

Cretaceous Birds – a short review of the first half of avian history

By Tommy Tyrberg

1. Introduction

The oldest known bird *Archaeopteryx lithographica* lived during the Tithonian stage of the Jurassic some 150 Ma (Megannum = million years) ago.

The Cretaceous period which lasted from ca 144 Ma to 65 Ma therefore constitutes approximately one half of known avian history (table 1). During these 80 Ma birds evolved from the primitive *Archaeopteryx* – in many ways intermediate between birds and reptiles – to essentially modern forms which in some cases are recognizable as members of extant avian orders. Unfortunately this process is very poorly documented by fossils. Fossil birds as a general rule are not common. The lifestyle of birds and their fragile, often pneumatized, bones are not conducive to successful fossilization, and even when preserved avian bones are probably often overlooked or misidentified. Collectors investigating Mesozoic continental deposits are likely to have their “search image” centered on either dinosaurs or mammals. It is symptomatic that of the five known specimens of *Archaeopteryx* two were originally misidentified, one as a pterosaur and the other as a small dinosaur *Compsognathus*.

Even when a fossil has been collected and identified as avian, problems are far from over. Avian skeletal elements are frequently badly preserved and rather undiagnostic, moreover birds (usually) lack teeth. This is a serious handicap since teeth are durable and frequently yield a remarkable amount of information about the lifestyle and taxonomic position of the former owners.

Last but not least paleornithology, whether it is considered as a branch of ornithology or of paleontology, is one of the most neglected branches of either science. All these factors combined means that only a handful of Cretaceous birds are known out of the multitude of species which must have evolved and gone extinct during 80 Ma (about 17,000 species according to an estimate by BRODKORB [1971]).

No Mesozoic birds are known from Africa or Antarctica, and from Asia and Australia there are only a few feather impressions (fig 1–2). Furthermore most known Cretaceous birds are marine forms while the terrestrial avifauna is virtually unknown. The distribution of the finds in time is also very uneven, with a strong concentration in the Upper Cretaceous, especially in the final, Maastrichtian, stage (table 1). Under these circumstances a review of Cretaceous birds must necessarily be rather speculative.

2. In the beginning

Archaeopteryx is still, more than a century after the first finds, the only well known Jurassic bird. In addition to the five *Archaeopteryx* specimens, all from the Eichstätt

area of Bavaria, Jurassic avian remains have only been reported from two localities. These are both late Jurassic of age. One is Montsech in Spain where a feather impression was found thirty years ago (CONDAL 1955). The other find locality is Karatau in Kazakhstan, a locality better known for its rich Jurassic insect fauna. The Karatau find consists of a single (slightly questionable) feather which, in what must be one of the more remarkable cases of taxonomic exuberance on record, has been used as the holotype both of a new species (*Praeornis sharovi*), genus (*Praeornis*), family (Praeornithidae), order (Praeornithiformes) and subclass (Praeornithes) (RAUTIAN 1978).

The most interesting Mesozoic feather impressions are those from Koonwarra in Victoria, Australia. There four impressions have been found in fresh water sediments from the Lower Cretaceous (Valanginian-Aptian) (TALENT et al 1966, WALDMAN 1970, RICH 1976).

The importance of the Koonwarra feathers lies in the fact that they prove, in conjunction with the finds from Europe and Central Asia, that birds already had a worldwide distribution in the Lower Cretaceous.

3. The setting

The Late Jurassic world, where the first birds evolved, was very different from today. Geographically, the breakup of Pangaea, the "World-continent", which had begun some 50 Ma earlier had not yet proceeded very far. All continents still either had land-connections or were separated only by narrow seas (fig 1), a circumstance which must have facilitated the dispersal of the ancestral birds.

The climate was apparently much milder and more equable than at present, with relatively small contrasts between low and high latitudes. Temperate conditions extended to the Arctics and probably no permanently snow-covered areas existed.

In the biosphere the contrast to present conditions was equally marked. On land, dinosaurs and other reptiles dominated. Mammals had already existed for a long time (since the Late Triassic), but they were small and primitive, perhaps still oviparous like the extant Monotremes.

The seas were populated by a variety of marine reptiles, while among the fishes the Holosteans were dominant.

The only flying animals were pterosaurs and insects. The latter were already a very old group, but many important groups e.g. the butterflies (Lepidoptera) did not yet exist. The Jurassic flora also differed greatly from the present one. The forests were constituted by primitive conifers, ginkgophytes and cycads sensu lato while the ground cover consisted largely of ferns and mosses. There were probably as yet no angiosperms and the whole flora was of a very low diversity compared to present conditions. According to an estimate by HUGHES (1976) the total number of vascular plant species was only some 3,000 in the Early Cretaceous compared to some 300,000 today.

Under these circumstances the range of ecological niches available to the ancestral birds was quite restricted. The opportunities must have been very limited for frugivores and granivores, and for nectar-eaters they were of course non-existent. Conditions were certainly more favourable for insectivores, but even here the range of prey must have been appreciably smaller than today. On the other hand conditions for sea-birds and waders were probably as favourable then as now, and the same is probably true for

carion-eaters and nocturnal hunters of small mammals (e g owls). Raptors, whether diurnal or nocturnal, however require highly developed senses and flying skills of a high order, which the ancestral birds probably lacked.

Another influence on early avian evolution, which is difficult to evaluate, is the possible competition from the pterosaurs.

These had been present since at least the late Triassic, and several species are known from the Jurassic, most of them fairly small. Not much is known about their way of life but many were probably piscivores.

During the Cretaceous pterosaurs tended to increase in size while the diversity of the order decreased. The number of known genera decreased from 11 or 12 in the Early Cretaceous to 6 in the Late Cretaceous (MOLNAR & THULBORN 1980). The trend towards gigantism culminated in the huge *Pteranodon* and *Quetzalcoatlus* from the Latest Cretaceous with wing-spans of 8 and 12–15 meters respectively.

Pteranodon was a marine form which probably caught fairly small surface-living prey (probably fish and crayfish) while *Quetzalcoatlus* was probably a scavenger on the plains of western North America, where dinosaur carrion was presumably plentiful.

The parallel with albatrosses and vultures is striking. For both these groups a large wing-span and excellent gliding abilities is apparently of paramount importance. Therefore it is probably significant that, while the Pterosaur “bat-wings” must in general be considered much inferior to the avian wing, they apparently allowed larger wing-spans than is possible for birds.

There is thus some reason to think that the evolution of birds during the Cretaceous successively restricted pterosaurs to the “vulture” and “albatross” niches. If this was the case, pterosaurs were competitively restricted by birds rather than the other way around.

During the Cretaceous several important changes in the biosphere must have exerted a profound influence on avian evolution.

Geographically the breakup of Pangaea continued (fig 1–2), a process which led to an increasing isolation of the continental fragments. This in turn must have promoted speciation through vicariance. The fragmentation of the Cretaceous landmasses was further accentuated by a general tendency towards rising sea-levels during most of the period. This trend culminated in the Campanian. At this time the sea-level was probably some 350 meters higher than currently and land only accounted for some 18 % of the Earth's surface compared to 28 % at present (HOWARTH 1981, VAIL et al 1977). The area covered by shallow epicontinental seas of course increased in proportion. In these warm, clear and relatively shallow seas, huge deposits of exceptionally pure and fine-grained limestones accumulated, the chalk (German: Kreide) which has given name to the Cretaceous. The final, Maastrichtian, stage of the Cretaceous was, in contrast, a time of falling sea-levels (regression).

Climate, on the other hand, seems to have remained fairly constant throughout the Cretaceous, though there is some evidence of lower temperatures near the end of the period (e g FRANKS 1979).

The change with the greatest long-term effect on avian evolution was probably the complete transformation of terrestrial vegetation during the Cretaceous. The first indisputable angiosperms seems to be of Barremian age (120 Ma) (HUGHES 1976), whereupon the flowering plants rapidly became dominant in the land flora (for details see e g

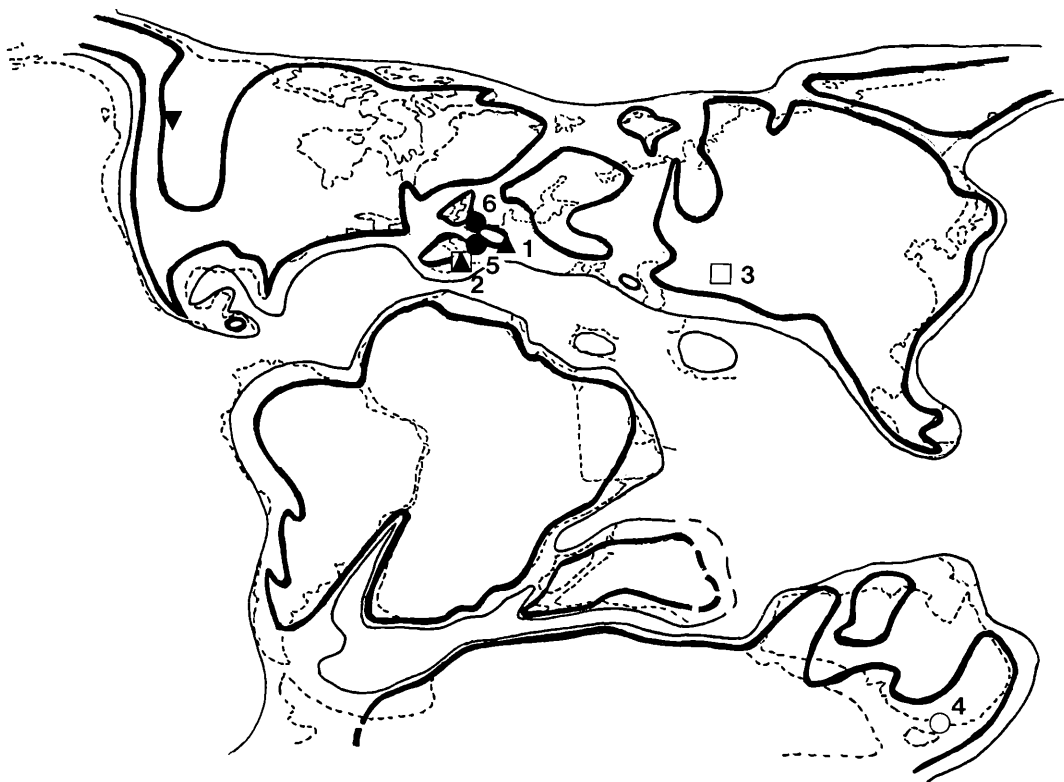


Figure 1:

Jurassic and Early Cretaceous avian remains. ▲ = Jurassic avian fossils, □ = Jurassic feather impressions, ● = Early Cretaceous avian fossils, ○ = Early Cretaceous feather impressions, ▼ = Early Cretaceous avian footprints, 1 = *Archaeopteryx*, 2 = Montsech, 3 = Karatau, 4 = Koonwarra, 5 = *Gallornis*, 6 = *Enaliornis*, 7 = Peace River.

