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BIRDS IN CRETACEOUS ECOSYSTEMS

ELŻANOWSKI, A.: Birds in Cretaceous Ecosystems. Acta Palaeont. Polonica, 28, 1—2, 75—92, 1983.

At least three ecological types are distinguished among the known Cretaceous birds: piscivores, shore birds and terrestrial birds. Striking rarity of terrestrial birds is considered as a special case of the rarity of smaller (1—10 kg) among the medium-sized vertebrate specimens in the Cretaceous record. This is probably caused, *inter alia*, by reptilian scavengers which swallow food items as large as possible, and decalcify bones completely or nearly so. Therefore, the smallest chance for preservation would be for those animals which are small enough to be swallowed whole and large enough to be well detectable and/or accessible. The great abundance of large and flightless piscivorous birds (Hesperornithes) in the warm seas of Western Interior contrasts with the lack of comparable forms in the Cenozoic warm seas. The extinction of toothed birds may have been caused by the explosive radiation of acanthopterygian fishes.

Key words: birds, Cretaceous, extinction, Hesperornithes, Ichthyornithes, marine communities, Mesozoic, North America, palaeoecology, scavenging, taphonomy, vertebrates.

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INTRODUCTION

Twenty three valid genera, including forty one species, have been established for the Cretaceous avian fossils. Undescribed or unnamed material of which I am aware, contains about seven genera with sixteen species, including new hesperornithiforms announced by Martin (1980) and the Enantiornithes described by Walker (1981). Thus the approximate total number of fossil genera known from Cretaceous deposits would be thirty.

Within the Cretaceous, the oldest avian fossils are isolated feathers coming from two remote areas of the world: Australia (Victoria) and Lebanon. The four Australian feathers (Rich 1976) come from the lacustrine claystones of Korumburra Group, now considered to be of Kimmeridgian to Albian (or later) date (Molnar 1980). The Lebanese feathers

(several fragments) were found in the amber of Hauterivian age (Schlee 1973). These finds indicate a worldwide distribution of birds by the early Cretaceous (Talent *et al.* 1966; Brodkorb 1971) unless feathers occurred in some archosaurs, close to the avian ancestry, as has been suggested (Jensen 1969).

Preserved in the Cretaceous beds are also footprints of birds. The oldest of them, named *Aquatilavipes swiboldi*, are of Aptian age and come from the deltaic Gething Formation, British Columbia, Canada (Currie 1982); they resemble the footprints of modern shorebirds, although this does not substantiate an ordinal allocation to the Charadriiformes as the describer did. Much younger tracks, also referred tentatively to Charadriiformes, were reported from the Maestrichtian Coli Toro Formation, Patagonia (Casamiquela 1980). Quite different avian footprints, having the impression of hallux and named *Ignotornis mcconnelli*, come from the Cenomanian sea shoreline deposits of the Dakota Sandstone, Colorado (Mehl 1931).

Besides feathers and footprints, the lower Cretaceous beds yielded only three genera of birds. Oldest of them, *Gallornis* and *Wyleyia*, do not reveal any trait that would be indicative of their habitats, *Gallornis straeleni* Lambrecht, coming from undetermined Neocomian beds of France (Department Yonne, Auxerre), is based on the proximal end of femur, which does not allow for any reliable assignment. *Wyleyia valdensis* was based on a single humerus from Weald Clay of England (Harrison and Walker 1973). Despite Brodkorb's (1978) statement that it is "almost certainly a reptilian humerus", the avian nature of *Wyleyia* is corroborated by comparison with Mongolian birds (Elzanowski 1981). The third early Cretaceous genus is *Enaliornis*, with two species described from the Upper Greensand of Albian age, England; they were foot-propelled divers, probably the oldest known hesperornithiforms (Martin and Tate 1976). The Albian occurrence of such a specialized form shows that birds had strongly diversified in the early Cretaceous. Moreover, the Albian marine limestones of the Toolebuc Formation, Queensland, Australia, yielded a small (length of centrum: 3.5 mm) vertebra which shows general similarities to the cervical vertebrae of *Ichthyornis* (pers. obs. based on the photographs furnished by R. Molnar, Queensland Museum) and thus appears to be avian.

