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EPIGENETIC EVIDENCE FOR THE ORIGIN OF BIRDS

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The question of heritability of epigenetic pathways is raised. Some theoretical predictions are made and tested on the example of the upper jaw structure in archosaurian reptiles and birds. Empirical evidence drawn from this example closely agrees with epigenetic predictions, but cannot be satisfactorily explained on the basis of the classical neo-Darwinism.

These results are used for discussing the origin of birds. They support Heilmann's view that birds originated from thecodont archosaurs. In addition, a new reconstruction of the Archaeopteryx' upper jaw is given, based on the restudy of the Berlin specimen.

Key words: epigenetics, heredity, upper jaw, Archosauria, Aves

In neo-Darwinian paradigm, phenotype had been considered simply as a direct result of information on development coded in the genotype. However, recent advances in molecular genetics and epigenetics revealed fundamental discrepancies in this paradigm, showing that the genotype-phenotype relation is by far not so simple as believed by the proponents of neo-Darwinism (cf., e.g., Løvtrup 1974, Wolsky and Wolsky 1976, Novák and Mlíkovský 1982, Bonner 1982, Chandebois and Faber 1983, Goodwin et al. 1983, Ho and Saunders 1984, and Mlíkovský and Novák 1985).

For purposes of this paper, the most important non-neo-Darwinistic concept is that of *epigenetics* (Waddington 1957, Løvtrup 1974). According to epigenetics, any phenotypic character develops through an *epigenetic pathway*, or *creode* in Waddington's (1942) terminology, which is more or

less resistant against evolutionary changes. The process leading to this phenomenon has been termed *canalization* by Waddington (1942) and *auto-regulation* by Šmal'gauzen (1938). The existence of epigenetic pathways has been proven in numerous embryological experiments (see especially Løvtrup 1974, Chandebois and Faber 1983, and Raff and Kaufmann 1983). However, although both Waddington and Šmal'gauzen have spoken about *evolutionary resistance* (evolutionary homeorhesis) of epigenetic pathways, all what has been testified in the above mentioned experiments was the *ontogenetic resistance* of them. Apparently, however, no evidence of ontogenetic resistance of epigenetic pathways can testify to, or even explain, the evolutionary resistance of them. Hence, this paper aims to contribute to testifying to the hypothesis of the evolutionary resistance of epigenetic pathways, i.e., in other words, the question of the heritability of them.

I believe that this question can be tested with relative ease by selecting a supraspecific taxon (or phyletic line) and identifying in it a phenotypic evolutionary change which had been actually achieved during evolution in more than one way. The theory of epigenetics predicts that the change required shall always be achieved through the relatively less stabilized epigenetic pathway.

If this selection is sound, the selection of the epigenetic pathway should be the same in related groups. Moreover, we may expect that in ancestral subgroup of the group under study, the distribution of destabilized epigenetic pathways should be more scattered among individual taxa included in that subgroup than in more advanced subgroups in which the originally destabilized epigenetic pathways are expected to be re-stabilized again.

To test these predictions I selected the structure of the upper jaw in archosaurian reptiles and in birds which are the former group's phylogenetic offshoot. In these animals, the length of the upper jaw is determined by the length of os premaxillare and os maxillare. In forms with short upper jaw, both premaxillare and maxillare are short. Then, if elongation of the upper jaw is required by the animal's feeding (or other) habits, it may be achieved either by the elongation of premaxillare, or maxillare, or both. Such changes require naturally destabilization of the

respective epigenetic pathways through which the respective bone develops. If, then, epigenetic claims are sound, the findings should be in agreement with respective predictions made above.

STRUCTURE OF THE UPPER JAW IN ARCHOSAURIA AND AVES

Long snouts build by long maxillare and short premaxillare have been found among Archosauria in all Crocodylia (Steel 1973, 1975), Pterosauria (Wellnhofer 1971, 1980), Saurischia (Steel 1970) and Ornithischia (Steel 1969). An exception are in this case ornithosuchian Hadrosauridae in which the form and relative size of premaxillare is very diverse (see Ostrom 1962, Hopson 1975).

On the other hand, all birds have beaks build by long premaxillare and short maxillare (Bellairs and Jenkin 1961), this being true already for the Jurassic Archaeopteryx (see below) which is still (in 1984) the oldest bird known.