The map is a reconstruction of geographical conditions during the Hauterivian (ca 130 Ma) and is based mainly on HOWARTH (1981) and SMITH, HURLEY and BRIDEN (1981) with several modifications. Cylindrical equidistant projection. Bold lines mark Hauterivian coastlines, thin lines the Hauterivian edges of continental shelves. Dotted lines indicate modern coastlines. This, like the other maps, is in part highly conjectural, i. a. in the Mediterranean, Caribbean and Bering Sound areas.

Funde von Vögeln aus dem Jura und der frühen Kreidezeit (Untere Kreide). ▲ = Jura-Fossilien; □ = Jura-Federabdrücke; ● = Untere Kreide-Fossilien; ○ = Untere Kreide – Federabdrücke; ▼ = Untere Kreide – Fußspuren von Vögeln, 1 = *Archaeopteryx*, 2 = Montsech, 3 = Karatau, 4 = Koonwarra, 5 = *Gallornis*, 6 = *Enaliornis*, 7 = Peace River.

Die Karte stellt eine Rekonstruktion der geographischen Verhältnisse vor 130 Millionen Jahren dar. Die kräftigen Linien bezeichnen den Küstenverlauf, die dünneren den Kontinentalschelf (Punktiert = heutige Küstenlinien). Der Kartenentwurf kann vorläufig nur eine ungefähre Vorstellung vermitteln, da Details, etwa im Mittelmeerraum, in der Karibik oder im Bereich der Beringstraße, noch weitgehend unbekannt sind. Das gilt analog für die anderen Karten.

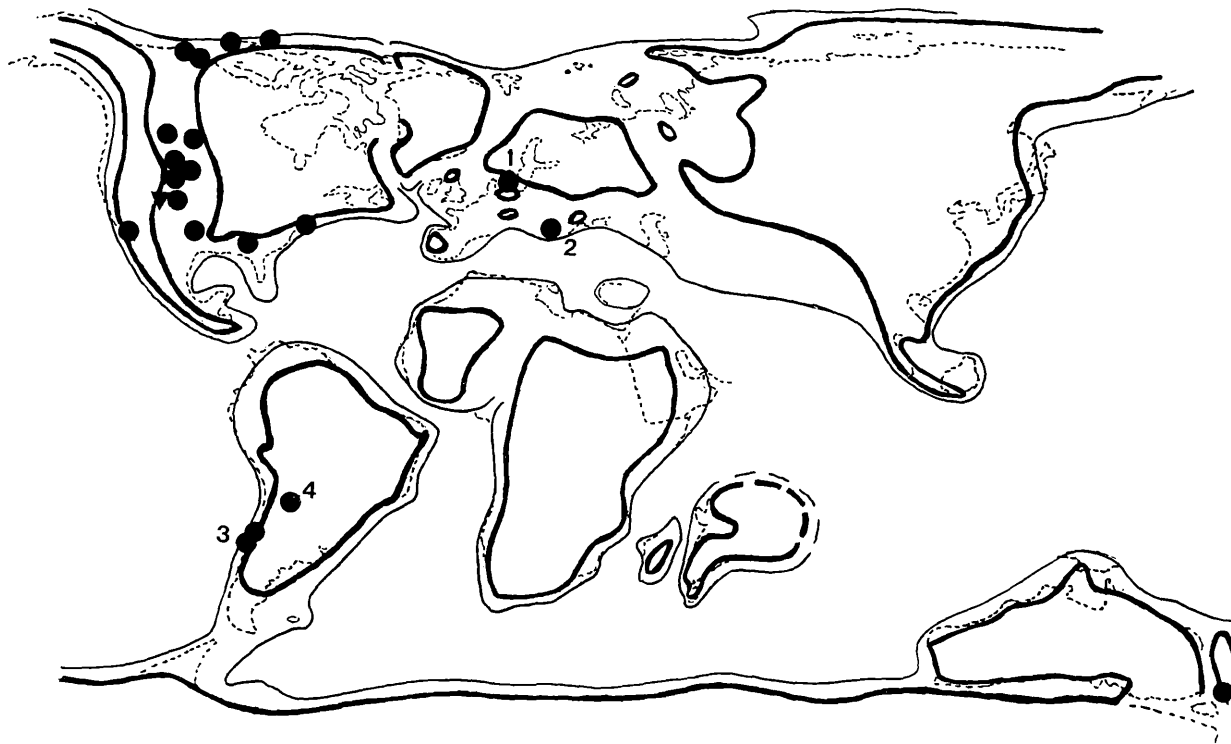


Figure 2:

Late Cretaceous avian remains. 1 = *Parascaniornis*, 2 = *Elopteryx*, 3 = *Neogaeornis*, 4 = *Enantiornis*, 5 = Waimakariri gorge. For details of North American finds see Fig. 3. Map based on conditions in the Campanian (ca 75 Ma), other details as in Fig 1.

Vogelfunde aus der späten Kreidezeit (Obere Kreide). Details zu den Funden in Nordamerika vgl. Abb. 3. Kartendarstellung der geographischen Verhältnisse vor etwa 75 Millionen Jahren. Angaben sonst wie Abb. 1.

DOYLE & HICKEY 1976, HUGHES 1976). This expansion of the flowering plants must have been matched by a corresponding proliferation of pollinating and seed-eating animals, i. e. mainly insects and birds. Frugivorous birds in particular, currently found mainly in tropical lowland forests, often form closely interdependent relationships with particular fruit-producing tree species which must have developed through co-evolution (for details see SNOW 1976, 1981). Among the insects the evolution of the Lepidoptera (butterflies) in particular was probably closely linked to the expansion of the angiosperms.

There was however one very important group still missing in the Late Cretaceous flora, the grasses (Graminae), which either did not yet exist, or only played a very minor role.

Among the vertebrates changes during the Cretaceous were less dramatic. Dinosaurs and marine reptiles still dominated land and sea at the end of the Cretaceous. The mammals had differentiated into placentals (Eutheria) and marsupials (Metatheria) in addition to archaic groups like the Multituberculata. But on the whole mammals still played a minor role in the terrestrial fauna. Among the fishes there had been larger changes, the Holostei having been largely supplanted by the modern bony fishes (Teleostei).

In aggregate, at the end of the Cretaceous period most of the ecological niches used by modern birds existed at least in potentiality. The most important remaining differences from modern conditions were probably the absence of arctic and grassland biomes and the absolutely and relatively much larger areas covered by tropical and subtropical lowland forest.

4. The toothed birds

The best known Cretaceous birds belong to the extinct orders Hesperornithiformes and Ichthyornithiformes. These, together with *Archaeopteryx*, are the only known birds with teeth. The two orders are therefore traditionally grouped in a separate subclass "Odontornithes" or "Odontognathae" (other names have also been proposed). There is however little that suggests any special relationship between the orders except the presence of teeth in both.

4.1 Hesperornithiforms

The order Hesperornithiformes comprises a number of medium-sized to very large non-volant seabirds. The two species of *Enaliornis*, *E. barretti* and *E. sedgwicki* from the Albion of Cambridgeshire (FISHER 1967, WALKER 1978), assigned to the family Enaliornithidae, are frequently regarded as the oldest known representatives of the order. The fossil material of *Enaliornis* is however fragmentary and it is not certain whether it belongs to Hesperornithiformes. If it does, *Enaliornis* might quite possibly have been the ancestor of the later hesperornithiforms. It would also be the only member of the order to be found in the Old World (at the time the British Isles were however situated quite close to northeastern North America [fig 3]). In contrast to other hesperornithiforms *Enaliornis* were fairly small birds, approximately pigeon sized (WALKER 1978).



Figure 3:

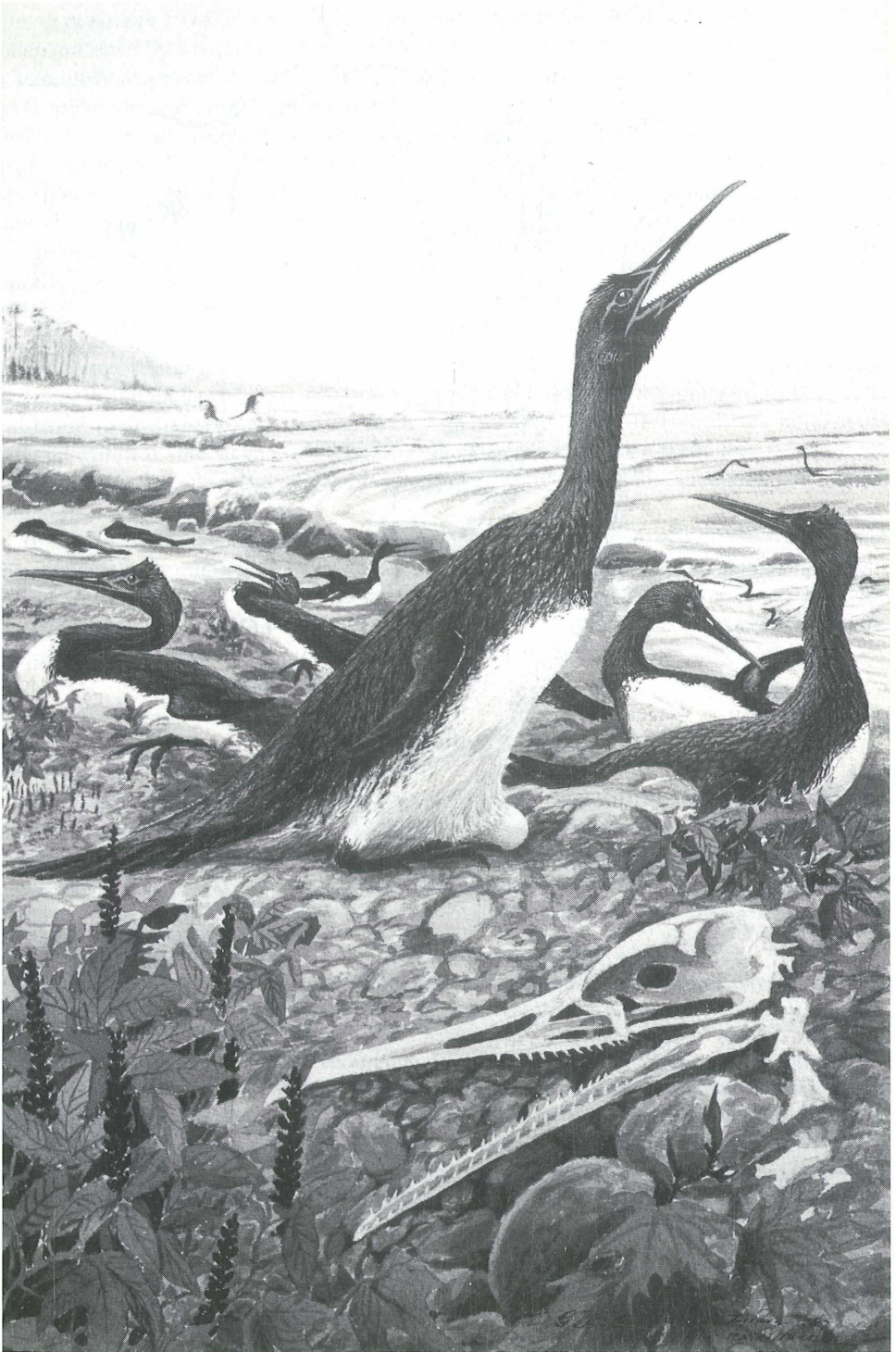
Cretaceous avian remains in North America. A = *Apatornis*, B = *Baptornis*, C = *Coniornis*, E = *Enaliornis*, H = *Hesperornis*, I = *Ichthyornis*, 1 = *Alexornis*, 2 = *Cimolopteryx*, *Ceramornis*, *Palintropus*, *Torotix*, *Lonchodytes* and *Apatornis*, 3 = *Graculavus*, *Telmatornis*, *Paleotringa* and *Laornis*, ▲ = avian footprints. Map based on conditions in the Campanian (ca. 75 Ma).