Late Cretaceous birds come mostly from marine or non-marine coastal deposits. Among a dozen of pre-Maestrichtian formations the most prolific have been those of the Western Interior basin in North America (see below). Also the Maestrichtian birds are known mostly from North America: from coastal plain deposits of the formations Lance, Wyoming, and Hell Creek, Montana; and seashore deposits of the formations Navesink and Hornerstown, both New Jersey. In Europe, the only Maestrichtian bird fossils come from the coastal plain deposits of the Hatég (Hatszég)

Table 1

Cretaceous genera of birds and their stratigraphic ranges

Stage / Genus		Subclass or order
Maestrichtian	<i>Wyleya</i>	—
Santonian	<i>Gobipteryx</i>	GOBIPTERYGIFORMES
Maestrichtian		ENANTIORNITHES
Turonian	<i>Ichthyornis</i>	ICHTHYORNITHES
Coniacian	<i>Apatornis</i>	?
Albian	<i>Enaliornis</i>	HESPERORNITHES
Coniacian	<i>Hesperornis</i>	
Coniacian	<i>Baptornis</i>	
Maestrichtian	<i>Neogaeornis</i>	
Maestrichtian	<i>Torotix</i>	?
Maestrichtian	<i>Lonchodytes</i>	CHARADRIIFORMES
Maestrichtian	<i>Cimolopteryx</i>	
Maestrichtian	<i>Palintropus</i>	
Maestrichtian	<i>Ceramornis</i>	
Maestrichtian	<i>Palaeotringa</i>	
Maestrichtian	<i>Telmatornis</i>	?
Maestrichtian	<i>Elopteryx</i>	?PELECANIFORMES
Maestrichtian	<i>Graculavus</i>	
Campanian	<i>Alexornis</i>	ALEXORNITHIFORMES
Valanginian	<i>Gallornis</i>	NO EVIDENCE FOR SYSTEMATIC PLACEMENT
Maestrichtian	<i>Laornis</i> *	
Santonian	<i>Parascaniornis</i>	

* Olson (1974) suggested that *Laornis* belongs with the suborder Lari of the Charadriiformes.

Basin, Romania (Grigorescu and Kessler 1980). True continental deposits with fossil birds are extremely scarce and represented only by the Santonian or Campanian Barun Goyot Formation, Mongolia (Gradziński and Jerzykiewicz 1974), and the ?Maestrichtian Lecho Formation, Argentina (Bonaparte and Powell 1980).

Recent discoveries brought about a profound change of views on the Cretaceous avifauna. Until now, only the toothed birds have been allowed, because of compelling evidence, to be primitive and not typically avian in all characters. Other avian fossils (as *Wyleyia* or *Gobipteryx*) have been either rejected as reptilian (Brodkorb 1978), but without showing similarities to any known group of reptiles, or included into modern taxa on the basis of more or less remote resemblances. Fortunately it has been recently shown that the affinities of Mesozoic (and even early Tertiary) birds are impossible to determine by small fragments (Olson and Feduccia 1980a) and, as in the case of leaves of Cretaceous plants, the placement of many fragmentary fossils of Cretaceous birds into modern taxa is unwarranted. A sceptical look at the earliest record leaves the Charadriiformes as the only recent group that is well evidenced in the Cretaceous (Feduccia 1980). Although this picture is certainly biased and several groups of modern birds have in all probability existed in continental areas (see below), the recent studies have demonstrated a great share of archaic (or aberrant) forms (*Wyleyia*, *Gobipteryx*, Enantiornithes, Ichthyornithes, Hesperornithes) in the Cretaceous avifauna.

