramus (0); above this margin (1).
91. Rostral part of the prearticular: deep, approaching the dorsal margin of the mandible (0); shallow, strap-like, not approaching the dorsal margin of the mandible (1).
92. Splenial: subtriangular, approaching the dorsal margin of the mandible (0); strap-like, shallow, not approaching the dorsal margin of the mandible (1).
93. Mandibular adductor fossa: rostrally delimited, occupying the caudal part of the mandible (0); large, rostrally and dorsally extended, not delimited rostrally (1).
94. Coronoid bone: well developed (0); reduced or absent (1).
95. Premaxillary teeth: present (0); absent (1).
96. Maxillary tooth row: extends at least to the level of the preorbital bar (0); does not reach the level of the preorbital bar (1); the maxillary teeth absent (2).
97. Dentary teeth: present (0); absent (1).
98. Number of the cervicals (excluding the cervicodorsal): not more than 10 (0); more than 10 (1).
99. Pleurocoels or lateral excavations on cervical centra: absent (0); at least one pair present (1).
100. Cranial articular facets of the centra in the anterior postaxial cervicals: subcircular (0); distinctly wider than deep (1).
101. Cranial articular facets of the centra in the anterior postaxial cervicals: not inclined or only slightly inclined (0); strongly inclined ventrocaudad, almost continuous with the ventral surfaces of the centra (1); ball-shaped (2).
102. Anterior cervical centra: not extending posteriorly beyond the respective neural arches (0); extending posteriorly beyond the respective neural arches (1).
103. Cervical neural spines: low and thin (0); powerful (1).
104. Epipophyses on the postaxial cervicals: in form of a low crest or rugosity (0); prong-shaped (1).
105. Cervical ribs: loosely attached to vertebrae in adults (0); firmly attached (1).
106. Shafts of the cervical ribs: longer than the respective centra (0), not longer than the respective centra (1).
107. Pleurocoels or lateral excavations on the dorsal centra: absent (0); present (1).
108. Postzygapophyses on the dorsals: not extending beyond the respective centra (0); markedly extending beyond the centra (1).
109. Number of vertebrae included in the synsacrum in adults: not more than five (0); more than five (1).
110. Sacral spines in adults: unfused (0); fused (1).
111. Continuous sulcus along the ventral side of the mid-sacral centra: absent (0); present (1).
112. Pleurocoels on the sacral centra: absent (0); present (1).
113. Transition point on the caudals: absent (0), present (1).
114. Number of caudals with the transverse processes: 15 or more (0); less than 15 (1).
115. Pleurocoels on the caudal centra: absent (0); present at least in the proximal part of the tail (1).
116. Neural spines on caudals: simple (0); divided into the cranial and caudal alae (1).
117. Neural spines confined to: 23 proximal caudals or more (0); at most 16 proximal caudals (1).
118. Distal caudal centra: about as long as the proximal ones or insignificantly shorter (0); longer than the proximal caudal centra (1); about half as long as the proximal caudal centra (2).
119. Number of the caudals: more than 35 (0); 30 or less (1).
120. Pygostyle: absent (0); present (1).
121. Distal caudal prezygapophyses: overlapping less than a half of the centrum of the preceding vertebra (0); overlapping at least a half of the preceding vertebra (1).
122. Hypapophyses in the cervicodorsal vertebral region: absent (0); small (1); prominent (2).
123. Distal chevrons: deeper than long (0); longer than deep (1).
124. Sternum: unossified or small (0); ossified, large (1).
125. Scapula length to humerus length ratio: 0.8–1.1 (0); 1.2 or more (1); 0.7 or less (2).
126. Acromion: projecting dorsad (0); everted laterad (1); projecting craniad (2).
127. Caudoventral process on the coracoid: absent (0); short, not extending beyond the glenoid diameter (1); long, caudoventrally extending beyond the glenoid (2).
128. Orientation of the glenoid on the pectoral girdle: caudoventral (0); lateral (1).

129. Deltopectoral crest: low, with the width equalling to or smaller than the shaft diameter (0); expanded, wider than the shaft diameter (1).
130. Internal tuberosity on the humerus: weakly pronounced or absent (0); well pronounced but low (1); subtriangular, distinctly extended medially (2); in form of a longitudinally short, tuber-like extension, sharply delimited from the shaft and usually also from the humeral head (3).