Kreidezeitliche Vogelfunde aus Nordamerika. (Schwarzes Dreieck = Fußabdrücke von Vögeln).

Geographische Verhältnisse etwa vor 75 Millionen Jahren. Vgl. Abb. 1

The other two families in Hesperornithiformes, Hesperornithidae and Baptornithidae occur in the upper Cretaceous of North and South America (fig 2–3).

Hesperornithidae comprises at least two genera *Hesperornis* (“Dawn bird”) and *Coniornis*, but other as yet undescribed genera are represented in the fossil material (MARTIN 1980). All Hesperornithids were large foot-propelled diving birds with greatly reduced wings. At least *Hesperornis sensu strictu* (whose cranial morphology is best



known) had sharp, slightly backward pointing teeth in the lower jaw and the middle part of the upper jaw. The hesperornithids were presumably piscivores.

In appearance the hesperornithids were large, somewhat diverlike birds with a streamlined body, fairly short neck and a long powerful beak (fig 4). The largest (and best known) species *Hesperornis regalis* was almost two meters long, three times the size of the great northern diver *Gavia immer*. As already mentioned, the beak was powerful, but not pointed. Apparently *Hesperornis* did not spear its prey but used its sharp teeth to seize it. The teeth were rooted in grooves on either side of the maxilla and were apparently shed alternately, like in many reptiles (MARTIN & STUART 1977).

That *Hesperornis* had retained the teeth of its Archosaurian ancestors was probably a direct consequence of its feeding strategy. For a piscivorous bird teeth must be very useful for holding on to wriggling and slippery prey. This view is supported by the fact that 'pseudo-teeth' has developed independently at least twice in other groups of fish-eating birds (the extinct Odonopterygiiforms and the mergansers *Mergus*).

The legs and feet of the hesperornithiforms were well adapted for swimming, probably with lobed toes like in grebes or coots. The Hesperornithiforms were undoubtedly powerful swimmers and divers, but on the other hand they must have been very clumsy on land since the legs were set far back on the trunk and poorly adapted for walking. The skeleton was heavy and little pneumatized and it is conceivable that they swam with the body largely underwater like anhingas. The small wings can hardly have been of much use for propulsion but may have been used for steering like the pectoral fins of fishes.

A closer study of the hesperornithiform skeleton reveals some primitive features in addition to the retention of teeth such as an unfused carpometacarpus (at least in *Baptornis*) and unfused clavicles. The latter may however be a secondary character since a furcula is present in *Archaeopteryx*. In *Enaliornis* the tarsometatarsus may also have been unfused (MARTIN 1980) but the only known proximal end of a *Enaliornis* tarsometatarsus may possibly belong to a young bird.

It is however quite clear that the hesperornithiforms had evolved from volant ancestors which were morphologically closer to modern birds than *Archaeopteryx*. One interesting recent finding is the presence of an apparently paleognathous palate in *Hesperornis* (GINGERICH 1976). This gives strong support to the view that the paleognathous condition is primitive in birds.

The affinities of the hesperornithiforms have been the subject of much debate. It has frequently been argued, most recently by CRACRAFT (1983), that they are related to the divers and grebes. However, it seems more likely that the similarities between these three groups are a result of convergence and not relationship and that the hesperornithiforms are not closely related to any extant birds. Against the specific phylogenetic theory of CRACRAFT (1983) speaks the fact that it either requires that the hesperornithiform lineage once having lost its teeth somehow regained them, or that teeth have been lost independently a minimum of four times among the ancestors of modern birds. Both hypotheses seem unlikely.

Fig 4:

A reconstruction of a *Hesperornis regalis* rookery. Painting by Gunnar BJÖRKMAN.

Rekonstruktion eines Brutplatzes von *Hesperornis regalis* (Gemälde von Gunnar BJÖRKMAN).

The systematics of the North American hesperornithiforms is currently under review, and according to MARTIN (1980) at least two undescribed genera and six species exist. One of these species, from the Campanian, is only grebe-sized and the Late Cretaceous hesperornithiforms were apparently of considerable diversity, presumably adapted to a variety of ecological niches.

Hesperornis is known from several North American localities ranging in age from the Coniacian to the Campanian (90–70 Ma). During this interval a shallow epeiric sea stretched far north from the Mexican Gulf across the present Great Plains of USA and Canada. For long periods this sea reached all the way to the Arctic Ocean and divided North America in two. It is in the sediments left by this sea, from Kansas in the south to the North West Territories in the north that *Hesperornis* has been found. Recently hesperornithiform remains belonging to a new subfamily have also been recovered from Maastrichtian freshwater deposits in North Dakota (MARTIN 1980). The find localities (marked in fig 3) seems to indicate a predominantly northern distribution.

This is supported by the variable abundance of the fossils. At the "classical" localities in Western Kansas *Hesperornis* constitutes less than 1 % of vertebrate remains, "among the rarest of fossils" according to MARSH (1880). In Manitoba the corresponding figure is about 10 % (BARDACK 1968) and at Andersson river near the Arctic coast it reaches 35 % (RUSSELL 1967).

The southern finds in Kansas are from the Niobrara chalk, which were probably deposited a fairly long distance from the nearest coast. The finds from this area are all from adult birds (unless the smaller *Hesperornis gracilis* are indeed juveniles of *H. regalis* as implied by MARTIN [1980]). It therefore seems likely that *Hesperornis* led a more or less pelagic life outside the breeding season.

In contrast to conditions in Kansas a considerable variation in size is found in specimens from Manitoba (BARDACK 1968) and a large proportions of the finds from the arctic part of Canada are of subadults or juveniles (RUSSELL 1967, STEEL 1979).

It therefore seems a reasonable guess that *Hesperornis*, like many recent seabirds, migrated to higher latitudes to breed. This is supported by the fact that all the Canadian finds seems to be of the same species (*Hesperornis regalis*) that predominates in the Niobrara chalk. Climate in the presumed breeding areas was however far from arctic at the time. Roughly contemporaneous plant remains from northern Alaska indicates temperate conditions with forests of Redwood *Sequoia*, *Torreya* and Planetrees *Platanus* in the lowlands and Pine *Pinus* and Spruce *Picea* on the uplands (SMILEY 1966). Seawater temperatures at the present Arctic coast have been estimated at 22 degrees Centigrade in summer and 14 in winter during the Mid-Cretaceous (LLOYD 1982).

This is roughly comparable to the temperature regime in the present-day Aegean Sea. Temperatures during the Campanian, the age of the *Hesperornis*-bearing deposits may however have been somewhat lower.

Even though the climate must have been mild and equable it seems doubtful whether the dominant Cretaceous predators, the Carnosaurs, could have existed north of the Arctic circle except during the summer, since they were presumably poikilothermic and could hardly have maintained body temperature during the winter darkness (cf HATTON 1980). Since the northernmost *Hesperornis* localities are located well inside the Arctic circle and were probably at approximately the same distance from the Pole during the Cretaceous (McELHINNY 1973) this might well mean that there were no large

terrestrial predators present in the area, at least during the winters. This must have been important since *Hesperornis*, on account of its clumsiness on land, was probably restricted to breeding on flat ground close to the shore (fig 5). Perhaps *Hesperornis* even bred during the winter darkness like the Emperor penguin *Aptenodytes forsteri*? The small mammals which could stay active during the winter probably did not pose much of a threat to such large birds.

4.2 The Baptornithids

The other hesperornithiform family, the Baptornithidae, is mainly known from the species *Baptornis advenus* which has only been found in the Niobrara chalk of Kansas (fig 5). *Baptornis* was similar to *Hesperornis*, but it was a much smaller bird (overall length some 70–90 centimeters) and perhaps slightly less well adapted to an aquatic existence. The wings were somewhat larger and the legs and feet slightly less modified for swimming than in *Hesperornis* (MARTIN 1980). A coprolith (fossilized excrement) which probably derives from *Baptornis* contains remains of a small species of the teleost genus *Enchodus* which was common in the Niobrara sea (MARTIN & TATE 1976) which supports the view that the hesperornithiforms were piscivorous.

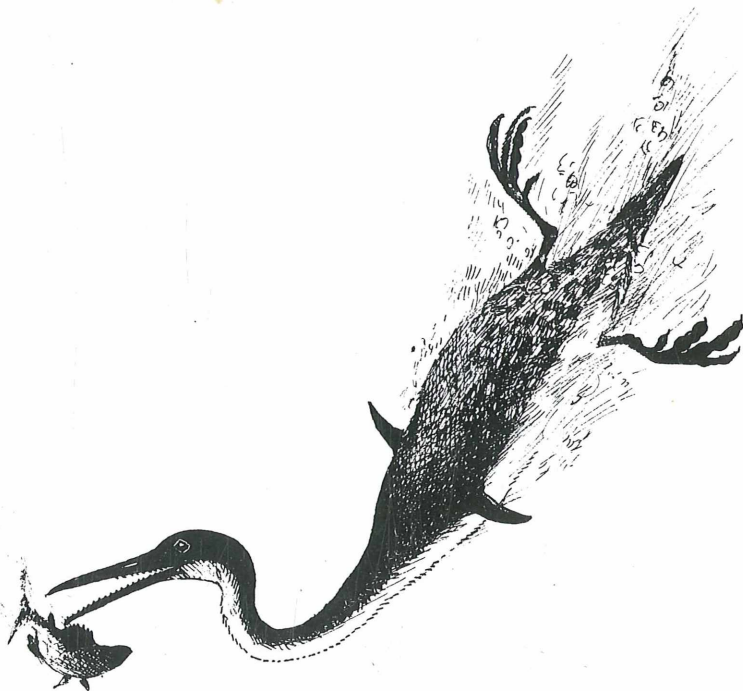


Fig 5:

A reconstruction of *Baptornis advenus*. Drawing by Gunnar BJÖRKMAN.
Rekonstruktion von *Baptornis advenus* (Zeichnung von Gunnar BJÖRKMAN).