ECOLOGICAL TYPES

At least three ecological types can be broadly defined among the described Cretaceous birds:

1. Piscivorous birds represented by seven (two undescribed) genera of Hesperornithes (see below) and two genera of Ichthyornithes (see below). Also two Maestrichtian genera may fall into this category whether or not they were correctly placed among the Pelecaniformes: *Elopteryx* from the Hațeg (Hatszég) Basin, Romania, and *Graculavus*, with two species from the Hornerstown Formation, New Jersey.

2. Shore birds represented by five genera of charadriiform birds, including *Lonchodytes* (Olson and Feduccia 1980a). *Telmatornis* may also belong to this category (Cracraft 1972). All they come from the Maestrichtian formations of North America: Lance (*Cimolopteryx*, *Palintropus*, *Ceramornis*, *Lonchodytes*); Hell Creek (*Cimolopteryx*), Navesink (*Palaeotringa*, *Telmatornis*) and Hornerstown (*Telmatornis*).

3. Terrestrial birds represented by *Gobipteryx* from the Barun Goyot Formation, Mongolia (Elżanowski 1977), and possibly also the Enantiornithes, described by Walker (1981) from Lecho Formation, Argentina. *Gobipteryx* has a robust, toothless beak, with strong edges, suggestive

of feeding on rather hard and easily available objects. Several embryonic skeletons, found in beds equivalent to Barun Goyot Formation, probably also belong to this genus (Elżanowski 1981).

Birds representing at least three other ecological types have been claimed to be found in the Cretaceous record. The flamingos, representing filter-feeding waders, became renowned for the antiquity of their alleged relatives, but this is probably a myth created by palaeornithologists (Feduccia 1980); the earliest unequivocal flamingo, based on sufficient material, is *Juncitarsus* from the middle Eocene (Olson and Feduccia 1980a) and the oldest known filter-feeding wader is *Presbyornis pervetus* from the early Eocene (Olson and Feduccia 1980b). However, filter-feeding waders might have arisen at earlier date and the Eocene *Presbyornis* may be a temporal relic (Feduccia 1977).

Harrison and Walker (1975) assigned to the owls (Strigiformes) two large tibiotarsi from the Haţeg Basin, Romania. However, the strigiform resemblances are inferred rather than visible and the bones do not warrant to be avian either (Brodkorb 1978).

Brodkorb (1976) described *Alexornis antecedens* from the (!)marine Bocana Roja Formation (Mexico) as a hypothetical ancestor of Piciformes and Coraciiformes. Seven fragments of postcranial bones display twenty characters, which are unique to *Alexornis*, and twenty one characters which are shared (or agreeing) with either Momotidae or Bucconidae, or both. The most striking among the unique characters is the transverse position of the external condyle of humerus, which approaches in this respect the condition found in Enantiornithes (Walker 1981). In functional terms, a transverse orientation of the external condyle suggests that the automatic flexion of the manus (as coupled with the humeroulnar flexion) was weak or nonexistent, which would be unusual among arboreal birds. These may have come into existence during late Cretaceous but we have no firm evidence for their occurrence prior to the Eocene.

Conspicuously lacking in the Cretaceous record are diurnal raptors, herons (fish-eating waders) and ducks which are all mainly and primarily continental birds. Therefore some uncertainty remains about the possibility of their Cretaceous existence. Both ducks and herons are apparently very likely to be preserved but the Cretaceous record of continental birds may be extremely biased. The oldest anseriform birds (Romainvillinae and other small forms) and herons are mentioned from the late Paleocene of central Asia (Kurochkin 1976).

SEA BIRDS

Almost all marine birds known from the Cretaceous are the toothed birds, Ichthyornithes and Hesperornithes. By the end of Cretaceous the marine habitat may have been also exploited by the modern flying birds,

as suggested by the Maestrichtian occurrence of *Elopteryx* and *Graculavus* in coastal plain deposits; and the beaches were certainly frequented by shorebirds.