131. Distal condyles of the humerus facing: distad (0); craniad or craniodistad (1).
132. Deltopectoral crest (measured from the humeral head to the apex) extending for: about the proximal third of the humerus length or less (0); about 40–50% of the humerus length (1).
133. Epicondyles on the humerus: absent or poorly developed (0); the ectepicondyle more prominent than the entepicondyle (1); the entepicondyle more prominent than the ectepicondyle (2); the ectepicondyle and entepicondyle about equally prominent (3).
134. Shaft of the ulna: straight (0); bowed, convex caudally (1); bowed, concave caudally (2).
135. Radius length to humerus length ratio: 0.80 or less (0); 0.85 or more (1).
136. Carpus including: more than four free carpals (0); three or four free carpals (1); the carpometacarpus present (2).
137. Distal carpals: flat, mostly separate (0); carpals I and II separate, carpal I with the proximal trochlea (1); carpals I and II fused, with the trochlea only on carpal I, covering only metacarpal I (2); carpals I and II fused, half-moon-shaped, with the trochlea on the proximal surface, covering metacarpals I and II (3).
138. Manual digit II: shorter than or subequal to manual digit III (0); longer than manual digit III (1).
139. Combined lengths of manual phalanges III-1 and III-2: greater than the length of phalanx III-3 (0); less than or equal to the length of phalanx III-3 (1).
140. Metacarpal I length to metacarpal II length ratio: 0.5 or more (0); less than 0.5 (1).
141. Proximal margin of metacarpal I in dorsal view: straight, horizontal (0); angled due to the medial extent of the carpal trochlea (1).
142. Metacarpal II relative to metacarpal III: shorter (0); subequal (1); longer (2).
143. Metacarpal II length to humerus length ratio: 0.4 or less (0); more than 0.4 (1).
144. Metacarpal III: unmodified (0); very slender (1).
145. Lip or nubbin on the proximodorsal edge of the manual unguals: absent (0); present (1).
146. Manus length to humerus plus radius length ratio: 0.50–0.65 (0); more than 0.65 (1); less than 0.50 (2).
147. Manus length to humerus length ratio: more than 1.0 (0); 0.8 or less (1).
148. Manus length to femur length ratio: 0.3–0.6 (0); more than 0.7 (1); less than 0.2 (2).
149. Humerus length to femur length ratio: 0.5–0.6 (0); less than 0.4 (1); 0.7 or more (2).
150. Dorsal margins of the opposite iliac blades: well separated from each other (0); close to or contacting each other along their medial sections (1).
151. Dorsal margin of the ilium along the central portion of the blade: straight (0); arched (1).
152. Preacetabular process relative to the postacetabular process (the lengths measured from the centre of the acetabulum): shorter or equal (0); longer (1).
153. Preacetabular process: not expanded or weakly expanded ventrally below the level of the dorsal acetabular margin (0); expanded ventrally well below the level of the dorsal acetabular margin (1).
154. Morphology of the ventral margin of the preacetabular process: the cuppedicus fossa absent, the margin transversely narrow (0); the cuppedicus fossa or wide shelf present (1); the margin flat, wide at least at the base of the pubic peduncle (2).
155. Cranioventral process on the preacetabular blade: absent (0); rounded (1); hook-like (2).
156. Distal end of the postacetabular process: truncated or broadly rounded (0); narrowed or acuminate (1).
157. Supracetabular crest: well developed (0); reduced or absent (1).
158. Craniocaudal length of the pubic peduncle: about as long as the ischiadic peduncle (0); distinctly longer than the ischiadic peduncle (1).
159. Dorsoventral extension of the pubic peduncle: level with the ischiadic peduncle (0); deeper than the ischiadic peduncle (1).
160. Pubic peduncle: directed craniad, often about parallel to the ventral margin of the preacetabular process (0); vertical or almost vertical (1).
161. Medial vertical ridge on the external surface of the ilium: absent (0); present (1).
162. Brevis fossa: absent or small (0); large (1).
163. Antitrochanter on the ilium: present (0); absent (1).
164. Ilium length to femur length ratio: 0.5–0.7 (0); 0.8 or more (1).
165. Pelvis: propubic (0); mesopubic (1); opisthopubic (2).
166. Pubic shaft: straight (0); concave cranially (1).
167. Pubic foot: with the cranial and caudal processes being about equally long (0); with the cranial process being longer than the caudal process (1); with the cranial process being shorter than the caudal process or absent (2); absent (3).