While juveniles of *Hesperornis* are missing from the Niobrara chalk several juveniles are represented in the much smaller *Baptornis* material (MARTIN & BONNER 1977). This may indicate that *Baptornis* bred somewhere close to western Kansas. Since *Baptornis* must have been almost as ungainly on land as *Hesperornis* breeding on offshore islands is perhaps most likely. In addition to *Baptornis advenus* one of the undescribed hesperornithiform genera mentioned above is a baptornithid from the Niobrara chalk smaller than *Baptornis advenus* (MARTIN 1980).

One more species probably belonging to Baptornithidae is known. This is *Neogaeornis wetzeli*, recorded from two localities of Maastrichtian age in Chile (LAMBRECHT 1933, BRODHORB 1963, MARTIN & TATE 1976). These finds are of great interest since they are both the youngest known hesperornithiforms and the only ones from the southern hemisphere. If *Neogaeornis* is a baptornithid this indicates that the Baptornithidae are the only non-volant seabirds ever to have a bipolar distribution.

All other groups belonging to this category (Penguins, Spheniscidae, Lucas auks, Mancallinae, Great auks *Pinguinus* and the Plotopteridae) have been restricted to one hemisphere. That the baptornithids managed to disperse across the equator means that they must have been well adapted to life in the warm and relatively barren tropical seas.

4.3 Ichthyornis

The other order of toothed birds, Ichthyornithiformes, consisting of the two families Ichthyornithidae and Apatornithidae, is in most respects very different from the hesperornithiforms.

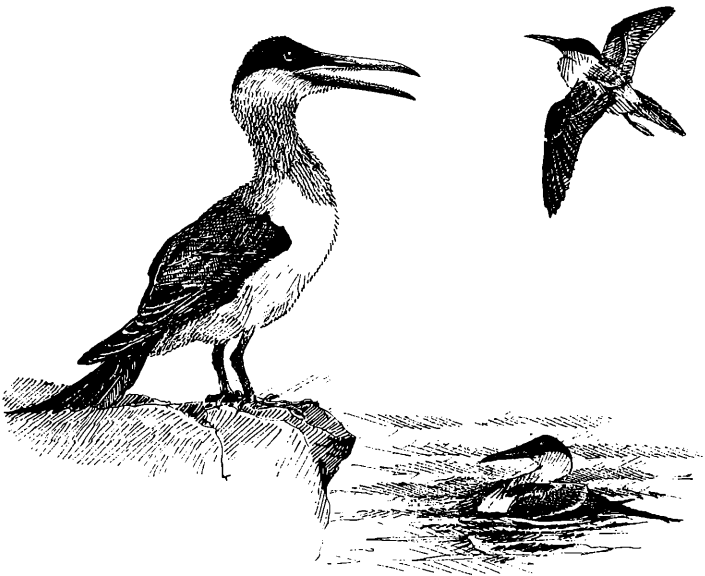


Fig 6:

A reconstruction of *Ichthyornis victor*. Drawing by Gunnar BJÖRKMAN.
Rekonstruktion von *Ichthyornis victor* (Zeichnung Gunnar BJÖRKMAN).

The ichthyornithiforms were tern-sized birds (overall length some 20 cm) with well-developed wings and flight muscles.

Like the hesperornithiforms they were apparently mainly marine birds. Most finds are of *Ichthyornis* the only known genus in Ichthyornithidae. The most important find locality is once again the Coniacian Niobrara chalk of western Kansas, but one species *I. antecessor* occurs in slightly younger (Santonian) layers in Alabama (OLSON 1975) and yet another, *I. lentus* has been found in Coniacian sediments in Texas (GREGORY 1952), though the assignment of the latter species to *Ichthyornis* has been questioned by MARTIN & STEWART (1982). Most reconstructions (including fig 6) are based on the best known Niobrara species, *I. victor*.

Ichthyornis seems to have had a more southern distribution than *Hesperornis* (fig 3) and Kansas and Manitoba (MARTIN & STEWART 1982) are the only areas where they have been found together.

The skeleton of *Ichthyornis* is rather similar in general features and proportions to some of the smaller auks', such as the rhinoceros auklet *Cerorhinca monocerata* or the tufted puffin *Lunda cirrhata* (BRODKORB 1971), and it seems likely that the ichthyornithiforms were more or less similar to gulls or auks in ecology and lifestyle.

Like the auks the ichthyornithiforms had a large head but the fairly long neck and the powerful beak with sharp teeth were quite different, and there seems to be few indications of affinities to any extant avian order, even though BRODKORB (1967, 1971) considered the ichthyornithiforms to be close to the charadriiforms.

Very little is known about the habits and ecology of the ichthyornithiforms. They were certainly good flyers and all finds of *Ichthyornis* to date have been from sediments probably deposited a fairly long distance from the nearest shore.

It also seems very likely that the ichthyornithiforms were piscivores but nothing concrete is known about their feeding habits. No juveniles have been found and the breeding biology is quite unknown. The shores bordering the seas where *Ichthyornis* has been found were probably low-lying so cliff-nesting seems unlikely unless the birds migrated to the Pacific coast or the Caribbean area to breed.

Apatornis, the only genus in Apatornithidae is found together with *Ichthyornis* in the Niobrara chalk (*A. celer*), but another species *A. retusus* has been recorded from the Maestrichtian Lance formation in Wyoming (BRODKORB 1963 a). The latter record is of considerable interest since the Lance formation is a freshwater deposit. *Apatornis* was of approximately the same size as *Ichthyornis* though it was perhaps a less capable flier than the latter. The remains of *Apatornis* are however so fragmentary the few definite conclusions can be drawn.

5. The extinction of the toothed birds

Both hesperornithiforms and ichthyornithiforms have been found up to the last Cretaceous stage, the Maestrichtian, but no trace of either group, nor of any other toothed birds, has ever been recorded from Cenozoic deposits. It therefore seems very likely that both orders became extinct at the Cretaceous-Tertiary boundary like many other taxa.

This crisis in the history of life is best known for the extinction of the dinosaurs, but the contemporaneous changes in the marine biosphere were even more drastic. Accord-

ing to some estimates as much as 75 % of all species became extinct at the Cretaceous-Tertiary boundary.

In the marine realm all large reptiles except turtles became extinct together with the marine pterosaurs, several cephalopod orders, the rudist bivalves and several other important groups. The extinctions apparently took place within a quite short period of time. The immediate cause of the marine extinctions was probably the almost complete disappearance of plankton (e.g. Hsu et al 1982). Such a reduction of primary production must have spread upwards in the food-webs with disastrous effects at higher trophic levels, e.g. marine birds like the hesperornithiforms and ichthyornithiforms.

The ultimate cause of the drastic decimation of both the terrestrial and the marine biosphere at the end of the Cretaceous is still doubtful but geochemical investigations in recent years has given strong support to the view that the extinctions were caused by the impact of a large (radius ≈ 10 km) asteroid as originally proposed by ALVAREZ et al (1980). If the extinctions were of a "catastrophic" character the disappearance of major groups like the toothed marine birds must have left many niches vacant for a time until they were filled through adaptive radiation of surviving species. Among the mammals this process is relatively well documented. The small and unspecialized late Cretaceous mammals had, by the early Eocene (some 10 Ma later), differentiated into rich and balanced faunas on all major continents (mammalian fossils of this age are however still unknown or very sparse from Australia, Antarctica, Madagascar and India).

Information about avian evolution in the early Tertiary is very fragmentary, but it seems possible that freshwater forms adapted to marine habitats and replaced the Cretaceous seabirds, since freshwater biomes seems, on the whole, to have been much less affected by the extinctions than the marine realm. It is suggestive that the oldest known representatives of such currently strictly marine families as frigatebirds (Fregatidae) and auks (Alcidae) has been found in freshwater deposits (FISHER 1967, OLSON 1977) and that gulls probably developed from pratincole-like ancestors in the earliest Tertiary (FJELDSÅ 1976).

6. The ancestral waders

The only avian order, in addition to hesperornithiforms and ichthyornithiforms, with a reasonable Cretaceous fossil record is the waders. The Cretaceous waders are of particular interest since taxonomic studies in recent years seem to indicate that several avian orders may be derived from charadriiform ancestors. Among these are the doves (Columbiformes), the sandgrouse (Pteroclediformes) (FJELDSÅ 1976, STEGMANN 1978), the plains-wanderer *Pedionomus* (OLSON & STEADMAN 1981), and possibly even the ducks (Anseriformes) and the flamingos (Phoenicopteriformes) (OLSON & FEDUCCIA 1980 a, b). If these views are correct, the early waders played a crucial role in avian evolution.

The Cretaceous charadriiform remains have all been found in two restricted areas in North America. One of these is the area around Hornerstown in New Jersey. Here fossils of several species of birds were found at the turn of the century in marine deposits of middle or late Maastrichtian age (BAIRD 1967).

Among the fossils assigned to Charadriiformes are three species of the genus *Paleo-tringa*, which are, however, too fragmentary to allow determination below ordinal level (CRACRAFT 1972, FJELDSÅ 1976, BRODKORB 1967, 1978). The other Hornerstown waders are three species of *Telmatornis* which were earlier thought to be related to the rails but have now been placed in a family of their own, Telmatornithidae, close to the thick-knees (Burhinidae) (CRACRAFT 1972).

The remaining Cretaceous waders are also of Maastrichtian age but from the Lance formation of Wyoming. They comprise four species belonging to an extinct family Cimolopterygidae, close to the avocets and stilts (Recurvirostridae) (BRODKORB 1963 a). There are also several other species of more or less definite charadriiform affinities (*Palintropus*, *Lonchodytes*, *Torotix*) (BRODKORB 1963 a, OLSON & FEDUCCIA 1980 a).

In spite of the fragmentary nature of the evidence it seems clear that by the end of the Cretaceous the waders were already a fairly diverse group which had begun to differentiate towards present-day families and were represented in both freshwater and marine habitats.