The toothed birds come predominantly almost exclusively from the region of Western Interior seaway (or basin), which supported a rich assemblage of fishes (mostly predatory) and other fish-eating vertebrates including the abundant birds. The vertebrate fauna contrasts with the invertebrate assemblages which are clearly impoverished as compared to those of fully marine deposits, and several large groups are lacking altogether; this is interpreted as evidence for special environmental conditions (Miller 1968; Kauffman 1977), not yet fully understood (?low salinity, ?oxygen shortage). On the other hand, the Hesperornithes at least are not likely to have been common in other seas since their solid bones and teeth, like those of cosmopolitan mosasaurs, would be certainly noticed. It appears therefore not unlikely that the toothed birds were attracted by opportunities of the epicontinental sea from inland waters where they had existed long before. After all, birds adapted probably first to inland waters and only thereafter some of them could invade seas.

Both the Ichthyornithes and Hesperornithes certainly fed largely on fishes; one of the coprolites referable to *Baptornis*, contained a jaw of the salmoniform fish *Enchodus* (Martin and Tate 1976). An additional source of food may have been provided by cephalopods, especially the squids which are not rare in the Smoky Hill Member of the Niobrara Formation (Miller 1968); squids constitute an important source of food for the modern sea bird communities (Ashmole and Ashmole 1967).

The Ichthyornithes are known only from the marine deposits of the southern half of North America (fig. 1), mostly from the Niobrara Formation, Kansas. *Ichthyornis* is being commonly compared with a tern, what may suggest catching of prey by surface plunging or dipping (Ashmole 1971). This comparison, however tempting as it is, may be misleading (e.g. in restoration of feeding habits) since the osteology of flight apparatus of *Ichthyornis* is very different from that of any modern bird and the differences are not understood functionally; if the flight was as different as the morphology is, this comparison would be hardly tenable.

Apatornis celer, known from a few remains from the Niobrara Formation, is usually placed in the Ichthyornithes, but it needs restudy (Brodkorb 1971). Howard (1955) noticed that "the available elements of *Apatornis* are so different from those of its famous contemporary [*Ichthyornis*] that it is entirely possible that the two are members of distinct orders".

The Hesperornithes include six late Cretaceous genera (*Hesperornis*, *Coniornis*, *Baptornis*, *Neogaeornis* and two undescribed) and probably also the Albian genus *Enaliornis* (Martin and Tate 1976, Martin 1980).

Except for *Neogaeornis* known from a single bone (tarsometatarsus)



Fig. 1. Records of *Hesperornis* (1—7, circles) and *Ichthyornis* (7—10, triangles). (1) **Ignek Formation**, Alaska: one specimen, species indeterminate (M. Brett-Surman and Laurie McDonald, pers. comm.). (2) **"Brown Beds"** Northwest Territories: remains of 10 individuals of *H. regalis* (Russell 1967). (3) **Foremost Formation**, Alberta: one specimen of *H. cf. regalis* (Fox 1974). (4) **Vermilion Formation**, Boyne and Pembina members, Manitoba: four specimens of *H. regalis* (Bardack 1968). (5) **Claggett Formation** (the upper part) or **Judith River Formation** (the basal part), Montana: two specimens of *Coniornis altus* which is recently considered to be congeneric with *Hesperornis* (Fox 1974, Martin 1980). (6) **Pierre Shale** (the lower part), South Dakota: possibly as many as four species, one of them including all larger, *regalis*-sized forms (Martin 1980). (7) **Niobrara Formation**, Smoky Hill Member, Kansas: *Hesperornis*: instead of the three species described by Marsh there are probably only two, *H. regalis* including all large forms and an undescribed species including smaller forms (Martin 1980); by the time of Lambrecht (1933) the Yale collections included the remains of about 50 individuals referred to *H. regalis* and *H. crassipes*. *Ichthyornis*: the minimum number of individuals, as inferred from Marsh's (1980) monograph, is fifty seven; they are referred to as many as six (!) species (Brodkorb 1967). (8) **Carlile Formation** (base) or **Greenhorn Formation** (top), Kansas: one specimen, species indeterminate (Walker 1967). (9) **Austin Chalk**, Texas: one specimen referred to *I. lentus* (Brodkorb 1967). (10) **Selma Chalk**, Alabama: one specimen of *I. antecessor* (Olson 1975).

