

Conflicting developmental and paleontological data: the case of the bird manus

MAX K. HECHT and BESSIE M. HECHT



Hecht, M.K. & Hecht, B.M. 1994. Conflicting developmental and paleontological data: the case of the bird manus. *Acta Palaeontologica Polonica* 38, 3/4, 329–338.

Phylogenetic inference is based on the distribution of characters across taxa. Characters and their states should be described in all of their complexity. The entire development of a structure should be considered to determine its significance in the search for homology and synapomorphy and for the determination of homoplasy. Simplistic description of characters often leads to comparisons of homoplasies. The pattern of development of the manus of living amniotes demonstrates a basic plan that has been retained in living birds but has been modified in theropod dinosaurs. The primitive pattern of digital and metacarpal reduction in buds (2-3-4) and other living amniotes is contrasted with manus reduction pattern of the theropods (1-2-3) based on comparative morphology. Neither digital pattern reduction is derivable from the other. The recent discovery of early dinosaurs with primitive stages of the derived reduction patterns indicates an earlier origin for buds than previously postulated. This study demonstrates the use of developmental data in distinguishing homologous structures from homoplastic structures which is important in cladistic analysis.

Key words: homology, homoplasy, amniote manus, avian manus, theropod manus, digital reduction pattern.

Max K. Hecht and Bessie M. Hecht, Department of Biology, Queens College of C.U.N.Y. Flushing, New York 11367 U.S.A.

Introduction

The basic data of phylogenetic inference are characters and taxa, and the distribution of the former across the latter. In most paleontological material characters are effectively fixed, because they are usually preserved in the adult condition, whereas in living taxa the ontogenetic pattern or 'the ontogenetic trajectory' (Alberch et al. 1979) is available for study. In the comparison of living and fossil groups, developmental data can be inferred based on relationships with extant forms. Furthermore, developmental data are derived from living crown groups in which ontogenetic patterns

may have been modified during their phylogeny from the ancestral ontogenetic trajectory (Alberch et al. 1979). The tracing of the history of developmental trajectories can be inferred by study of the distribution of these characters (ontogenetic trajectories) across taxa on a cladogram or a phylogeny.

A case in point is the numbering convention of the digits of bird manus by paleontologists and by developmental biologists. These two groups of investigators have differed in their interpretation for at least one hundred years.. Owen (1836) identified the bird digits as 2-3-4, Parker (1888) numbered them 1-2-3. Since that time developmental biologists have numbered the digits as 2-3-4 and paleontologists as 1-2-3 (Hinchliffe & Hecht 1984). The disagreement resolves itself to a question of whether the similarity in the number of digits between birds and other reptilian groups is a synapomorphic feature or a case of homoplasy.

The neontological debate on the homologies of the digital developmental trajectories has been ignored by most paleontologists (Padian 1992, Weishampel et al. 1990). Recently however, Clark (1992) in his review of the paleornithological section of a symposium on controversies in tetrapod evolution (Schultze & Trueb 1991), pointed out the general failure of the participants in considering the digital data. Clark (1992: p. 534) stated: The only substantive problem with the theropod-bird hypothesis remains the discrepancy between the homology of the digits of the manus as indicated by the fossils and the development of extant birds (Hinchliffe 1985), something touched upon, but not elucidated...' by the participants (Martin 1991; Ostrom 1991; Tarsitano 1991; Witmer 1991). It is important to note that Clark (1992) is a supporter of the theropod-bird relationship hypothesis. The discrepancy has been the basis of previous reconsiderations of this problem (Tarsitano & Hecht 1980; Hinchliffe & Hecht 1984; Hinchliffe 1985; Thulborn & Hamley 1982). New data on dinosauriform diversity (Sereno & Novas 1992) require reconsideration of the two interpretations 1-2-3 or 2-3-4 digital homologies, since one pattern can not be directly derived from the other.