The “ancestral wader” must have lived fairly far back in the Cretaceous. Since there seems to be fairly general agreement that the plovers (Charadriidae) is the most primitive group within the charadriiforms it seems likely that the first waders were plover-like. They may also have had some similarities to the thick-knees and coursers *Cursorius*, which also seem to have retained some primitive characters. Some homologies apparently exist in both adult and juvenile plumages of plovers, sandgrouse, pratincoles and perhaps doves. This applies to i. a. the pectoral bands that many species in these

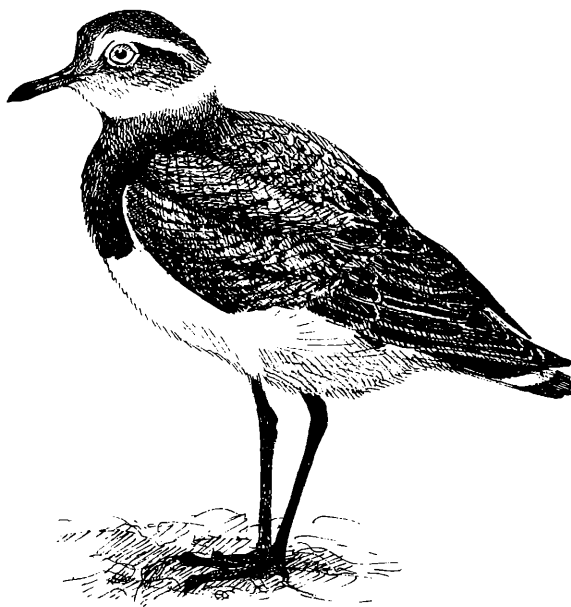


Fig 7:

A conjectural reconstruction of an ancestral wader. Drawing by Gunnar BJÖRKMAN.
Versuch einer Rekonstruktion eines kreidezeitlichen Vorläufers der Kiebitze (Charadriiformes)
(Zeichnung Gunnar BJÖRKMAN).

groups possess and to many details in the cryptic plumage of the young (for details see FJELDSÅ 1976). This, in concert with the supposed primitiveness of the plovers makes it possible to make a (very speculative!) reconstruction of what the "ancestral wader" may have looked like sometime in the Middle/Late Cretaceous (fig 7).

7. Other Cretaceous birds

The remaining Cretaceous avian fossils are quickly enumerated.

Gallornis straeleni has been found in "Neocomian" (Valanginian?) deposits in Auxerre, France. It has been regarded as an anseriform (LAMBRECHT 1933) or a phoenicopteriform (BRODKORB 1963 b), but considering its fragmentary state (the proximal part of a femur and a fragment of the humerus) and great age it can probably not be determined even at ordinal level.

In spite of this *Gallornis* is of considerable interest since it indicates that avian evolution had proceeded quite far from the *Archaeopteryx* level already by the Early Cretaceous. *Alexornis antedecens* from Campanian sediments in Baja California, Mexico, is of great interest since it is the only indisputable Cretaceous landbird. *Alexornis* is apparently related to Coraciiformes and Piciformes and shows some particular similarities to the motmots (Momotidae) and the puffbirds (Bucconidae) (BRODKORB 1976). This is not very remarkable since it seems likely that the piciforms and the coraciiforms are fairly closely related. Furthermore both the fossil record and the current distribution pattern of piciforms and coraciiforms seems to indicate that Coraciiformes is primarily an Old World group while piciform differentiation has mainly taken place in the New World. *Alexornis* may well be a representative of an ancestral perching-bird group from which piciforms, coraciiforms and possibly passerines evolved through the increasing isolation of the Continents in the Late Cretaceous.

Parascaniornis stensioi, also of Campanian age and found in detrital limestone on Ivön, Sweden, has been regarded as a phoenicopteriform (LAMBRECHT 1933). Since it is only represented by a single vertebra *Parascaniornis* is, however, probably indeterminate.

Avian fossils of Maastrichtian age are somewhat more common (table 1).

From the Hornerstown area comes, in addition to the waders already mentioned, *Laornis edvardianus* and two *Graculavus* species.

Laornis has been assigned to a family of its own (Laornithidae) close to the rails by CRACRAFT (1973). This assignment has been questioned by BRODKORB (1978) who regards *Laornis* as indeterminate, but possibly pelecaniform. If *Laornis* was indeed a rail, it was a very large one, larger than the Takahe *Notornis* the largest living rail. It is also rather surprising to find a rail or near-rail in marine deposits.

Graculavus are usually considered to be early cormorants (e.g. BRODKORB 1963 b) but this probably needs to be confirmed by re-study of the specimens.

Elopteryx nopcsai has been found in freshwater deposits of latest Cretaceous age in Roumania. There has been some doubt whether *Elopteryx* is of latest Cretaceous or earliest Tertiary age, but new finds has recently confirmed the assignment to the Cretaceous (GRIGORESCU & KESSLER 1980). *Elopteryx* is referred to the extinct family Elopterygidae within the Pelecaniformes. Elopterygids are so far only known from Europe (BRODKORB 1963 b) and from the time span from Maastrichtian to Middle Eocene.

Recently some very peculiar avian fossils have been reported from the Maastrichtian of Northwestern Argentina (WALKER 1981). They have been assigned by WALKER (1981) to a new subclass Enantiornithes and several species seem to be represented. The remains show some remarkably primitive features such as an only partially fused tarso-metatarsus and the Enantiornithes are probably not closely related to any known birds. WALKER (1981) suggest that they may be the sister group of all birds except *Archaeopteryx*.

Finding such an archaic group of birds in South America is not very surprising by itself since that continent was largely isolated during most of the Cretaceous and the Tertiary and evolution there proceeded in isolation resulting in the preservation of archaic forms of both animals and plants. As far as known, South America had no land connections to any other continent except possibly Antarctica from the Mid Cretaceous to the Pliocene, a period of some 100 Ma. This is still very evident in extant Neotropical biota with their remarkably high incidence of endemism and relict forms.

PERIOD	STAGE	AGE (MA)	AVIAN FOSSILS
TERTIARY	Paleocene	65	<u>Enantiornis, Neogaeornis, Elopteryx</u>
			<u>Graculavus, Cimolopteryx, Ceramornis</u>
	Maestrichtian	73	<u>Palintropus, Telmatornis, Paleotringa</u>
			<u>Lonchodytes, Torotix, Laornis</u>
	Campanian	83	<u>Coniornis</u>
			<u>Parascaniornis</u>
			<u>Alexornis</u>
	Santonian	87,5	<u>Baptornis</u>
			<u>Ichthyornis</u>
	Coniacian	88,5	<u>Apatornis</u>
UPPER	Turonian	91	<u>Hesperornis</u>
	Cenomanian		
CRETACEOUS		97,5	
	Albian		<u>Enaliornis</u>

PERIOD	STAGE	AGE (MA)	AVIAN FOSSILS
		113	
	Aptian		
		119	
	Barremian		
		125	
	Hauterivian		(?Koonwarra)
LOWER		131	
	Valanginian		?Gallornis
		138	
	Berriasian/Ryazanian		
		144	
JURASSIC			Archaeopteryx, (Montsech, Karatau)

Tab. 1. A synopsis of Mesozoic birds. A question mark before a find denotes that the exact age is uncertain. For genera known from more than one stage the generic name marks the first appearance and a vertical line the stratigraphic range of the genus. Timescale from HARLAND et al. (1982). – *Synopsis der Mesozoischen Vögel. Ein ? vor dem Fund bedeutet, daß das genaue Alter unbekannt ist. Für Gattungen, die in mehr als einer Periode vorkommen, wird die Zeit des ersten Auftretens angegeben und durch die senkrechte Linie die Spannweite des stratigraphischen Vorkommens aufgezeigt. Zeitskala nach HARLAND et al. (1982).*

Finally a few unidentified avian remains are known from the Cretaceous. There is an unidentified tarsometatarsus, probably of Maastrichtian age, from Waimakariri gorge in New Zealand (FLEMING 1979). Avian footprints have been recorded from the Cenomanian of Colorado (MEHL 1931) and from the Aptian of Peace River, British Columbia (CURRIE 1981). These records are of limited importance except insofar as they attest the worldwide distribution of Cretaceous birds. Fragmentary avian fossils of Mesozoic age must however be treated with caution since on several occasions reptilian remains have been erroneously identified as avian. This is understandable considering the Archosaurian origin of birds and the considerable osteological similarities that still remain.

Such “birds” which are in fact reptiles or whose avian character is at least questionable include *Laopteryx* (MARSH 1881), *Caenagnathus* (STERNBERG 1940, CRACRAFT

1981), *Bradycneme* and *Heptasteornis* (HARRISON & WALKER 1975), *Wyleyia* (HARRISON & WALKER 1973) and *Gobipteryx* (ELZANOWSKI 1974, 1976, 1977, 1981).

The opposite error is of course also possible, *Archaeopteryx* specimens has repeatedly been mistaken for pterosaurs or small dinosaurs and the toothed jaw of *Ichthyornis* was thought by GREGORY (1952) to belong to the Mosasaur genus *Clidastes*!

8. The late Cretaceous avifauna

An interesting question is whether the fossil record is a representative sample of the Cretaceous avifauna. This seems unlikely for several reasons.

According to an, admittedly hypothetical, estimate by BRODKORB (1971) the world avifauna consisted of some 2,000 species in 40 families at the end of the Cretaceous. Of these rather less than 1 % has yet been found. Furthermore it seems clear that the fossil record is biased both geographically (in favour of North America) and ecologically (towards aquatic and marine species). To some extent sampling errors can however be rectified through study of younger fossils and biogeographic data.

9. Cretaceous birds and the Paleogene avian record

Several avian orders are known from the Paleocene or Eocene. Some of these are rather specialized groups which must have had a fairly long previous history, presumably reaching back into the Upper Cretaceous. Among the more convincing cases are Penguins (Sphenisciformes), Parrots (Psittaciformes) and Owls (Strigiformes).

In addition to these there were undoubtedly other, now extinct, avian groups in existence in the Late Cretaceous and Early Tertiary. An interesting example is afforded by the recent find of medium sized, fully volant, paleognathous birds in the Paleocene – Early Eocene of Wyoming (HOUDE & OLSON 1981). These birds show no affinities to the ratites nor to the tinamoes, the only extant volant paleognaths. Presumably they were part of an early radiation of paleognath birds of which the surviving paleognaths are but “waifs and strays” (HUXLEY 1867). An interesting sidelight is shed on the difficulties of interpretation in avian palaeontology by the fact that, except for the palaeognathous palates, the skeletons of these birds are unremarkable, and skeletal elements found in isolation would very likely either have been left indeterminate or assigned to living avian orders (HOUDE & OLSON 1981).

10. Biogeographic evidence

In addition to the groups mentioned above, where early fossil evidence is available, it is in some cases possible to postulate a Cretaceous origin for groups with no early fossil record on the basis of biogeographic evidence.

A classical case in point is the “superorder” Ratitae which consists of some eight families of flightless, mainly large, birds (see table 2).