168. Dorsoventral length of the pubic apron: longer than the half total length of the pubis (0); not longer than the half total length of the pubis (1).
169. Caudal margin of the ischiadic shaft: straight or almost straight (0); strongly concave (1).
170. Position of the obturator process on the ischium: proximal (0); at about mid-length (1); distal (2); obturator process lacking (3).
171. Distal end of the ischium: not expanded (0); expanded (1).
172. Ischium length to pubis length ratio: 0.75 or more (0); 0.70 or less (1).
173. Posterior (greater) trochanter: weakly separated or not separated from the femoral head (0); distinctly separated from the femoral head (1).
174. Craniocaudal extent of the posterior trochanter: short (0); long (1).
175. Anterior (lesser) trochanter: non-aliform (0); aliform (1).
176. Anterior and posterior trochanters: well separated (0); contacting (1); fused (2).
177. Dorsal extremity of the anterior trochanter: well below the posterior trochanter (0); about level with the posterior trochanter (1).
178. Fourth trochanter: well developed (0); weakly developed or absent (1).
179. Adductor fossa and associated craniomedial crest on the distal femur: weak or absent (0); well developed (1).
180. Strong distal projection of the fibular condyle on the femur: absent (0); present (1).
181. Number of the cnemial crests on the tibia: one, cranial (0); two, cranial and lateral (1).
182. Medial surface of the fibular head: flat or shallowly concave (0); with a deep fossa (1).
183. Contact of the distal end of the fibula with the tarsus: present (0); absent (1).
184. Height of the ascending process of the astragalus: less than a quarter of the tibiotarsus length (0); a quarter of the tibiotarsus length or more (1).
185. Ascending process of the astragalus: as tall as wide across the base (0); taller than wide (1).
186. Ascending process of the astragalus: narrower across the base than across the distal end of the astragalus (0); as broad across the base as across the distal end of the astragalus (1).
187. Distal tarsals: not fused with metatarsals (0); fused with metatarsals (1).

188. Proximal coossification of metatarsals II–IV: absent (0); present (1).
189. Arctometatarsus: absent (0); present (1).
190. Metatarsals II and IV: not in contact on the plantar surface (0); contacting distally (1).
191. Metatarsal I length: more than 50% of metatarsal II length (0); less than 50% of metatarsal II length (1); metatarsal I absent (2).
192. Metatarsal IV length relative to the metatarsal II length: about equal (0); longer (1).
193. Pedal digit II: not modified (0); hyperextensible (1).
194. Tibia length to femur length ratio: less than 1 (0); more than 1 (1).
195. Metatarsus length to femur length ratio: 0.4–0.6 (0); about 0.3 (1); 0.7–0.8 (2).

Appendix 2

Distribution of the states of 195 characters (Appendix 1) in four outgroup (*Herrerasaurus ischigualastensis*, *Coelophysis bauri*, Allosauroidea, Tyrannosauridae) and 16 ingroup taxa. The taxa that were excluded from the final cladistic analysis are in parentheses. The characters that proved to be parsimony-uninformative and therefore were excluded from the cladistic analysis are preceded by superscript P (preliminary analysis) or F (final analysis). Missing data are indicated by "?" (unknown state) or "–" (inapplicable character). The percentage of missing records for each taxon is given in the final columns.

Taxon	Characters																			
	1	2	3	4	5	6	$^{PF}7$	8	9	10	11	12	13	14	15	16	17	18	19	20
Herrerasaurus ischigualastensis	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
Coelophysis bauri	0	0	0	1	0	1	0	0	0	0	?	0	0	0	0	0	1	0	0	0
Allosauroidea	0	0	0	0	0	0, 1	1	0	0	0	–	0	1	0	0, 1	0	0	0, 1	1	0
Tyrannosauridae	0	0	1	2	0	0, 1	0	0	0	0	0	0	0, 1	0	1	0	0, 1	0	0	0
Ornithomimosauria	0	0	0	0	1	0	?	0	0	0	1	0	0	0	?	0	1	0	0	0
Dromaeosauridae	0	0	0	0, 1	0	0	?	0	0	0	1	0	0, 1	0	1	0	1	1	0	0
(Troodontidae)	0	0	0	2	0	1	?	0	0	0	?	0	0	0	1	0	1	0	0	0
(Alvarezsauridae)	0	0	0	?	0	0	?	?	0	0	1	0	?	0	1	1	1	?	0	0
Therizinosauria	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0
Archaeopteryx lithographica	0	0	0	?	0	1	?	0	0	0	?	0	1	0	1	1	1	0	1	1
Confuciusornis sanctus	0	0	?	1	1	1	?	?	0	0	?	?	?	0	1	1	1	?	1	?