The morphological data

The classic paleobiological interpretation can be illustrated by Romer's treatment (1956, 1966). He used early reptiles as an archetype for the primitive reptilian carpus and manus in which the reptilian digital (Roman letters) and phalangeal formula (numerals) is:

(I)2-(II)3-(III)4-(IV)5-(V)3 (with the postaxial side marked by the presence of the pisiform and metacarpal 5). Thus he oriented his numbering of the digits of *Archaeopteryx* to fit the archetypal number of phalanges. Since he considered *Archaeopteryx* as the most primitive known bird, to him the homologies were clear. The only paleontological studies which have not accepted these homologies are Tarsitano & Hecht (1980) and Thulborn &

Hamley (1982). The former accepted the embryological interpretation (2-3-4) which required the loss of a single phalanx from each digit of Archaeopteryx. This observation oriented Tarsitano & Hecht's entire analysis. The latter, Thulborn, & Hamley (1982) requires new homologies for the theropodan manus for which there is no evidence. Most paleontologists have followed the 1-2-3 digital convention.

The developmental data

The 2-3-4 digital convention has been followed by developmental anatomists since the beginning of this century, and had been reinforced by the work of Montagna (1945) and Holmgren (1955). These two authors based their interpretations on tetrapod archetypes of the manus, which required finding the number of carpal blastema elements of a hypothetical primitive tetrapod in the chick and other amniotes. These older observations have since been disputed by Hinchliffe (1985, 1989a, b, 1991). Using radiographic techniques he demonstrated that the primitive carpal elements have been lost or fused independently early in the history of the lissamphibians and amniote lineages, and that earlier interpretations were in error. Despite these earlier errors, however, interpretation of the pattern of digital development has remained stable. The views of Holmgren and Montagna were primarily Haeckelian based on strict recapitulation without consideration that crown groups have evolved from their primitive condition by modifying their ontogenetic trajectories.

Modern evidence and interpretation of metacarpal and digital development has been reviewed by Hinchliffe & Hecht (1984) and Hinchliffe (1985). These reviews have concluded that the development of extant birds supports the 2-3-4 pattern of digital and metacarpal homologies. Furthermore, the developmental sequence of the appearance of the digits that is characteristic of the chick has been found in five orders of birds examined (Hinchliffe & Hecht 1984) and therefore should be considered plesiomorphic for extant birds. Despite these ontogenetic findings, the century-old dichotomy of interpretation of the homology of the digits of birds persists.

The amniote pattern of digital development of the manus

Recent studies on developmental programs of the basic pattern of limb development allow for the development of a general groundplan (or blueprint) for the tetrapod limb without a Haeckelian backdrop (Shubin 1991). Chondrogenesis of the metacarpals and digits, with its accompanying developmental processes (condensation, segmentation, fusion of elements and the digital arch), accounts for known morphology diversity of the manus, but at the same time retains a general pattern for almost all amniotes (Shubin & Alberch 1986; Burke & Alberch 1985; Muller 1991,

Hinchliffe 1989b; Shubin 1991). The development of metacarpals and digits is constrained and apparently determined by the digital arch of the developing manus (Shubin & Alberch 1986).

The general reduction and associated morphological changes of tetrapod limbs and digits was summarized by Lande (1978) and described in lizards by Raynaud (1985). In most amniotes the general order of reduction of metacarpals and digits (5→1→2→3→4) is the reverse of the sequence of the appearance of metacarpals and digits (4→3→2→1→5). The last digital elements formed are usually the first elements lost in digital reduction (Greer 1991; Raynaud 1985). The late development of the fifth and first digit is characteristic of most amniotes and is known in chelonians (Burke & Alberch 1985), crocodylians (Muller & Alberch 1990), lizards (Greer 1991), birds (Hinchliffe 1985) and in virtually all mammals (Holder 1983; Shubin & Alberch 1986). This basic tetrapod pattern of the digital arch in the manus is found in frogs and modified in the urodeles (Shubin and Alberch 1986; Oster *et al.* 1988). The distribution among living amniotes of the developmental or reductional sequence of the manus indicates that the program is primitive or plesiomorphic in the amniotes.

One of the arguments for the relationship of birds to the crocodylomorph clade has been the retention by the latter of the amniote digital and metacarpal chondrogenic program (Muller & Alberch 1990). The pattern of development revealed by their study of the *Alligator* forelimb was interpreted as being primitive for the Archosauria.