The relationships of the ratites have been hotly debated for more than a century. The main point of contention is whether the ratites are a monophyletic, primarily flightless

PERIOD	STAGE	AGE (MA)	AVIAN FOSSILS
		113	
	Aptian		
		119	
	Barremian		
		125	
	Hauterivian		(?Koonwarra)
LOWER		131	
	Valanginian		<u>?Gallornis</u>
		138	
	Berriasian/Ryazanian		
		144	
JURASSIC			<u>Archaeopteryx, (Montsech, Karatau)</u>

Tab. 1. A synopsis of Mesozoic birds. A question mark before a find denotes that the exact age is uncertain. For genera known from more than one stage the generic name marks the first appearance and a vertical line the stratigraphic range of the genus. Timescale from HARLAND et al. (1982). – *Synopsis der Mesozoischen Vögel. Ein ? vor dem Fund bedeutet, daß das genaue Alter unbekannt ist. Für Gattungen, die in mehr als einer Periode vorkommen, wird die Zeit des ersten Auftretens angegeben und durch die senkrechte Linie die Spannweite des stratigraphischen Vorkommens aufgezeigt. Zeitskala nach HARLAND et al. (1982).*

Finally a few unidentified avian remains are known from the Cretaceous. There is an unidentified tarsometatarsus, probably of Maastrichtian age, from Waimakariri gorge in New Zealand (FLEMING 1979). Avian footprints have been recorded from the Cenomanian of Colorado (MEHL 1931) and from the Aptian of Peace River, British Columbia (CURRIE 1981). These records are of limited importance except insofar as they attest the worldwide distribution of Cretaceous birds. Fragmentary avian fossils of Mesozoic age must however be treated with caution since on several occasions reptilian remains have been erroneously identified as avian. This is understandable considering the Archosaurian origin of birds and the considerable osteological similarities that still remain.

Such "birds" which are in fact reptiles or whose avian character is at least questionable include *Laopteryx* (MARSH 1881), *Caenagnathus* (STERNBERG 1940, CRACRAFT

1981), *Bradycneme* and *Heptasteornis* (HARRISON & WALKER 1975), *Wyleyia* (HARRISON & WALKER 1973) and *Gobipteryx* (ELZANOWSKI 1974, 1976, 1977, 1981).

The opposite error is of course also possible, *Archaeopteryx* specimens has repeatedly been mistaken for pterosaurs or small dinosaurs and the toothed jaw of *Ichthyornis* was thought by GREGORY (1952) to belong to the Mosasaur genus *Clidastes*!

8. The late Cretaceous avifauna

An interesting question is whether the fossil record is a representative sample of the Cretaceous avifauna. This seems unlikely for several reasons.

According to an, admittedly hypothetical, estimate by BRODKORB (1971) the world avifauna consisted of some 2,000 species in 40 families at the end of the Cretaceous. Of these rather less than 1 % has yet been found. Furthermore it seems clear that the fossil record is biased both geographically (in favour of North America) and ecologically (towards aquatic and marine species). To some extent sampling errors can however be rectified through study of younger fossils and biogeographic data.

9. Cretaceous birds and the Paleogene avian record

Several avian orders are known from the Paleocene or Eocene. Some of these are rather specialized groups which must have had a fairly long previous history, presumably reaching back into the Upper Cretaceous. Among the more convincing cases are Penguins (Sphenisciformes), Parrots (Psittaciformes) and Owls (Strigiformes).

In addition to these there were undoubtedly other, now extinct, avian groups in existence in the Late Cretaceous and Early Tertiary. An interesting example is afforded by the recent find of medium sized, fully volant, paleognathous birds in the Paleocene – Early Eocene of Wyoming (HOUDE & OLSON 1981). These birds show no affinities to the ratites nor to the tinamoes, the only extant volant paleognaths. Presumably they were part of an early radiation of paleognath birds of which the surviving paleognaths are but “waifs and strays” (HUXLEY 1867). An interesting sidelight is shed on the difficulties of interpretation in avian palaeontology by the fact that, except for the palaeognathous palates, the skeletons of these birds are unremarkable, and skeletal elements found in isolation would very likely either have been left indeterminate or assigned to living avian orders (HOUDE & OLSON 1981).

10. Biogeographic evidence

In addition to the groups mentioned above, where early fossil evidence is available, it is in some cases possible to postulate a Cretaceous origin for groups with no early fossil record on the basis of biogeographic evidence.

A classical case in point is the “superorder” Ratitae which consists of some eight families of flightless, mainly large, birds (see table 2).

The relationships of the ratites have been hotly debated for more than a century. The main point of contention is whether the ratites are a monophyletic, primarily flightless

Tab. 2: Geographic and stratigraphic range of the ratites. The assignment of *Stromeria* and *Eremopezus* to Aepyornithidae is very doubtful as is the status of the probable ratite *Eleutherornis* from the Eocene of Switzerland. – *Geographische und stratigraphische Verbreitung der Flachbrustvögel (Ratites). Die Zuordnung von Stromeria und Eremopezus zu den Aepyornithidae ist sehr zweifelhaft. Das gilt auch für den Status von Eleutherornis aus dem Eozän der Schweiz, einem möglichen Angehörigen der Ratiten.*

Family	Recent range	Oldest record	Age	Fossil range extension	Sources
Struthionidae (Ostriches)	Africa, SW Asia	<i>Struthio</i> cf. <i>brachydactylus</i> (Turkey) <i>Struthio</i> sp. (Tunisia, Kenya)	Early-Middle Miocene Middle-Late Miocene	E Europe, Central Asia, N India, Canaries?	SAUER 1979 RICH 1974
Rheidae (Rheas)	Southern S America	<i>Ophistodactylus patagonicus</i> (Argentina)	Early Miocene	–	TONNI 1980
† Dromornithidae (Mihirungs)	Australia	Dromornithidae sp.	Early Miocene	–	RICH 1979, 1980
Casuariidae (Cassowaries)	N Australia, New Guinea	<i>Casuaris</i> sp.	Pliocene	S Australia	RICH 1976
Dromaiidae (Emus)	Australia	Dromaiidae sp.	Middle Miocene	–	RICH 1976
† Dinornithidae (Moas)	New Zealand	<i>Anomalopteryx antiquus</i> <i>Pachyornis mappini</i>	Late Miocene– Early Pliocene	–	BRODKORB 1963 b FLEMING 1979
Apterygidae (Kiwis)	New Zealand	Several species Footprints?	Pleistocene Late Miocene	–	BRODKORB 1963 b FLEMING 1979
† Aepyornithidae (Elephant birds)	Madagascar	<i>Stromeria fajumensis</i> ? (Egypt). <i>Eremopezus eocaenus</i> ? (Egypt) Several species (Madagascar)	Early Oligocene Late Eocene– Early Oligocene Pleistocene	Egypt?	BRODKORB 1963 b

group or not. No consensus has yet been reached (for two recent contrary views on the matter see CRACRAFT 1974 and FEDUCCIA 1980). Recent studies, however, seems mainly to support ratite monophyly.

If the ratites are a monophyletic, primarily flightless, group their presence on all important fragments of old Gondwanaland (except India and Antarctica where fossils of the relevant age are largely unknown) and their virtual absence from the northern continents assumes considerable significance. This is particularly true since the Cretaceous and Tertiary faunas of the northern continents are by and large much better known than those of Gondwanaland. The only well attested northern ratites are Neogene and Pleistocene ostriches from Asia and Eastern Europe and these were presumably immigrants from Africa. The same is probably true of the eocene *Eleutherornis* of Switzerland if this species is really a ratite.

The widespread occurrence of ratites in old Gondwanaland on the other hand strongly suggest that the ancestral ratites dispersed while there was still land connection between the present-day fragments of the southern Supercontinent (for a detailed review of this hypothesis see CRACRAFT (1973 b). A difficulty for this view of ratite evolution has been the presence of the ostriches in Africa since there is strong evidence that the ostriches and the South American rheas are sister-groups and that the split of the ostrich-rhea lineage must fall fairly late in ratite phylogeny. Since there is good evidence that the opening of the South Atlantic had broken land connection between Africa and the rest of Gondwanaland by the Albian, or the Turonian by the latest (REYMENT 1968) this would imply that several of the ratite lineages were already in existence by the Mid Cretaceous which seems improbably early. In recent years there has however been several very surprising finds of animals with otherwise strictly South American distribution in the Paleogene of Western Europe and North Africa. These include ziphodont mesosuchian crocodiles (BUFFETAUT 1980, 1982), phorusrhacid birds (MOURER-CHAUVIRE 1981) and even an anteater (*Eurotamandua joresi*) (STORCH 1981).

These finds prove that some sort of connection between South America and the Old World must have existed in the early Tertiary. This might have been by way of North America and the well-attested Paleocene-Eocene North Atlantic land bridge between North America and Western Europe as suggested by HOCH (1983). Several mammalian groups (condylarths, didelphid marsupials and notoungulates) certainly managed to make the crossing between North and South America in the Late Cretaceous or Paleocene. However, no trace of either ratites nor of any of the Neotropic groups found in Europe have been recorded in the rich and well-researched North American Tertiary faunas.

It therefore seems that some dispersal across the South Atlantic must have been possible early in the Tertiary. This may have taken the form of an sweepstake route across a partially emergent Walvis ridge-Rio Grande Rise (BUFFETAUT 1982) or by way of now submerged islands in the still relatively narrow strait between Liberia and Northeast Brazil (AXELROD & RAVEN 1978). No direct evidence for such a route has been found in Africa except for a ziphodont crocodile from the Eocene of Algeria (BUFFETAUT 1982) but this lack of evidence is not surprising considering the paucity of African Paleogene land vertebrate faunas.

If such a route allowed dispersal of the ostrich-rhea lineage from South America to Africa (and from there across the closing Tethys into Eurasia), the timetable for the evolution and isolation of the ratite lineages becomes much more reasonable. The first

part of Gondwana to become isolated was then probably New Zealand which was split off from Australia-Antarctica by the Maastrichtian or earlier (FLEMING 1979). India and Madagascar probably also had parted from each other and Antarctica before the end of the Cretaceous, but probably not much earlier given the similarities of the Late Cretaceous dinosaur faunas of South America, Madagascar and India. Finally Australia separated from Antarctica in the early Eocene while the find of an polydolopid marsupial of South American affinities in the Late Eocene of West Antarctica (WOODBURN & ZINSMEISTER 1982) shows that some dispersal across the Drake passage was still possible in the Early Tertiary.

This sequence of events means that the ratite lineages in the various Gondwanaland fragments would have become isolated from each other over a period ranging perhaps from the Campanian to the Early Eocene (80–50 Ma) with the New Zealand and Madagascar forms being isolated first. This fits fairly well with current views of ratite relationships (e.g. CRACRAFT 1973, RICH 1980).