Avimimus portentosus	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Caudipteryx zoui	1	0	?	1	?	?	?	0	1	?	?	?	?	1	1	1	?	?	1	1
Chirostenotes pergracilis	?	?	?	?	?	?	?	?	?	0	1	1	0	1	0	?	?	?	?	1
Nomingia gobiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
(*Microvenator celer*)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
"*Oviraptor*" *mongoliensis*	1	1	1	2	0	0	0	1	1	1	1	1	0	1	1	1	0	1	2	1
Oviraptor philoceratops (GIN 100/42)	1	1	2	2	1	0	0	1	1	1	1	1	0	1	1	1	0	1	2	1
Conchoraptor gracilis	1	0	1	2	1	0	0	1	1	1	1	1	0	1	1	1	0	1	2	1
Ingenia yanshini	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?

Taxon	Characters																			
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Herrerasaurus ischigualastensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelophysis bauri	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0
Allosauroidea	0	1	0	1	0	0	0	0, 1	0	1	0, 1	0	0	0	0	2	0, 2	0	0	0
Tyrannosauridae	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	2	0	0	0	1
Ornithomimosauria	0	?	0	0	1	0	0	0	1	1	1	?	0	0	0	2	1	1	0	1
Dromaeosauridae	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	2	1	0	0	0
(Troodontidae)	1	0	?	1	1	0	0	1	1	1	1	1	?	0	?	1	1	0	?	1
(Alvarezsauridae)	?	?	1	0	0	0	?	0	?	3	1	?	1	1	2	1	3	?	1	?
Therizinosauria	0	0	?	2	0	0	0	0	1	1	1	?	1	0	0	2	–	1	0	0
Archaeopteryx lithographica	0	0	?	2	0	0	0	0	1	?	?	1	1	1	1	1	?	1	?	?
Confuciusornis sanctus	1	?	1	?	0	?	?	0	1	1	1	?	1	0	?	?	?	1	1	0
Avimimus portentosus	?	?	?	?	?	1	0	1	1	3	?	?	1	1	2	2	3	?	?	0
Caudipteryx zoui	?	1	?	?	?	1	0	?	?	?	?	0	1	0	1	2	2	0	0	?
Chirostenotes pergracilis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nomingia gobiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
(*Microvenator celer*)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
"*Oviraptor*" *mongoliensis*	1	1	1	2	?	1	1	1	?	2	1	1	1	0	1	2	2	1	1	1
Oviraptor philoceratops (GIN 100/42)	1	1	1	2	1	1	1	1	1	2	1	1	1	0	1	2	2	1	1	1
Conchoraptor gracilis	1	1	1	2	0	1	1	1	1	2	1	1	1	0	1	2	2	1	1	1
Ingenia yanshini	?	1	1	?	?	?	?	?	?	?	?	?	1	0	1	2	2	1	1	1

Taxon	Characters																			
	41	42	43	44	45	46	47	48	49	50	^{F}51	52	53	54	55	56	57	58	59	60
Herrerasaurus ischigualastensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelophysis bauri	0	0	2	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Allosauroidea	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0
Tyrannosauridae	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ornithomimosauria	0	0	2	1	0, 1	1	0, 1	0	1	0	1	0	1	?	1	1	0	0	0	0
Dromaeosauridae	0	0	1	0	0	?	0	1	0	0	0	0	0	0	0, 1	0	0	0	0	0
(Troodontidae)	0	?	1	0	0	1	0	0, 1	1	0	1	0	1	1	1	0	0	0	0	0
(Alvarezsauridae)	?	?	2	1	0	?	1	?	?	0	0	?	?	1	1	0	?	0	?	?
Therizinosauria	0	0	2	0	0	1	0	0	1	1	0	0	1	1	1	0	1	?	0	0
Archaeopteryx lithographica	0	0	2	0	?	?	?	?	0	0	?	?	?	?	1	0	?	0	0	0
Confuciusornis sanctus	0	1	?	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	0	?
