

Arctometatarsalia revisited: The problem of homoplasy in reconstructing theropod phylogeny

Thomas R. Holtz, Jr.

Department of Geology, University of Maryland
College Park, MD 20742 U.S.A.
E-mail: tholtz@geol.umd.edu

Abstract

Recent analyses demonstrate that ornithomimosaur, troodontid, tyrannosaurid, therizinosaurid, oviraptorosaur, dromaeosaurid and birds form a clade apart from other theropod dinosaurs. However, these recent studies differ on which clades share a more recent common ancestor with birds (Maniraptora) or with ornithomimosaur (Arctometatarsalia). Some of the differences in tree topology may be due to the use of different taxa as outgroups. Additionally, resolution of theropod phylogeny is hindered in part by the incomplete nature of some of the relevant fossils. But ambiguity also comes from seemingly conflicting data; for example, troodontid cranial and metatarsal anatomy support an arctometatarsalian position, while forelimb, other hind limb, and caudal anatomy favor a maniraptoran placement. No phylogenetic hypothesis that eliminates homoplasy (convergence, reversals, or both) is possible at present, but increased outgroup information and new data from primitive members of the various clades may help to resolve these relationships.

Keywords

Theropoda, Coelurosauria, Maniraptoriformes, Maniraptora, phylogenetic reconstruction, bird origins, feathers.

Appendix 1: List of deleted characters

Appendix 2: Character states for *Caudipteryx*, *Confuciusornithidae* and *Protarchaeopteryx*

Appendix 1: List of deleted characters

The morphological characters used in the present study were derived from the data matrix of Holtz (2000). However, several characters for which the derived condition was not expressed in the coelurosaur taxa were deleted to reduce the size of the matrix. The following characters were deleted.

5, 9, 11, 20–25, 27, 35–36, 41, 48–50, 52–53, 56, 62, 66, 68, 75, 84, 96–97, 99, 105, 131, 142–143, 150, 159, 167, 170, 179, 193, 214, 300, 302, 308, 321, 324, 356, 365

Appendix 2: Character states for *Caudipteryx*, *Confuciusornithidae* and *Protarchaeopteryx*

The following observations supplement the data matrix in Holtz (2000). The complete list of 386 characters is provided; those numbers in bold italics represent characters culled for the analyses presented in the present study (see Appendix 1).

| | 10 | 20 | 30 | 40 | 50 | 60 | 70 |
|----------------------------|-------------|-------------|-------------|-------------|-------------|--------------|--------------|
| <i>Caudipteryx</i> | 000?01?0?0? | 0000111100 | 000?000000 | 010?00??? | 000000?00 | 0000???? | 0?0?0?0?0?? |
| <i>Confuciusornithidae</i> | 21?0011101 | 01001????? | 0000000000 | 00?0?01?00 | 0000000?00 | 0000?0011? | 000??0?002 |
| <i>Protarchaeopteryx</i> | ?00?0????? | 00???????? | ????? ????? | ???? ????? | ?????????? | ?????????? | ????? ????? |
| | 80 | 90 | 100 | 110 | 120 | 130 | 140 |
| <i>Caudipteryx</i> | ?????????? | ?? ? ?????? | ?????????? | ???100?1?0 | ?2?00?0?? | ??1100?200 | 00???0???? |
| <i>Confuciusornithidae</i> | ?1?? ?????? | ?20?? ?1??? | ????? ????? | 1??1010000 | 000000?0?? | ?01010???? | ?????20???? |
| <i>Protarchaeopteryx</i> | ???? ?????? | ?? ? ?????? | ????? ????? | ???0?0?0?? | ?????????? | ?????????0?? | ???????????? |
| | 150 | 160 | 170 | 180 | 190 | 200 | 210 |
| <i>Caudipteryx</i> | ?????01010 | 11?11??100 | ??110? ???? | ???0?01?? | ??1?3????? | ?1?0012002 | 00?11?021? |
| <i>Confuciusornithidae</i> | ?????01010 | 111110?100 | 0?111?00?0 | 10?10??101 | ?0??5?0112 | ?101013040 | 0????????? |
| <i>Protarchaeopteryx</i> | ?????0?0?0? | ??1?0?100 | ????? ????? | ??????????? | ??????????? | ???01200? | ???????????? |
| | 220 | 230 | 240 | 250 | 260 | 270 | 280 |
| <i>Caudipteryx</i> | 1100001010 | 002?100000 | 0201111??? | 10??1000?0 | 0021133001 | 110111?101 | 110100?000 |
| <i>Confuciusornithidae</i> | 1100013111 | 1111122101 | 0211111111 | 1110111110 | 0021133001 | 111111?111 | 1110001100 |
| <i>Protarchaeopteryx</i> | ?? ? ?????? | 002?11?1?0 | 02111????? | ????1000?0 | 0021133001 | 111111?101 | 110000?000 |
| | 290 | 300 | 310 | 320 | 330 | 340 | 350 |
| <i>Caudipteryx</i> | 0?0101?1?1 | ?011101100 | ?00110???? | 0110??1?11 | 0220001012 | 2111222??? | ?????1???? |
| <i>Confuciusornithidae</i> | 1100010000 | 0010011110 | 1011111030 | 0120000110 | 0?30101112 | 2112432220 | 101101???? |
| <i>Protarchaeopteryx</i> | 0?0101???? | ?00??????? | ????? ???? | 0110?????? | ?? ? ?????? | ??????????? | ??????????? |
| | 360 | 370 | 380 | 386 | | | |
| <i>Caudipteryx</i> | 2111? ???01 | 020100?000 | 01?0??0121 | 0?0?00 | | | |
| <i>Confuciusornithidae</i> | 2111? ?0102 | 0201010121 | 01010?0122 | 100101 | | | |
| <i>Protarchaeopteryx</i> | 2111? ???01 | 020100?000 | ?1?0??0111 | 010?00 | | | |