from the Quiriquina beds, Concepcion Province, Chile, all the Late Cretaceous Hesperornithes come from the western half of North America between Kansas and the latitude 69°N (fig. 1). The most common is the genus *Hesperornis*, reported to be especially abundant in the "Brown Beds" (Russell 1967) and the Vermilion River Formation (Bardack 1968). In the Niobrara Formation the relative abundance is lower but a high absolute number of specimens testifies that the birds were common in this area. The youngest *Hesperornis* fossils are those from the Campanian deposits of the Foremost Formation, Pierre Shale and Pembina Member of the Vermilion (Fox 1974). "Brown Beds" and the Boyne Member of the Vermilion are thought to be approximately isochronous to the Smoky Hill Member, which, according to Kauffman (1977), extends from the late Coniacian to the earliest Campanian.

Other hesperornithiforms from Niobrara Formation are *Baptornis advenus* known from more than ten individuals (Martin and Tate 1976) and two undescribed genera (Martin 1980). New nonmarine hesperornithiforms have been recently announced from the Maestrichtian deposits of South Dakota (Martin 1980).

The Hesperornithes covered a size range between larger grebes and largest living penguins. Like the penguins, they are good indicators of a high productivity of marine waters. The diving achievements of larger hesperornithiforms, as *Hesperornis regalis* or *Baptornis advenus*, must have been significantly greater than those of much smaller loons and diving ducks which are known to reach 55 m of depth (Kooyman 1975). Thus the larger hesperornithiforms could probably reach a bottom dwelling prey — at least in shallow areas like the Niobrara sea, which was presumably about 40 m deep during Smoky Hill Member deposition (Miller 1968).

In spite of being flightless, the Hesperornithes apparently had to co-exist with the isurid (*Isurus*, *Lamna*, *Squalicorax*) and carchariid (*Scaipanorhynchus*) sharks, as well as many large teleost predators (Lane 1944; Bardack 1968) including the huge *Xiphactinus audax*. It is therefore quite probable that for breeding and raising their young they had to seek protected sites in coastal areas (Fox 1974).

The abundance of great flightless and foot-propelled divers in the warm seas of the Cretaceous constitutes a striking difference in comparison with the Cenozoic seas. Tertiary seas supported only wing propelled divers which, with a minor exception of the Pliocene mancallas (Howard 1970) extending to the Baja California (Mexico), flourished mainly in the temperate seas; this applies first of all to the largest Tertiary penguins and pterosaurs which vanished in the Miocene, being probably displaced by porpoises and seals (Stonehouse 1969; Simpson 1975; Olson and Hasegawa 1979; Olson 1980). In the Quaternary seas the flightless wing propelled divers (penguins and auks) appear to have been

ousted toward the polar zones. The modern communities of sea birds in tropical and subtropical zones consist almost exclusively of terns, gulls, pelecaniforms and procellariiforms (Bourne 1963; Ashmole 1971), which are all good flyers. Most of them (especially the smaller ones) depend partly or entirely on schools of predatory fish, mainly tunas, to drive their prey closely to the surface and so make it available (Ashmole and Ashmole 1967). In tropical waters, the avian pursuit divers would probably find the food too deep or too scattered for economical hunting (Brown 1976) and, at the same time, would have to compete with large and swift perciform predators as the scombroids (including the tunas which are partly homeotherms!), the sphyraenids (including the barracudas) and several percoids. Thus, the rise of large perciform predators must have been of crucial importance for the evolution of sea bird communities.