Avimimus portentosus	0	–	1	0	2	?	1	1	?	1	0	?	?	?	?	1	?	?	?	?
Caudipteryx zoui	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chirostenotes pergracilis	?	?	?	?	2	1	1	0	?	1	?	?	?	?	1	?	?	0	?	?
Nomingia gobiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
(*Microvenator celer*)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
"*Oviraptor*" *mongoliensis*	1	1	1	?	2	1	1	1	1	2	0	1	?	1	?	0	1	1	1	1
Oviraptor philoceratops (GIN 100/42)	1	1	1	1	2	1	1	1	1	2	0	1	1	1	1	0	1	1	1	1
Conchoraptor gracilis	1	1	1	1	2	1	1	1	1	2	0	1	1	1	1	0	1	1	1	1
Ingenia yanshini	1	1	1	?	?	1	1	1	1	?	?	?	1	1	1	?	?	1	?	?

Taxon	Characters																			
	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Herrerasaurus ischigualastensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelophysis bauri	0	0	0	?	?	?	0	0	0	0	0	0	0	0	0	1	1	0	0, 1	0
Allosauroidea	0	0	0	0	0	0, 1	0	0	0	0	0	0	0	0	0	0	0	0	0, 1	0
Tyrannosauridae	0	0	0	0	0	1	0	0	0, 1	0	0	0	0	0	0	0	0	0	1	0
Ornithomimosauria	0	0	0	?	?	?	?	0	1	0	1	2	0	1	1	0	0	0	0, 1	0
Dromaeosauridae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
(Troodontidae)	?	0	0	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	1	?
(Alvarezsauridae)	?	0	0	1	?	?	?	?	?	0	?	?	?	0	0	?	1	0	0	0
Therizinosauria	?	0	0	1	1	?	1	1	1	0	0	0	0	1	1	0	0, 1	0	0	0
Archaeopteryx lithographica	0	0	0	1	?	1	?	?	?	?	1	0	0	0	0	1	1	2	3	0
Confuciusornis sanctus	?	?	0	?	?	?	?	?	?	0	1	1	?	0	0	0	1	0	0	?
Avimimus portentosus	?	?	?	?	?	?	?	?	?	0	?	?	?	?	1	1	?	?	?	1
Caudipteryx zoui	0	?	?	?	?	?	?	?	?	?	0	?	?	1	1	1	?	?	2	?
Chirostenotes pergracilis	?	?	?	?	?	?	?	?	?	1	1	2	1	0	1	1	0	0	2	1
Nomingia gobiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
(*Microvenator celer*)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
"*Oviraptor*" *mongoliensis*	1	1	1	2	1	1	1	1	0	1	1	1	1	1	1	1	2	1	2	0
Oviraptor philoceratops (GIN 100/42)	1	1	1	2	1	1	1	1	0	1	1	1	1	1	1	1	2	1	2	0
Conchoraptor gracilis	1	1	1	2	1	1	1	1	0	1	1	1	1	1	1	1	2	1	2	0
Ingenia yanshini	1	1	1	?	1	?	?	?	?	1	1	1	1	1	1	1	2	1	2	0

Taxon	Characters																			
	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	^{PF}99	100
Herrerasaurus ischigualastensis	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Coelophysis bauri	0	0	0	1	0	0	1	0	0	0	?	0	0	?	0	0	0	0	1	0
Allosauroidea	0	0	0, 1	1	0	0	0, 1	0	0	0	0	0	0	0	0	1	0	0	1	0
Tyrannosauridae	0	0	1	1	0	0	0, 1	0	0	0	0	0	0	0	0	1	0	0	1	0
Ornithomimosauria	0	0	0, 1	1	0	0	0	0	0	0	0	0	0	1	0, 1	1, 2	0, 1	0	1	1
Dromaeosauridae	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
(Troodontidae)	0	0	1	1	0	0	0	?	?	0	?	0	?	?	?	?	0	?	1	1
(Alvarezsauridae)	0	0	?	?	?	0	?	?	?	0	?	?	?	1	?	1	0	?	0, 1	?