The theropod digital pattern

In the recent review of the Dinosauria (Weishampel *et al.* 1990) all the contributors identified the digits of theropods using a numbering system indicating a reduction program starting on the postaxial side (5-4-3-2-1). Within this clade there are varying degrees of reduction in the manus from the loss of a single digit to the loss of four digits. Assuming this interpretation is correct, this pattern of reduction is unique in the Amniota and could therefore be regarded as a synapomorphy for the Theropoda. Across the component theropodan taxa there are many examples of parallel reduction sequences.

Recognition of this reduction pattern is based on comparative morphology. Thulborn & Hamley (1982) regarded the reduction pattern in this clade as a typical amniote pattern and thought it matched the bird pattern. Further criticism of the conflict in digital homologies was expressed by Ostrom (1985), who stated that there can be no comparison of the homologies of the theropod and bird manus because there is no ontogenetic data for theropods. His criticism overlooks the morphological series within the Theropoda (which supports his 1-2-3 hypothesis) and the primitive chondrogenic pattern common to all living amniotes (Hinchliffe 1989a, b; Shubin 1991; Muller 1991).

Benton (1990) and Sues (1990) in a summary of the classification and phylogeny showed that the Herrerasauridae represents a basal sister group to most of the Saurischia if not to the Theropoda. Sereno & Novas (1993) with new material of the Triassic *Herrerasaurus* illustrate the complete manus with well-developed first, second and third digits and metacarpals but with reduced fourth and fifth digits and their metacarpals. In a cladogram Sereno et al. (1993) place the Herrerasauridae as basal to the Theropoda.

These new data, the reduction of the fourth and fifth digits and fifth metacarpal, demonstrate that the reduction pattern in the Theropoda is much older than previously thought. *Herrerasaurus*, either as a basal dinosauromorph or theropod, illustrates an adult morphology unique to amniotes. It is evident that to arrive at this adult morphology the reduction sequence from the postaxial side is required and not the primitive amniote reduction pattern. In cladistic terms the digital reduction pattern could be coded as either the primitive amniote pattern (developmental bauplan of Shubin 1991) or the derived theropod pattern [with reduction starting from the postaxial side]. Stated in such terms it is apparent that the theropod condition is unique in the evolution of the amniote manus.

The phyletic significance of the reduction pattern of the bird manus

The relationship of birds to dinosaurs was originally espoused by Huxley (1870) and advocated by Ostrom (1976, 1985). Gauthier (1986) has listed a series of synapomorphies, minimally ten, which unite birds with the theropod lineage. Among these synapomorphies is the reduction sequence of the metacarpals and digits. As a result of this inclusion of the birds and *Archaeopteryx* within the theropod clade, the digits must be renumbered in order to remain a synapomorphy and contrary to the developmental data.

There are several hypotheses of the distribution of the metacarpal and digital reduction pattern ascribed to birds; they are:

- (1) Crocodylomorph affinity of birds (Martin 1985, 1991; Tarsitano 1991);
- (2) Dinosauro-morph affinity of birds (Ostrom 1991; Witmer 1991; Weishampel et al. 1990; Gauthier & Padian 1985);

(2A) Ostrom's interpretation of *Archaeopteryx* as a bird with digits 1-2-3;

(2B) *Archaeopteryx* as a theropod (Gauthier 1986) and modern birds as surviving theropods;

(2C) Birds including *Archaeopteryx*, as a sister group to the Saurischia or the Theropoda in particular;

(2D) Alternatively, a mutational (or possibly epigenetic or heterochronic) change took place in development within the early history of the avian clade causing a reversal to the primitive program.

Hypothesis 1. — There is no conflict between the chondrogenic developmental program of crocodylians and the developmental pattern of birds. The similarity of chondrogenic pattern may simply be a synplesiomorphy and not an indicator of relationships. Furthermore, this hypothesis of relationships requires complex functional transformations and many parallelisms to dinosauromorph taxa. This hypothesis implies a large gap in the fossil record and perhaps saltational steps.

Hypothesis 2. — Many similarities in locomotor adaptations which can be used as synapomorphies for monophyly of birds and theropods require the use of many reversal or loss state synapomorphies. There are many variants or subhypotheses of this basic hypothesis. These subhypotheses require that birds are characterized by a derived developmental theropodal pattern [metacarpals and digits] in contrast to the developmental data available for living birds. These subhypotheses may be compared with a cladogram (Fig. 1) modified from Sereno *et al.* (1993).