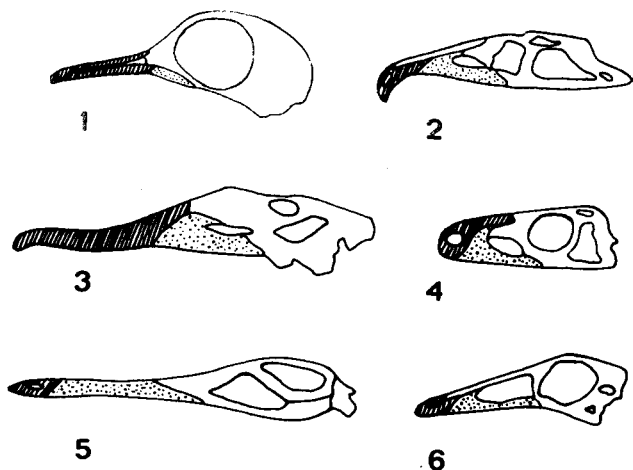


Fig. 1. Skulls (in norma lateralis sinistra) of some archosaurs and birds showing schematically structure of their upper jaw. Lower jaw and teeth have been omitted for the sake of simplicity. Shaded = os premaxillare, dotted = os maxillare. 1 = Columba (Aves), 2 = Chasmatosaurus (Thecodontia: Proterochampsidae), 3 = Machaeropsopus (Thecodontia: Phytosauria), 4 = Euparkeria (Thecodontia: Pseudosuchia), 5 = Geosaurus (Crocodylia), 6 = Ornithomimus (Ornithischia). Redrawn from Müller (1968) after various authors.

All these advanced groups originated with all probability from ancestral Triassic archosaurs known as Thecodontia (Colbert 1969, Krebs 1974). As stated above, we may expect that in the latter (ancestral) group we shall find both variants of the upper jaw structure. This proved to be true, although the interpretation of the findings is rather difficult, owing to the still insufficiently known phylogeny of Thecodontia which had presumably consisted of three main subgroups: Pseudosuchia, Phytosauria, and Proterosuchia, while the family Proterochampsidae is still considered as incertae sedis (cf. Hofstetter 1955, Hughes 1963, Romer 1972, Kuhn 1976, Chatterjee 1982a,b, Thulborn 1982). Pseudosuchia, which had been probably closely allied with Crocodylia (Krebs 1974), possessed short premaxillare and long maxillare (Krebs 1976). However, in late Triassic pseudosuchia Stagonolepididae, premaxillare is modified, toothless, and somewhat elongated (Walker 1961, Krebs 1976). All Phytosauria, on the other hand, possessed long premaxillare and short maxillare (Westphal 1976). The mainly Middle Triassic family Proterochampsidae, the affinities of which still remain enigmatic (Sill 1967, Sues 1976), possessed long maxillare, but also their premaxillare seems to had been somewhat elongated (see Sues 1976) when compared with typical reptiles of the "short premaxillare - long maxillare" type. Among the Proterosuchia, the most ancestral, late Permian to early Triassic thecodonts, all Erythrosuchidae possessed short premaxillare and long maxillare, while all Proterosuchiae appear to had possessed long maxillare and somewhat elongated, ventrally bent premaxillare (Charig and Reig 1970, Cruickshank 1972, Charig and Sues 1976).

EPIGENETICS OF THE UPPER JAW EVOLUTION IN ARCHOSAURS

As expected by the theory of epigenetics (see above), in early archosaurs epigenetic pathways leading to maxillare and premaxillare had still not been completely stabilized, what may be evidenced by elongation of maxillare in Erythrosuchidae and Pseudosuchia, by elongation of premaxillare in Phytosauria, and by elongation of maxillare with variously modified and somewhat elongated premaxillare in Proterosuchidae, Stagonolepididae and Proterochampsidae. Although the latter condition is known also in earliest thecodonts (Proterosuchidae), it seems probable that epigenetic

pathways leading to maxillare had been less stable than those leading to premaxillare, because premaxillare really elongated only in Phytosauria.

Before they became extinct at the end of Triassic, thecodonts gave rise to several more advanced groups. In accordance with patterns found in Thecodontia, nearly all of them (Crocodylia, Pterosauria, Saurischia, and Ornithischia) possessed less stable epigenetic pathways leading to maxillare, because it is this bone which always elongated in these groups. In the ornithischian family Hadrosauridae, epigenetic pathways leading to premaxillare became secondarily destabilized. On the other hand, birds are the only advanced archosaurian group in which the elongation of the upper jaw had been realized by the destabilization of epigenetic pathways leading to premaxillare.