The biogeographic arguments for the antiquity of ratites can be extended to some other avian groups with similar Transantarctic, "Gondwanan" relationships. The most persuasive cases are the Caprimulgiforms, the suboscine passerines (FEDUCCIA & OLSON 1982, SIBLEY, WILLIAMS & AHLQUIST 1982) and some Gruiform and Charadriiform families (CRACRAFT 1973 b, 1982 a, OLSON & STEADMAN 1982). A "Gondwanan" origin and dispersal has been argued for several other groups including doves, parrots and cuckoos (CRACRAFT 1973 b) but the evidence in these cases is flimsy. As a matter of fact the relative rarity of clear transantarctic relationships among birds compared to groups such as plants and insects could be used as an argument for the relatively low age of many avian lineages.

The inevitable blurring of biogeographic patterns among such mobile organisms as birds also limits the usefulness of biogeographic data for the reconstruction of avian phylogenies.

Summary

A study of paleoecological conditions shows that at the beginning of the Cretaceous period the range of ecological niches available to birds was quite limited while at the end of the period it was roughly similar to present conditions. The best known Cretaceous birds are two orders of marine toothed birds, Hesperornithiformes and Ichthyornithiformes. The fossil record and probable life-styles of both orders is reviewed. Neither order was probably closely related to any modern birds. It seems likely that both became extinct at the Cretaceous-Tertiary boundary and were replaced by unrelated birds who adapted to marine conditions during an Early Tertiary adaptive radiation. The Cretaceous record of forms ancestral to extant birds is very sparse and largely restricted to a few Late Cretaceous charadriiforms. There is also an possible ancestor to coraciiforms and piciforms (*Alexornis*) and some possible pelecaniiforms and gruiforms. In addition to the birds attested through fossils some other groups may be inferred to have existed in the Late Cretaceous through Paleogene fossils or biogeographic considerations. The latter applies to groups with a southern "Gondwanan" distribution, in particular if transantarctic relations are indicated e.g. the ratites.

Zusammenfassung

Die Vögel der Kreidezeit – eine kurze Übersicht über die erste Hälfte der Geschichte der Vögel

Die Ergebnisse der palökologischen Forschungen lassen darauf schließen, daß zu Beginn der Kreidezeit die für Vögel nutzbaren ökologischen Nischen in noch recht geringem Umfang zur Verfügung standen. Gegen Ende der Kreidezeit hingegen entsprachen die Lebensbedingungen in etwa den heutigen Verhältnissen.

Die bestbekannten Vögel der Kreidezeit gehören zu den beiden marinen Ordnungen der Hesperornithiformes und Ichthyornithiformes. Beide Gruppen besaßen Zähne („Zahnvögel“). In ihrer Lebensweise ähnelten sie flugunfähigen Meeresvögeln, etwa den großen Pinguinen oder Alken. Ihre Vorkommen, zumindest an den Brutplätzen, scheinen auf Gebiete beschränkt gewesen zu sein, in denen es keine Raubtiere gab (Bodenfeinde): Inseln abgelegener Meeresküsten der borealen Bereiche. Die Bruten fanden wahrscheinlich auf flachem Untergrund statt. Die fossilen Belege und weitere Aspekte ihres Lebensstiles werden diskutiert, soweit die verfügbaren Befunde dies zulassen. Keine der beiden Ordnungen stellt einen Vorläufer heutiger Vögel dar.

An der Grenze von der Kreide zum Tertiär starben diese Vögel, wie so viele andere größere Organismen auch, ganz plötzlich aus. Sie wurden durch nicht näher verwandte Formen in der weiteren Evolution der Vögel ersetzt. Die Ursache dieses abrupten Verschwindens war möglicherweise der Einschlag eines Riesenmeteoriten von etwa 10 km Durchmesser. Die dabei freigesetzten Staubmengen verminderten die Einstrahlung von Sonnenlicht so sehr, daß große Teile der Landvegetation und fast das gesamte pflanzliche Plankton im Meer abstarben. Diese Unterbrechung der Nahrungsketten wurde den größeren Tierarten zum Verhängnis: Die Dinosaurier starben bis auf wenige kleine Gruppen ebenso aus, wie große Tintenfische im Meer – und die großen Vögel der Kreidezeit, die die doppelte Größe eines Eistauchers erreicht hatten.

Dieses Freiwerden von ökologischen Nischen setzte die Vorbedingungen für den weiteren Weg der Evolution der Vögel, der Säugetiere und der Reptilien. Besonders die Säugetiere gewannen rasch an Boden und entfalteten eine große Anpassungsvielfalt. Ähnlich starke Evolutionsprozesse waren bei den Vögeln festzustellen.

Die fossilen Funde zu den aus der Kreidezeit stammenden Vorfahren moderner Vogelgruppen sind recht spärlich und hauptsächlich – vielleicht aus ökologischen Gründen – beschränkt auf die Regenpfeiferartigen (Charadriiformes). Die Gattung *Alexornis* stellt vielleicht einen Vorläufer der Racken (Coraciiformes) und Spechte (Piciformes), zweier nahe miteinander verwandter Ordnungen, dar. Auch Vorläufer von Ruderfüßern (Pelecaniformes) und Kranichen (Gruiformes) liegen möglicherweise bereits vor. Neben diesen mehr oder weniger sicheren Nachweisen von Ausgangsformen heutiger Vogelordnungen müssen weitere Gruppen aufgrund der tiergeographischen Gegebenheiten als existent in der späten Kreidezeit angenommen werden. Für die wahrscheinlich stammesgeschichtlich einheitliche (monophyletische) Gruppe der Flachbrustvögel (Ratites) mit einer typisch „südlichen“ Verbreitung über die Teile des Riesenkontinents Gondwanaland werden Landverbindungen „trans-antarktischer“ Natur gefordert. Eine Ausbreitung in die Südkontinente über die Nordkontinente erscheint wenig wahrscheinlich.

Insgesamt gibt die „erste Hälfte“ der Evolution der Vögel viele Rätsel auf, so daß die engeren Zusammenhänge zwischen den einzelnen Vogelordnungen und ihre genaueren evolutionären Wege noch reichlich unbekannt bleiben. Immerhin wird angenommen, daß gegen Ende der Kreidezeit bereits etwa 2 000 Vogelarten in 40 Familien existierten; eine Vielfalt, die fast einem Viertel des heutigen Wertes entsprechen würde.

Literatur

- ALVAREZ, L. W., ALVAREZ W., ASARO, F. & MICHAEL, H. V. (1980): Extraterrestrial Cause for the Cretaceous-Tertiary Extinctions. *Science* 208: 1095–1108.
- AXELROD, D. I. & RAVEN P. H. (1978): Late Cretaceous and Tertiary vegetation history of Africa. WERGER, M. J. A. (Ed). *Biogeography and Ecology of Southern Africa*: 77–130. The Hague.
- BAIRD, D. (1967): Age of fossil birds from the greensands of New Jersey. *Auk* 84: 260–262.
- BARDACK, D. (1968): Fossile vertebrates from the Marine Cretaceous of Manitoba. *Can. J. Earth Sci.* 5: 145–153.
- BRODKORB, P. (1963 a): Birds from the upper Cretaceous of Wyoming. *Proc. XIII Intern. Ornithol. Congr.*: 55–70.
- — (1963 b): Catalogue of fossil birds. Part 1. (Archaeopterygiformes through Ardeiformes). *Bull. Fla. State Mus.* 7: 179–293.
- — (1967): Catalogue of fossil birds. Part 3. Ralliformes, Ichthyornithiformes, Charadriiformes. *Bull. Fla. State Mus.* 11: 99–220.
- — (1971): Origin and Evolution of Birds. *Avian Biology*: 19–55.
- — (1976): Discovery of a Cretaceous bird, apparently ancestral to the Orders Coraciiformes and Piciformes (Aves. Carinatae). *Smithson. Contrib. to Paleobiology* 27: 67–73.
- — (1978): Catalogue of fossil birds. Part 5 (Passeriformes). *Bull. Fla. State Mus.* 23(3): 139–228.
- BUFFETAUT, E. (1980): Histoire biogéographique des Sebecosuchia (Crocodylia, Mesosuchia): un essai d'interprétation. *Ann. Paleont., (Vert.)*, 66: 1–18.
- — (1982): A ziphodont mesosuchian crocodile from the Eocene of Algeria and its implications for vertebrate dispersal. *Nature* 300: 176–178.
- CONDAL, L. F. (1955): Notice préliminaire concernant la présence d'une plume d'Oiseau dans le Jurassique Supérieur du Montsec (Province de Lerida, Espagne). *Proc. XI Intern. Ornithol. Congr.*: 268–269.
- CRACRAFT, J. (1971): Caenagnathiformes: Cretaceous birds convergent in jaw mechanism to dicyonodont reptiles. *Journal of Paleontology* 45(5): 805–809.
- — (1972): A new Cretaceous Charadriiform family. *Auk* 89: 36–46.
- — (1973 a): Systematics and Evolution of the Gruiformes (Class Aves). 3. Phylogeny of the suborder Grues. *Bulletin of the American Museum of Natural History* Vol 151: Article 1.
- — (1973 b): Continental drift, paleoclimatology, and the evolution and biogeography of birds. *J. Zool. Lond.* 169: 455–545.
- — (1974): Phylogeny and evolution of the ratite birds. *Ibis* 115: 494–521.
- — (1982 a): Phylogenetic relationships and transantarctic biogeography of some gruiform birds. *Geobios Spec. Mem.* 6: 25–36.
- — (1982 b): Phylogenetic relationships and monophyly of Loons, Grebes and Hesperornithiform birds, with comments on the early history of birds. *Syst. Zool.* 31(1): 35–56.
- CURRIE, P. J. (1981): Bird footprints from the Gething Formation (Aptian, Lower Cretaceous) of northeastern British Columbia, Canada. *J. Vertebr. Paleontol.* 1(3/4): 257–264.
- DOYLE, J. A. & HICKEY, L. J. (1976): Pollen and leaves from the mid-Cretaceous Potomac group and their bearing on early angiosperm evolution. BECK C. B. (ed). *Origin and Early evolution of Angiosperms*: 139–206. New York.
- ELZANOWSKI, A. (1974): Preliminary Note on the Paleognathous Bird from the Upper Cretaceous of Mongolia. *Paleont. Polonica* 30: 103–109.
- — (1976): Paleognathous bird from the Cretaceous of Central Asia. *Nature* 264: 51–53.
- — (1977): Skulls of *Gobiapteryx* (Aves) from the Upper Cretaceous of Mongolia. *Paleont. Polonica* 37: 153–165.
- — (1981): Embryonic bird skeletons from the Late Cretaceous of Mongolia. *Paleont. Polonica* 42: 147–179.