Hypothesis 2A. — If Archaeopteryx is a bird (Aves) this hypothesis would require reidentification of the metacarpals and digits of Archaeopteryx in the primitive amniote pattern. It would also require an earlier origin for the Archaeopteryx lineage as a basal bird as suggested by Elzanowski & Wellnhofer (1993). The hypothesis of Ostrom (1976, 1985, 1990) requires modification in order to incorporate the primitive amniote bauplan of digital and metacarpal reduction as a bird character.

Hypothesis 2B. — This hypothesis reduces the number of convergences between theropods and birds but implies that all developmental data on the manus of modern birds are incorrect. Furthermore, if Bryant and Russell (1993) are correct then the furcula was redeveloped in the bird lineage as is indicated by its presence in Archaeopteryx. Muller & Streicher (1989) provide developmental data on the reduction and fusion of elements of the hindlimb of birds. They compared this developmental process in the bird hind limb as evidence for theropod relationship, but stated that such simple patterns have often been demonstrated to have developed in parallel in related lineages (Hecht 1983, 1985) because of developmental constraints.

Hypothesis 2C. — This hypothesis requires that the bird lineage [including Archaeopteryx] diverged from the saurischian base prior to the origin of the theropods and the developmental switch to a new manus reduction program (dotted lines Fig. 1). Therefore other morphological similarities to the theropods are homoplasies or primitive states. This hypothesis requires the retention of the furcula [as clavicles] in birds as a primitive state or possibly as a neomorph (Bryant & Russell 1993). If this hypothesis is accepted, then birds diverged from the Theropoda in the early Triassic predating Chatterjee's (1991) disputed *Protoavis*.

Hypothesis 2D. — This hypothesis, reversal from the derived condition of theropods to the primitive condition of birds, requires modification of the 'developmental bauplan' (Shubin 1991) of the amniotes. It has been suggested that a shift of the central developmental axis from the fourth

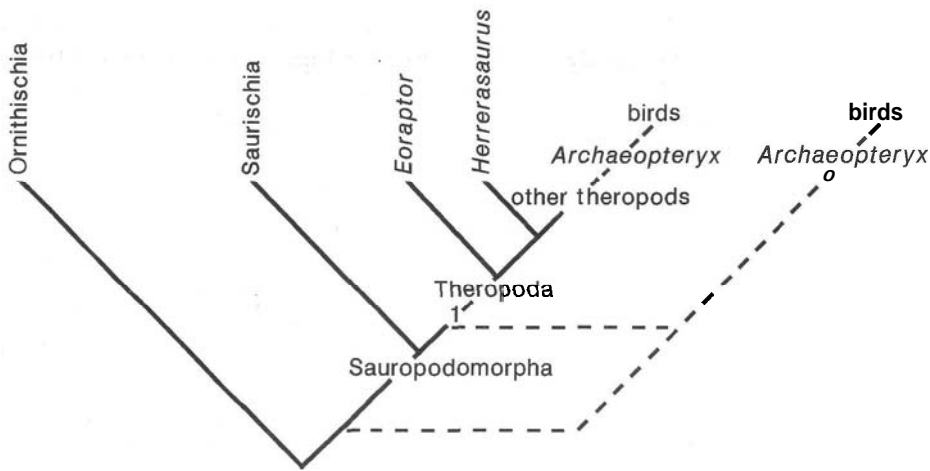


Fig. 1. Cladogram of postulated relationships of dinosaur groups and birds. Solid lines following Sereno *et al.* (1993). Dotted lines are postulated relationships of birds. Dotted lines [on left] represent relationships based on 1-2-3 hypothesis. Dotted lines [on right] represent relationships based on the 2-3-4 hypothesis. 1 - minimal age of origin of the derived digital reduction pattern.

digit (see Shubin 1991: Fig. 2b) to the third digit could accomplish this reversal. This proposed change simplifies the difference in the reduction patterns of these two groups because it omits the symmetry of metacarpal and digital loss in amniotes. The wide taxic distribution of the developmental bauplan and its reduction pattern among the living amniote groups is certainly an argument for stability of the system. Developmental processes are constrained (Alberch *et al.* 1979; Shubin & Alberch 1986) as demonstrated by the amniote chondrogenic pattern (Hinchliffe 1989a, b). The theropod condition having evolved once, would need a mutational event affecting symmetry and central axis to reverse the process. In such a complex process as development of the manus it is highly improbable that a program could be altered with all evidences of prior history erased.