Therizinosauria	0	0	1	1	0	0	?	0	0	0	0	0	0	1	1	1	0	1	1	1
Archaeopteryx lithographica	0	0	1	1	–	0	1	0	0	0	0	0	0	1	0	1	0	0	1	?
Confuciusornis sanctus	0	0	0	0	1	0	0	?	0	0	?	?	?	?	1	2	1	0	1	?
Avimimus portentosus	?	?	?	?	?	1	1	0	0	0	?	?	?	1	0	?	1	1	1	1
Caudipteryx zoui	?	0	0	0	1	?	?	?	?	?	?	1	?	?	0	2	1	0	?	?
Chirostenotes pergracilis	1	1	0	0	1	1	1	1	1	1	1	1	1	1	?	2	1	?	1	?
Nomingia gobiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
(*Microvenator celer*)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
"*Oviraptor*" *mongoliensis*	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1
Oviraptor philoceratops (GIN 100/42)	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1
Conchoraptor gracilis	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1
Ingenia yanshini	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	2	1	?	1	1

Taxon	Characters																			
	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	$^{\mathrm{PF}}116$	117	118	119	120
Herrerasaurus ischigualastensis	0	0	0	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelophysis bauri	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0
Allosauroidea	2	0, 1	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0
Tyrannosauridae	0	0	1	1	0	0	1	0	0	1	?	1	1	0	0	0	0	0	0	0
Ornithomimosauria	0	1	0	0	0	1	0	0	0, 1	0	1	1	1	1	0	0	0, 1	0	0	0
Dromaeosauridae	1	0	0, 1	1	1	0, 1	1	1	1	1	1	0	1	1	0	0	1	0	0	0
(Troodontidae)	?	1	?	0, 1	0	?	0	?	1	1	0	0	1	1	0	0	1	1	1	0
(Alvarezsauridae)	0	?	0	0	0	?	0	1	1	?	?	?	?	1	0	0	1	0	?	?
Therizinosauria	?	0	0	0	0, 1	1	0, 1	1	1	0	?	1	1	1	0	?	1	2	1	0
Archaeopteryx lithographica	?	?	0	0	1	0	1	1	0	0	?	?	1	1	0	0	1	1	1	0
Confuciusornis sanctus	?	?	0	?	0	1	1	?	1	?	?	?	–	1	?	0	1	–	1	1
Avimimus portentosus	0	0	0	0	1	1	0	1	1	1	1	0	?	?	0	0	?	?	?	?
Caudipteryx zoui	?	?	?	?	?	?	0	?	0	?	?	?	?	?	0	?	?	0	1	0
Chirostenotes pergracilis	?	?	0	?	0	?	1	?	1	1	1	1	?	?	1	?	?	?	?	?
Nomingia gobiensis	?	?	0	0	?	?	1	0	0	0	1	1	0	0	1	0	1	0	1	1
(*Microvenator celer*)	?	?	0	0	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?
"*Oviraptor*" *mongoliensis*	1	1	0	0	0	1	1	1	1	0	1	1	0	0	1	0	0	0	1	0
Oviraptor philoceratops (GIN 100/42)	1	1	0	0	1	1	1	1	1	0	1	1	0	0	1	0	0	0	1	0
Conchoraptor gracilis	1	1	0	0	1	1	1	1	1	0	1	1	0	0	1	0	0	0	1	0
Ingenia yanshini	1	1	0	0	0	1	1	1	1	0	1	1	0	0	1	0	0	0	1	0

Taxon	Characters																			
	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140
Herrerasaurus ischigualastensis	1	0	0	0	?	0	?	0	0	–	0	1	0	0	1	0	0	0	?	?