- FEDUCCIA, A. (1980): The Age of Birds. Cambridge, Mass.
- FEDUCCIA, A. & OLSON, S. L. (1982): Morphological similarities between the Menurae and the Rhinocryptidae, relict passerine birds of the southern hemisphere. *Smithson. Contrib. Zool.* 366: 1–22.
- FISHER, J. (1967): Fossil birds and their adaptive radiation. *The Fossil Record*: 133–154, 733–762. Geological Society of London.
- FJELDÅ, J. (1976): The Systematic affinities of Sandgrouse, Pteroclididae. *Vidensk. Medd. naturh. Foren.* 139: 179–243.
- FLEMING, C. A. (1979): The Geological History of New Zealand and its life. Auckland.
- FOX, R. C. (1974): A Middle Campanian, Nonmarine Occurrence of the Cretaceous Toothed Bird *Hesperornis* Marsh. *Can. J. Earth Sci.* 11: 1335–1338.
- FRAKES, L. A. (1979): Climates throughout Geologic Time. Amsterdam.
- GINGERICH, P. D. (1973): Skull of *Hesperornis* and the early evolution of birds. *Nature* 243: 70–73.
- — (1976): Evolutionary significance of the Mesozoic toothed birds. *Smithson. Contrib. to Paleobiology* 27: 23–33.
- GREGORY, J. T. (1952): The Jaws of the Cretaceous toothed birds *Ichthyornis* and *Hesperornis*. *Condor* 54: 73–88.
- GRIGORESCU, D. & KESSLER, E. (1980): A new specimen of *Elopteryx nopsai* Andrews from the dinosaurian beds of Hateg Basin. *Revue Roum. Geol. Geophys. Geogr. (Se Geol)* 24: 171–175.
- HARLAND, W. B., COX, A. V., LLEWELLYN, P. G., PICKTON, C. A. G., SMITH, A. G. & WALTERS, R. (1982): A geologic time scale. Cambridge.
- HARRISON, C. J. O. & WALKER C. A. (1973): *Wyleyia*: a new bird humerus from the Lowerer Cretaceous of England. *Palaeontology* 16: 721–728.
- — (1975): The Bradynemidae, a new family of owls from the Upper Cretaceous Romania. *Palaeontology* 18: 565–566.
- HATTON, N. III (1980): An alternative to dinosaur endothermy, the happy wanderers. *Am. Assoc. Adv. Sci. Selected Symposium* 28: 311–350.
- HOCH, E. (1983): Fossil evidence of Early Tertiary North Atlantic events viewed in European context. BOTT et al (eds). *Structure and Development of the Greenland-Scotland Ridge*: 401–415.
- HOUDE, P. & OLSON, S. L. (1981): Paleognathous carinate birds from the Early Tertiary of North America. *Science* 241: 1236–1237.
- HOWARTH, M. K. (1981): Paleogeography of the Mesozoic. COCKS L. R. M. (ed). *The Evolving Earth*: 197–220. Cambridge.
- HSÜ, K. J. et al (1982): Mass mortality and its environmental and evolutionary consequences. *Science* 216: 249–256.
- HUGHES, N. F. (1976): *Paleobiology of Angiosperm Origins*. Cambridge.
- HUXLEY, T. H. (1867): On the Classification of the Birds; and on the Taxonomic value of the Modification of Certain of the Cranial Bones observable in that Class. *Proc. of the Zoological Society of London* 1867: 415–472.
- LAMBRECHT, K. (1933): *Handbuch der Paleornithologie*. Berlin.
- LLOYD, C. L. (1982): The Mid-Cretaceous Earth. *Journal of Geology* 90: 393–413.
- MARSH, O. C. (1880): *Odontornithes*. a monograph on the extinct toothed birds of North America. Report of the U. S. Geological Exploration of the Fortieth Parallel No 7 Washington D. C.
- — (1881): Discovery of a fossil bird in the Jurassic of Wyoming. *Amer. J. Sci.* (3)21: 341–342.
- MARTIN, L. D. (1980): Foot-Propelled Diving Birds of the Mesozoic. *Proc. XVII Intern. Ornith. Congr.* (II): 1237–1242.
- MARTIN, L. D. & BONNER, O. (1977): An immature specimen of *Baptornis advenus* from the Cretaceous of Kansas. *Auk* 94: 787–789.
- MARTIN, L. D. & STEWART, J. D. (1977): Teeth in *Ichthyornis* (Class: Aves). *Science* 195: 1331–1332.

- — (1982): An ichthyornithiform bird from the Campanian of Canada. *Can. J. Earth Sci.* 19 (2): 324–327.
- MARTIN, L. D. & TATE JR, J. (1967): A *Hesperornis* from the Pierre shale. *Proc. Nebraska Acad. of Science* 77: 49.
- — (1969): New information on *Baptornis advenus*. *Proc. Nebraska Acad. of Science* 79: 49–50.
- — (1976): The Skeleton of *Baptornis advenus* (Aves. Hesperornithiformes). *Smithson. Contrib. to Paleobiology* 27: 35–66.
- McELHINNY, M. W. (1973): *Paleomagnetism and Plate Tectonics*. Cambridge.
- MEHL, M. G. (1931): Additions to the vertebrate record of the Dakota sandstone. *Am. J. Sci.* 21: 441–452.
- MOLNAR, R. E. & THULBORN, R. A. (1980): First pterosaur from Australia. *Nature* 288: 361–363.
- MOURER-CHAUVIRÉ, C. (1981): Première indication de la presence de phorusracidés, famille d'oiseaux géants d'Amerique du sud, dans le Tertiaire Européen: *Ameghinornis* nov. gen. (Aves, Ralliformes) des phosphorites de Quercy, France. *Geobios (Lyon)* 14 (5): 637–648.
- OLSON, S. L. (1975): *Ichthyornis* in the Cretaceous of Alabama. *The Wilson Bulletin* 87: 103–105.
- — (1977): A lower Eocene frigatebird from the Green River Formation of Wyoming (Pelecaniformes. Frigatidae). *Smithson. Contrib. to Paleobiology* 35: 1–33.
- OLSON, S. L. & FEDUCCIA, A. (1980a): Relationships and Evolution of Flamingos (Aves. Phoenicopteridae). *Smithson. Contrib. to Zool.* 316.
- — (1980b): *Presbyornis* and the Origin of the Anseriformes (Aves. Charadriomorphae). *Smithson. Contrib. to Zool.* 323.
- OLSON, S. L. & STEADMAN, O. W. (1981): The Relations of the Pedionomidae (Aves. Charadriiformes). *Smithson. Contrib. to Zool.* 337.
- RAUTIAN, A. S. (1978): Unikalnoe pero ptitsi iz otloshenii orskogo ozero u khrebte Karatau. *Paleontologicheskii zhurnal* 1978: 106–114.
- REYMENT, R. A. (1969): Ammonite stratigraphy, continental drift and oscillating transgressions. *Nature* 224: 137–140.
- RICH, P. V. (1974): Significance of the Tertiary Avifaunas from Africa (with emphasis on a Mid to Late Miocene Avifauna from Southern Tunisia). *Annals of the Geological Survey of Egypt* IV: 167–210.
- — (1976): The History of Birds on the Island Continent Australia. *Proc. XVI Intern. Ornith. Congr.*: 53–64.
- — (1979): The Dromornithidae, a family of large extinct ground birds endemic to Australia. *Canberra Bur. Min. Res. Bull.* 184: 1–196.
- — (1980): The Australian Dromornithidae: A group of extinct large Ratites. *Contrib. Sci. Natur. Hist. Mus. Los Angeles County* 330: 93–103.
- RUSSELL, D. A. (1967): Cretaceous Vertebrates from the Andersson River N. W. T. *Can. J. Earth Sci.* 4: 21–38.
- SIBLEY, C. G., WILLIAMS, G. R. & AHLQUIST, J. E. (1982): The relationships of the New Zealand Wrens (Acanthisittidae) as indicated by DNA-DNA hybridization. *Notornis* 29: 113–130.
- SAUER, E. G. F. (1979): A Miocene Ostrich from Anatolia. *Ibis* 121: 494–501.
- SMILEY, C. J. (1966): Cretaceous Floras from the Kuk River Area. *Stratigraphic and Climatic Interpretations*. *Geol. Soc. of America Bulletin* 77: 1–14.
- SMITH, A. G., HURLEY, A. M. & BRIDEN, J. G. (1981): *Phanerozoic paleocontinental world maps*. Cambridge.
- SNOW, D. W. (1976). *The Web of Adaption*. New York.
- — (1981): Coevolution of birds and plants. FOREY, P. L. (ed). *The Evolving Biosphere*: 169–178. Cambridge.
- STEEL, R. (1979): Cretaceous. STEEL, R. & HARVEY, A. (ed). *The Encyclopedia of Prehistoric Life*: 50–52, London.

- STEGMANN, B. C. (1978): Relationships of the Superorders Alektoromorphae and Charadriomorphae (Aves). A comparative study of the Avian Hand. Publ. of the Nuttall Ornithological Club No 17. Cambridge, Masse.
- STERNBERG, R. M. (1940): A toothless bird from the Cretaceous of Alberta. *Journal of Paleontology* 14: 81–85.
- STORCH, G. (1981): *Eurotamandua joresi*, ein Myrmecophagid aus den Eozän der „Grube Messel“ bei Darmstadt (Mammalia, Xenarthra). *Senckenberg. leth.* 61: 247–289.
- TALENT, J., DUNCAN, P. & HARDY, P. (1966): Early Cretaceous Feathers from Victoria. *Emu* 64: 81–86.
- TONNI, E. P. (1980): The present state of knowledge of the Cenozoic birds of Argentina. *Contrib. Sci. Natur. Hist. Mus. Los Angeles County* 330: 105–114.
- VAIL, P. R., MITCHUM, J. R. M. & THOMPSON, S., III (1977): Global cycles of relative changes of sea level. *Am. Assoc. Pet. Geol. Mem.* 26: 83–97.
- WALDMAN, M. (1970): A third Specimen of a lower Cretaceous feather from Victoria, Australia. *Condor* 72: 377.
- WALKER, C. A. (1978): Hesperornithiformes. HARRISON, C. J. O. (ed) *Bird families of the world*: 15–17. Oxford.
- — (1981): New subclass of birds from the Cretaceous of South America. *Nature* 290: 51–52.
- WOODBURNE, M. O. & ZINSMEISTER, W. J. (1982): Fossil land mammal from Antarctica. *Science* 218: 284–286.

Author's address:

Tommy Tyrberg, Kimstadsvägen 37,
S-61020 Kimstad, Schweden

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Verhandlungen der Ornithologischen Gesellschaft in Bayern](#)

Jahr/Year: 1986

Band/Volume: [24_2-3_1984](#)

Autor(en)/Author(s): Tyrberg Tommy

Artikel/Article: [Cretaceous Birds - a short review of the first half of avian history 249-275](#)