Summarizing this evidence we can conclude that since earliest archosaurs, epigenetic pathways leading to maxillare had been somewhat less stable than those leading to premaxillare in most archosaurs, although both of these epigenetic pathways had been apparently relatively unstable in many Triassic ones. This made possible the elongation of premaxillare in a few groups, particularly in Phytosauria and birds, although the reverse pattern is the typical one. After the elongation of the upper jaw took place in individual archosaurian subgroups, the respective epigenetic pathways became secondarily stable, what is evidenced by the phenotypic invariance of the upper jaw structure in all of these more advanced groups. Exceptionally, a secondary destabilization of some of these epigenetic pathways could happen, as it has been observed in hadrosaurs.

Thus, the observed pattern of the archosaurian upper jaw evolution is in full agreement with that predicted by the theory of epigenetics. Moreover, it is evident that these findings cannot be satisfactorily explained in the frame of the neo-Darwinian paradigm, because it can hardly be expected that, at the phenotypic level, long premaxillare and short maxillare had been selectively advantageous in some groups whereas the opposite had been true in other ones.

IMPLICATIONS FOR THE ORIGIN OF BIRDS

There is common agreement among contemporary paleontologists that birds originated from archosaurian reptiles. However, uncertainty prevails regarding the subgroup of Archosauria from which birds originated (see Ostrom 1975, Tarsitano and Hecht 1980, Thulborn and Hamley 1982, and Martin 1983 for current reviews). From five main subgroups of Archosauria in four (Pterosauria, Ornithischia, Saurischia, and Crocodylia), upper jaw is constructed from short premaxillare and long maxillare (see above). Only in Triassic Thecodontia, an ancestral group among Archosauria, we find forms with long premaxillare and short maxillare, too, i.e. the condition occurring in all birds, incl. Archaeopteryx (see below).

With respect to theoretical epigenetic considerations presented above, this strongly supports the view of Heilmann (1926) and his followers (e.g., Swinton 1960, Brodkorb 1971, Tarsitano and Hecht 1980) that birds originated directly from Thecodontia and parallelly to other advanced archosaurian groups listed above. Unfortunately, as mentioned above, phylogenetic relations in Thecodontia are still so little understood and so contradictory that to discuss the problem from which thecodontian subgroup birds originated seems to me to be meaningless at this time, although Proterosuchia (cf. above) may be probably excluded from the consideration.

THE CASE ARCHAEOPTERYX

It is commonly believed that Archaeopteryx had long maxillare and short premaxillare. This belief which goes back at least to Dames (1884) had been undoubtedly provoked by the then widely accepted view that birds originated from dinosaurs (see Ostrom 1975 for review), all of which possessed upper jaws constructed from long maxillare and short premaxillare. However, all Recent birds (Bellairs and Jenkin 1960) as well as the Mesozoic Hesperornis (Marsh 1880, Gingerich 1973, 1976) and Ichthyornis (Marsh 1880), in short all birds in which the structure of their upper jaw is known, have the reverse arrangement: short maxillare and long premaxillare. This may have three alternative explanations: (1) Archaeopteryx did not belong to true

birds (Aves); (2) the structure of the Archaeopteryx' upper jaw has been reconstructed incorrectly, or (3) a reversal in respective epigenetic strategies occurred in the evolution of birds.

Because the explanation (3) is highly improbable on theoretical grounds discussed above, I tested the former two alternatives by examining the Berlin specimen of Archaeopteryx. The results strongly support the alternative (2). What appears to be a sutura between maxillare and premaxillare when the specimen is observed macroscopically, is in reality a caudal border of a piece of bone broken out during the taphonomic process. The break occurred at the place where it could be expected with highest probability: below large external nares where premaxillare is relatively slender and fragile in Archaeopteryx.

By a close microscopic examination which I performed, it is possible to see that the supposed "sutura" includes a rectilinear angle with the ventral border of external nares, and runs from its caudoventral angle straight into the alveola of the 6th teeth. Slightly rostral, a parallel break runs into the alveola of the 5th teeth. This outbroken piece of bone is slightly displaced, so that the caudal break is well visible by simple examination by eye and has been misinterpreted as a true sutura between maxillare and premaxillare. The rostral break appears only after microscopic examination. Because the most caudal parts of Archaeopteryx upper jaw are lacking in the Berlin specimen, the only I could examine, I cannot comment upon the exact place where premaxillare joints maxillare in this ancient bird. However, this is of no importance for the present paper.

In any case, we may conclude that in Archaeopteryx, too, its upper jaw was built by long premaxillare and short maxillare, just as in all other birds. This supports the view that Archaeopteryx belonged in an early (probably first) radiation of birds (e.g., Mlíkovský 1982).

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