Coelophysis bauri	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Allosauroidea	1	0, 1	0	0	1	0	1	0	0	2	0	1	2	0	0	0	2	1	0	1
Tyrannosauridae	0	0	1	0	1	0	1	0	0	1	0	0, 1	0	0	0	0	0	1	–	0
Ornithomimosauria	1	0	1	0	0	0	2	0	0	1	0	0	0	2	0	?	0	0	1	0
Dromaeosauridae	1	1	1	1	0	2	1, 2	1	0, 1	2	0	0	2	1	0	1	3	1	1	0, 1
(Troodontidae)	0	1	1	0	?	1	2	?	1	?	0	0	?	1	1	1	3	1	1	1
(Alvarezsauridae)	1	2	1	1	1	0	2	?	1	1	1	1	1	0	0	2	–	?	?	0
Therizinosauria	0	0	0	?	1	0	1, 2	0, 1	0, 1	1, 3	0, 1	1	2, 3	0	0	0	1	1	1	0
Archaeopteryx lithographica	0	0	1	1	2	2	2	1	0	0	?	0	?	1	1	1	3	1	1	1
Confuciusornis sanctus	?	1	–	1	2	–	–	1	1	2	1	0	2	0	0	2	3	1	0	1
Avimimus portentosus	?	2	?	?	0	1	2	0	0	1	1	1	1	1	1	2	3	?	?	1
Caudipteryx zoui	?	?	1	1	0	?	?	?	1	?	0	0	?	1	1	1	3	1	?	1
Chirostenotes pergracilis	?	1	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Nomingia gobiensis	1	2	–	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
(*Microvenator celer*)	0	?	?	?	?	?	1	?	0	2	0	0	0	1	1	?	?	?	?	?
"*Oviraptor*" *mongoliensis*	0	2	?	1	1	1	2	0	1	2	0	0	1	0	0	?	?	?	?	?
Oviraptor philoceratops (GIN 100/42)	0	2	1	1	0	1	2	0	1	2	0	0	1	1	1	1	3	1	0	1
Conchoraptor gracilis	0	1	1	1	1	1	2	0	1	2	0	1	1	1	1	1	3	1	0	0
Ingenia yanshini	0	1	0	1	1	1	2	0	1	2	0	1	1	0	0	1	3	1	0	0

Taxon	Characters																			
	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
Herrerasaurus ischigualastensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelophysis bauri	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Allosauroidea	0	2	0	0	0	1	0	0	1	0	0	0	0	0	2	0	0	1	0, 1	0
Tyrannosauridae	0	2	0	1	0	0	1	2	1	1	0, 1	0	1	0	1	0	1	1	0	1
Ornithomimosauria	0	1	0	0	0	0, 2	0, 1	0, 1	0, 2	1	0	0	1	1	2	0	0	1	0	1
Dromaeosauridae	1	2	0	1	1	1	0	1	2	0	0	0	0	1	1	0, 1	1	1	1	1
(Troodontidae)	1	1	1	1	0	1	0	1	0	1	1	0	0	1	1	1	0	?	1	1
(Alvarezsauridae)	–	2	0	–	0	2	0	1	1	?	?	0	0	1	0	0	0	1	0	0
Therizinosauria	0	2	0	1	1	1	0	?	2	0	0	1	0	0	2	0	1	0	1	0, 1
Archaeopteryx lithographica	1	1	1	1	1	0	0	1	2	0	1	1	0	1	0	1	1	1	1	1
Confuciusornis sanctus	?	2	1	1	?	?	0	1	2	0	0	1	0	?	0	1	?	?	?	?
Avimimus portentosus	?	?	?	?	?	?	?	?	0	0	0	0	0	?	0	1	1	0	?	1
Caudipteryx zoui	0	1	0	1	?	1	0	0	0	?	0	0	1	2	1	0	1	1	1	1
Chirostenotes pergracilis	?	?	?	1	1	?	?	?	?	?	1	1	?	?	?	1	1	1	0	1
Nomingia gobiensis	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	0	1	1	0	1
(*Microvenator celer*)	?	?	?	?	1	?	0	?	0	?	0	?	1	1	2	?	1	1	0	1
"*Oviraptor*" *mongoliensis*	?	?	?	?	1	?	?	?	0	1	1	0	1	1	2	1	1	1	0	1
Oviraptor philoceratops (GIN 100/42)	1	1	1	1	1	1	0	1	0	1	0	0	1	2	1	1	1	0	0	1
Conchoraptor gracilis	1	1	1	1	1	1	0	1	0	1	0	0	0	2	1	0	1	0	0	1
Ingenia yanshini	1	1	0	1	1	2	1	0	0	1	0	0	1	2	1	0	1	0	0	1

Taxon	Characters																			
	^{PF}161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
Herrerasaurus ischigualastensis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelophysis bauri	0	0	0	?	0	0	3	0	0	0	1	0	1	0	0	0	0	0	1	0
Allosauroidea	0, 1	1	0, 1	0, 1	0	0	0, 2	0, 1	0	0	1	0	0	0	1	0	0	0	1	0
Tyrannosauridae	0, 1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0
Ornithomimosauria	0	1	1	1	0	0	0	1	0	0	1	0	0	0	1	0	1	1	1	1
Dromaeosauridae	0	0, 1	0	1	2	0	2	1	0	1	0, 1	1	0	0, 1	0	1	1	0, 1	0	0
(Troodontidae)	0	0	0	0	0	0	3	?	0	1	1	0	1	1	0	1	1	1	?	?