Conclusions

The above discussion is a study in the interpretation of characters and of different classes of characters. The use of a simplified character description, such as three digits, conceals the complexity of character development. The description of a character should be considered within its entire ontogenetic trajectory within taxa and compared across taxa. By comparing the ontogenetic trajectories of characters across taxa as synapomorphies in corroborated cladograms, it is possible to determine primitive states and patterns of polarity.

The relationships of birds, an often discussed problem, is further complicated by the similarity of the developmental bauplan of the amniote

manus. In order to relate birds to the saurischian or theropod clade, it is necessary to deny the reductive amniote sequence which has been inferred from many studies on the development of the manus of modern birds. A hypothesis of bird-crocodylomorph relationships implies only the retention of a primitive amniote developmental bauplan – a primitive state.

If one accepts the derived theropod developmental program [determined from morphology] as a synapomorphy supporting theropodan monophyly, one can approach the solution to the bird relationship problem. The fossil record requires this reduction developmental program to have evolved by the early Triassic as indicated in *Herrerasaurus*. This discovery requires birds, retaining the primitive amniote bauplan, to have diverged from the clade earlier than the origin of the hypothesized development program for the theropod manus. Therefore the many other similarities between theropods and birds may be a mix of plesiomorphies and homoplasies.

In this analysis it appears that the developmental program of the manus has been heavily weighted. The validity of this criticism depends as to whether the developmental program is considered a very complex set of characters or a simple character of little phylogenetic weight. The time of origin and homologies of the manus are important to further research in developmental evolutionary biology. In our opinion the new data from paleontology and developmental biology require a reanalysis of all putative theropod-avian synapomorphies. The theropod-bird relationships have not been satisfactorily established to the exclusion of alternative hypotheses until the contradicting ontogenetic data for the bird manus is considered. As in all phylogenetic inference more corroborative data are needed to test hypotheses.

Acknowledgements

This article is in memory of our friend and colleague, Antoni Hoffman, with whom we had spent many pleasant hours of stimulating discussion on two continents and over several years. The authors wish to thank the many colleagues who criticized and evaluated this paper, they are: Dr. W. Bock, Dr. A. Boucot, Dr. B. Hall, Mr. A. Kellner, Dr. J. Maisey, Dr. J. Ostrom, Dr. O. Rieppel, Dr. U. Sornhannus, Dr. S. Tarsitano and Dr. R. Wassersug. MKH thanks the City University of New York Research Foundation grant no. 661167 for aid in the completion of this study.

References

- Alberch, P., Gould, S.J., Oster, G.F., & Wake, D.B. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology* 5, 296–317.
- Benton, M.J. 1990. Origin and Interrelationships of Dinosaurs. In: D. Weishampel, P. Dodson, & H. Osmolska (eds) *The Dinosauria*, 11–30. University of California Press, Berkeley.
- Bryant, H.N. & Russell, A.P. 1993. The occurrence of clavicles within Dinosauria: Implications for the homology of the avian furcula and the utility of negative evidence. *Journal of Vertebrate Paleontology* 13, 171–184.

