Acta Palaeontologica Polonica
Vol. 28, No. 1—2 pp. 133—136 Warszawa, 1983
Second Symposium on Mesozoic Terrestial Ecosystems, Jadwisin 1981

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ARCHAEOPTERYX AND ITS PALEOECOLOGY

HECHT, M. K. and TARSITANO, S.: *Archaeopteryx* and its paleoecology. Acta Palaeont. Polonica, 28, 1—2, 133—136, 1983.

The various reptilian relationships of *Archaeopteryx* are reviewed. Crocodilian and theropod ancestry for *Archaeopteryx* and therefore birds is rejected because of the specialized morphology of both these taxa. In contrast the known morphology of certain thecodonts, provides the necessary features from which the primitive avian morphology of *Archaeopteryx* can be derived. The origin of flight in birds is discussed within the context of the ecological setting of the Solnhofen environment. The primitive level of the flight morphology of *Archaeopteryx* is used to interpret the flight capabilities of these early birds.

Key words: *Archaeopteryx*, phylogenetic inference, flight.

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INTRODUCTION

Recent interest in the origin of higher taxa has refocused attention on *Archaeopteryx* as the earliest bird or *Urvogel*. The three major theories of relationship of *Archaeopteryx* are those of crocodilian (Walker 1972), theropod (Ostrom 1976) and of thecodontian (Heilmann 1926; Tarsitano and Hecht 1980) ancestry. Of these three hypotheses it is possible to select the most probable relationship by an evaluation of the characters and their states.

That *Archaeopteryx* is a sister group of crocodilians can be discounted by the following criteria:

1) the pubis is excluded from the acetabulum in all crocodilians
2) the carpals are elongate in all crocodilians
3) the presence of clavicles is unknown in the crocodilian lineage
4) crocodilians have a flat, forward sloping quadrate which is broadly sutured to the skull
5) the complete lack of synapomorphies uniting the two groups.

The theropod hypothesis is supported by a list of plesiomorphic characters and disputable interpretations of poorly preserved areas of pertinent fossil material. This hypothesis is also falsified by the following data:

1) the fusion of the proximal tarsals to the tibia forming a tibiotarsus in *Archaeopteryx*

2) the absence of a reflexed hallux in theropods (Dr. Ph. Taquet's personal communication)

3) the presence of a non-reduced and unique bent coracoid in *Archaeopteryx*

4) the pubis in *Archaeopteryx* reflexed at the avian level of development

5) the presence of a semilunate-like element in the carpus of *Archaeopteryx* and theropods cannot be used as a synapomorphy because of the similar occurrence of this character state in thecodontians (Walker 1961) and some lepidosaurians.

The third hypothesis proposing a thecodontian ancestry is supported by the presence of primitive features in *Archaeopteryx* indicating an ancestry among early archosaurs. Furthermore, the presence of ectodermal feathers and a furcula is paralleled by the bizarre thecodontian, *Longisquama*. The thecodontian level of organization can easily be considered ancestral to the Crocodylia, theropods and birds. The fragmentary nature of the thecodontian record makes the direct comparison between *Achaeopteryx* and thecodonts at this time difficult. However, the morphology of known thecodonts provides the necessary features from which the primitive avian level of organization can be derived.

ECOLOGICAL INTERPRETATIONS

The presence of feathers indicates that *Archaeopteryx* required insulation and therefore was probably homeothermic. Its phylogenetic relationship with the Thecodontia precludes the use of homeothermy in *Archaeopteryx* as evidence for homeothermy in theropods.

The presence of asymmetrical remiges in *Archaeopteryx* (Feduccia and Tordoff 1979; Olsen and Feduccia 1979) indicate that it could attain high speeds during gliding and weak powered flight. Therefore the presence of an airfoil as evidenced by the feather structure precludes the development of an insect net (Ostrom 1976). The presence of a furcula and a bent coracoid implies that *Archaeopteryx* was capable of some powered flight (Olsen and Feduccia 1979; Tarsitano and Hecht 1980). The vertical component of the wing beat is limited by the ventrally directed glenoid and the lack of an avian *M. supracoracoideus* pulley system. The presence of an elongate (as compared to modern birds) caudal vertebral column and its associated feathers provides greater lift during gliding but limits maneuvrability in certain environments.

The environment of the Solnhofen indicates a large inland sea divided into basins with the possibility of scattered islands (Barthel 1979). The presence of large open areas is consistent with the flight capabilities of *Archaeopteryx*. It is our interpretation that the limited flight capabilities of *Archaeopteryx* precludes its inhabiting dense forest.

The poorly developed flight mechanism required that *Archaeopteryx* attained height by climbing in order to initiate flight. Therefore, the large hand claws were not vestiges but functioned in climbing (Heilmann 1926). Furthermore, the limited flight capability of *Archaeopteryx* was such that it could not catch food on the wing, such as insects, but used flight to locate food. The large areas of open space and beaches of the Solnhofen sea provided the environment which could be exploited by a gliding and weakly flying animal searching for detritus along the shore line.

CONCLUSION

In summary, *Archaeopteryx*, a primitive bird, shares no synapomorphies with theropods or crocodilians that are not present in thecodonts. The morphology of both theropods and crocodilians are too specialized to be ancestral to birds. The ecological conclusions that can be drawn from the morphology of *Archaeopteryx* and its depositional environment indicates a glider with limited powered maneuvrability searching open areas for carrion and other detritus.

ACKNOWLEDGMENTS

We wish to acknowledge the support of the PSC/BHE faculty research fund of the City University of New York and the Sonderforschungsbereich 53. We also thank the Institut and Museum für Geologie und Paläontologie of the University of Tübingen for their hospitality. This paper is Konstruktionsmorphologie, Nr. 137.

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