(Alvarezsauridae)	0	1	0	?	2	0	3	1	0	3	0	0	1	1	–	2	–	1	0	1
Therizinosauria	1	0	1	1	2	0, 1	0, 1	0, 1	0	2	0	0	1	1	0, 1	0	1	0	0	?
Archaeopteryx lithographica	0	?	1	0	2	0	2	1	–	?	–	1	1	?	0	?	0	1	0	0
Confuciusornis sanctus	?	0	0	?	2	?	3	1	?	?	0	1	1	–	–	2	–	?	?	?
Avimimus portentosus	0	0	0	1	0	0	1	1	0	?	?	1	1	1	0	0	1	0	0	1
Caudipteryx zoui	0	?	?	0	?	0	1	1	1	1	0	1	1	1	0	0	0	?	?	?
Chirostenotes pergracilis	0	?	?	?	?	0	1	1	1	1	0	1	?	?	?	?	?	1	?	1
Nomingia gobiensis	0	0	0	1	1	0	0	1	1	1	0	1	1	1	0	1	1	1	?	1
(*Microvenator celer*)	?	0	?	?	?	1	?	0	?	?	?	?	1	1	0	0	1	1	?	0
"*Oviraptor*" *mongoliensis*	0	0	0	1	?	?	?	?	?	?	?	?	1	1	0	1	1	1	1	1
Oviraptor philoceratops (GIN 100/42)	0	0	0	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1
Conchoraptor gracilis	0	0	0	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1
Ingenia yanshini	0	0	0	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1

Taxon	Characters															Missing records (%)	
	181	182	183	184	185	186	187	188	189	190	191	192	^{F}193	194	195	Unknown states	Inapplicable characters
Herrerasaurus ischigualastensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.6	0.5
Coelophysis bauri	0	?	0	0	0	0	1	0	0	0	1	0	0	1	0	4.6	0
Allosauroidea	0, 1	1	0	0	0	0, 1	0	0	0	0	1	0	0	0	0	0.5	0.5
Tyrannosauridae	1	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0.5	0.5
Ornithomimosauria	0	1	0	1	1	1	1	0	1	0, 1	2	1	0	1	2	5.1	0
Dromaeosauridae	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	1.0	0
(Troodontidae)	?	?	1	1	1	1	?	0	1	1	1	1	1	1	2	20.0	0
(Alvarezsauridae)	1	0	1	0	0	0	0	0	1	1	1	0	0	1	?	30.3	2.6
Therizinosauria	1	0	0	1	0, 1	1	0	0	0	0	0	1	0	0, 1	1	6.2	0.5
Archaeopteryx lithographica	0	?	0	0	?	?	1	1	0	?	1	0	0	1	2	19.5	1.5
Confuciusornis sanctus	0	0	1	?	?	?	1	1	0	0	1	1	0	1	0	38.5	4.1
Avimimus portentosus	0	1	0	0	1	1	1	1	1	1	2	0	0	1	2	44.1	0.5
Caudipteryx zoui	?	?	0	0	1	1	0	0	0	0	1	0	0	1	2	49.2	0
Chirostenotes pergracilis	?	?	?	?	?	?	0	?	1	0	1	0	?	1	0	60.0	0
Nomingia gobiensis	0	0	0	?	1	1	?	?	?	?	?	?	?	1	?	71.3	0.5
(*Microvenator celer*)	?	0	0	0	1	1	0	0	?	?	?	0	?	1	?	77.4	0
"*Oviraptor*" *mongoliensis*	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	20.5	0
Oviraptor philoceratops (GIN 100/42)	0	0	?	0	1	1	0	0	0	0	1	0	0	1	0	0.5	0
Conchoraptor gracilis	0	0	?	0	1	1	0	0	0	0	1	0	0	1	0	0.5	0
Ingenia yanshini	0	0	1	0	1	1	0	0	0	0	1	0	0	1	0	22.6	0