- Burke, A.C. & P. Alberch 1985. The development and homologies of the chelonian carpus and tarsus. *Journal of Morphology* 186, 119–131.
- Chatterjee, S. 1991. Cranial anatomy and relationships of a new Triassic bird from Texas. *Philosophical Transactions of the Royal Society of London* **B332**, 277–342.
- Clark, J. 1992. "What good are fossils?" *Journal of Vertebrate Paleontology* 12, 532–536.
- Elzanowski, A. & Wellnhofer, P. 1993. Skull of Archaeornithoides from the upper Cretaceous of Mongolia. *American Journal of Science* 293-A, 235–252.
- Gauthier, J. 1986. Saurischian Monophyly and the Origin of Birds. *Memoirs of the California Academy of Sciences* **8**, 1–47.
- Gauthier, J. & Padian K. 1985. Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. In: M. Hecht, J. Ostrom, G. Viohl, & P. Wellnhofer (eds) *The Beginnings of Birds*, 185–197. Jura Museum, Eichstatt.
- Greer, A.E. 1991. Limb reduction in Squamates: Identification of the Lineages and Discussion of the Trends. *Journal of Herpetology* 25, 166–173.
- Hecht, M.K. 1983. Microevolution, developmental processes, paleontology, and the origin of vertebrate higher categories. *Geobios Memoire Speciale* 12, 207–216.
- Hecht, M.K. 1985. The Biological Significance of Archaeopteryx In: M. Hecht, J. Ostrom, G. Viohl, & P. Wellnhofer (eds) *The Beginnings of Birds*, 149–160. Jura Museum, Eichstatt.
- Hinchliffe, J.R. 1985. One, two, three or Two, three, four. An embryologist's view of the homologies of the digits and carpus of modern birds. In: M. Hecht, J. Ostrom, G. Viohl, & P. Wellnhofer (eds) *The Beginning of Birds*, 141–147. Jura Museum, Eichstatt.
- Hinchliffe, J.R. 1989a. An evolutionary perspective of the developmental mechanisms underlying the patterning of the limb skeleton on birds and tetrapods. *Geobios Memoire Speciale* **12**, 217–225.
- Hinchliffe, J.R. 1989b. Reconstructing the Archetype: Innovation and Conservatism in the Evolution and Development of the Pentadactyl Limb. In: D. Wake & G. Roth (eds) *Complex Organismal Functions: Integration and Evolution in Vertebrates*, 171–189. John Wiley & Sons, London.
- Hinchliffe, J.R. 1991. Developmental approaches to the problem of transformation of limb structure in evolution. In: J.R. Hinchliffe, J. Hurle, & D. Summerbell (eds) *Developmental Patterning of the Vertebrate Limb*, NATO Advanced Study Institute Series A 205, 313–323. Plenum Press, New York.
- Hinchliffe, J.R. & Hecht, M.K. 1984. Homology of the Bird Wing Skeleton. *Embryological versus Paleontological Evidence*. *Evolutionary Biology* 18, 21–39.
- Holder, N. 1983. Developmental Constraints and the Evolution of Vertebrate Digit Patterns. *Journal of Theoretical Biology* **104**, 451–71.
- Holmgren, N. 1955. Studies on the phylogeny of birds. *Acta Zoologica* 36, 243–328.
- Huxley, T.H. 1870. On the classification of the Dinosauria with observations of the Dinosauria of the Trias. *Quarterly Journal of Geological Society of London* 26, 31–50.
- Lande, R. 1978. Evolutionary mechanisms of limb loss in tetrapods. *Evolution* 32, 73–92.
- Martin, L.D. 1985. The relationship of *Archaeopteryx* to other birds, In: M. Hecht, J. Ostrom, G. Viohl & P. Wellnhofer (eds) *The Beginnings of Birds*, 177–183. Jura Museum Eichstaett.
- Martin, L.D. 1991. Mesozoic birds and the origin of birds. In: H. Schultze & L. Trueb (eds) *Origin of the higher groups of tetrapods*, 485–540. Comstock Publishing Company, Ithaca.
- Montagna, W. 1945. A re-investigation of the development of the wing of the bird. *Journal of Morphology* 76, 87–118.
- Muller, G.B. 1991. Evolutionary transformation of limb pattern: Heterochrony and secondary fusion. In: J.R. Hinchliffe, J. Hurle, & D. Summerbell (eds) *Developmental Patterning of the Vertebrate Limb*, NATO Advanced Study Institute Series A 205, 395–405. Plenum Press, New York.
- Muller, G.B. & Alberch, P. 1990. Ontogeny of the limb skeleton in *Alligator mississippiensis*: Developmental invariance and change in the evolution of archosaur limbs. *Journal of Morphology* 203, 151–164.

- Müller, G.B. & Streicher, J. 1989. Ontogeny of the syndesmosis tibiofibularis and the evolution of the bird hindlimb: a caenogenetic feature triggers phenotypic novelty. *Anatomy and Embryology* 179, 327–339.
- Oster, G.F., Shubin, N., Murray, J.D., & Alberch, P. 1988. Morphogenetic rules and evolution. *Evolution* 42, 862–884.
- Ostrom, J.H. 1976. Archaeopteryx and the origin of birds. *Biological Journal of Linnean Society London* 8, 91–182.
- Ostrom, J.H. 1985. The meaning of Archaeopteryx. In: M. Hecht, J. Ostrom, G. Viohl, & P. Wellnhofer (eds) *The Beginning of Birds*, 161–176. Jura Museum, Eichstatt.
- Ostrom, J.H. 1991. The question of the origin of birds. In: H. Schultze & L. Trueb (eds) *Origin of the higher groups of tetrapods*, 467–484. Comstock Publishing Co. Ithaca.
- Owen, R. 1836. Aves. In: *Todd's Cyclopaedia in Anatomy and Physiology* 1, 265–358.
- Padian, K. 1992. A proposal to standardize phalangeal formula designations. *Journal of Vertebrate Paleontology* 12, 260–262.
- Parker, W.K. 1888. On the structure and development of the wing in the common fowl. *Philosophical Transactions of the Royal Society of London* B179, 385–395.
- Raynaud, A. 1985. Development of limbs and embryonic limb reduction. In: C. Gans (ed) *Biology of the Reptilia* 15b, 59–148. Wiley, New York.
- Romer, A.S. 1956. *The Osteology of the Reptiles*. 772 pp. University of Chicago Press, Chicago.
- Romer, A.S. 1966. *Vertebrate Paleontology*, 3rd ed. 468 pp. University of Chicago Press, Chicago.
- Schultze, H.P. & Trueb, L. (eds) 1991. *Origins of the higher groups of Tetrapoda*. 724 pp. Comstock Publishing Company, Ithaca, New York.
- Sereno P.C. & Novas, F.E. 1992. The Complete Skull and Skeleton of an Early Dinosaur. *Science* 258, 1137–1140.
- Sereno P.C., Forster C.A., Rogers R.R., & Monetta, A.M. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature* 361, 64–66.
- Sues, H.D. 1990. *Staurikosaurus* and *Herposauridae*. In: D. Weishampel, P. Dodson, & H. Osmolska (eds) *The Dinosauria*, 143–147. University of California Press, Berkeley.
- Shubin, N. 1991. The implications of "The Bauplan" for Development of the Tetrapod Limb. In: J.R. Hinchliffe, J. Hurle, & D. Summerbell (eds) *Developmental Patterning of the Vertebrate Limb*, 411–421. Plenum Press, New York.
- Shubin, N. & Alberch, P. 1986. A morphogenetic approach to the origin and basic organization of the tetrapod limb. *Evolutionary Biology* 20, 319–387.
- Tarsitano, S. 1991. Archaeopteryx Quo Vadis? In: H. Schultze & L. Trueb (eds) *Origin of the higher groups of tetrapods*, 541–576. Comstock Publishing Co. Ithaca.
- Tarsitano S. & Hecht, M.K. 1980. A reconsideration of the reptilian relationships of Archaeopteryx. *Zoological Journal of Linnean Society* 69, 149–182.
- Thulborn, R.A. & Hamley, T.A. 1982. The reptilian relationships of Archaeopteryx. *Australian Journal Zoology* 30, 611–34.
- Weishampel, D., Dodson, P., & Osmólska, H. 1990. *The Dinosauria* 733 pp. University of California Press, Berkeley.
- Witmer, L.M. 1991. Perspectives on Avian Origins. In: H. Schultze & L. Trueb (eds) *Origins of the higher groups of tetrapods*, 427–466. Comstock Publishing Co., Ithaca.

Streszczenie

Wyprowadzony z danych embriologicznych styl redukcji metakarpaliów w skrzydle ptaków (2-3-4) jest odmienny od udokumentowanego paleontologicznie stylu redukcji dłoni teropodów (1-2-3). Jeśli uznać zasadność tej rozbieżności ptaki wyodrębniły się z gałęzi ewolucyjnej dinozaurów przed powstaniem teropodów.