It would be surprising if the profound change in the fish faunas towards the close of Cretaceous had no influence on the communities of piscivores. The acanthopterygians, which first appear in the Cenomanian, remained almost constant in numbers until the end of the period (Patterson 1964) and the fish faunas were strongly dominated by the lower teleosts; in the Niobrara Formation the only acanthopterygian fish is the small (7 cm long) *Kansius sternbergi*, a holocentrid berycoid (Patterson 1964). By the end of Cretaceous the lower teleosts succumbed to the pressure of competition from the beryciforms and their derivatives (Goody 1969) especially the perciforms which began to radiate into a great range of forms (Patterson 1964); large and swift predators have apparently arisen very early since the first tunas (*Palaeothunnus*) are known from the Paleocene (Bannikov 1978). Being well protected by specialized spines, the acanthopterygians, and especially the perciforms (Marshall 1971) owe their success to the radical improvement in locomotion, especially the manoeuvrability, and feeding techniques, and therefore their impact on the fish-eating birds and reptiles must have been twofold: the piscivores became subject to powerful competition and, at the same time, deprived of the usual prey they were adapted to feed on, since the lower teleosts (e.g. myctophoids) had been displaced to deeper sea layers (Marshall 1971). The explosive radiation of acanthopterygians appears thus to be an important factor of extinction of both the marine reptiles and toothed birds although the process may have involved also other factors and the disappearance of the Western Interior basin may have strongly reduced the populations of toothed birds.

Oelofsen (1978) extended on *Hesperornis* his elegant hypothesis of O_2/CO_2 imbalance as the cause of extinction of larger, homeothermic and oviparous vertebrates. Yet not all *Hesperornithes* were large and also the *Ichthyornithes* disappeared although they were small. On the other hand, small birds may be also affected by O_2/CO_2 imbalance if they

bury their eggs as do the recent megapodes. As usual, there are too much of possible extinction factors and the competing hypotheses are hardly verifiable.

TERRESTRIAL BIRDS

Aside from *Gobipteryx* and Enantiornithes, there are good reasons to believe that the terrestrial birds had been significantly diversified during the Cretaceous (Brodkorb 1971; Mayr 1976). The prime candidates for the Cretaceous ground-feeding birds are small flying ancestors of the modern palaeognathous birds which include the tinamous and ratites, and appear now what they were thought to be by Thomas H. Huxley i.e. the "waifs and strays" of an old (Cretaceous) radiation (Prager *et al.* 1976; Simpson 1980). Among modern birds the palaeognaths retained the most primitive characters in the structure of skull and pelvis as well as in the reproductive biology (Elżanowski in prep.). These characters, shared by small and flying tinamous, have nothing to do with either flightlessness or giantism, and the claim for their neotenic origin is a pure *ad hoc* hypothesis. The gruiform origin of the ostrich, recently postulated by Feduccia (1980) is unacceptable since the ostrich's palaeognathous characters, which conspicuously do not appear in any neognathous flightless bird, would be then unexplained. The present distribution of the palaeognaths also strongly suggests the Mesozoic occurrence of their ancestors which may be safely assumed to have been flying not better than do the tinamous and therefore unable to cross sea barriers (tinamous are apparently unable to colonize any neotropical island). Thus the hypothesis that the ratites are monophyletic and derived from a flightless ancestor, as stated recently by Cracraft (1974) and challenged by Feduccia (1980) is unnecessary to postulate the Mesozoic dispersal. Palaeognathous birds are remnants of a primitive grade of avian evolution characterized i.a. by a limited power of flight. Most similar to the ancestral palaeognaths are certainly the South American tinamous, which are short distance flyers, with a conspicuously deficient manoeuvrability. Tinamous are otherwise galliform in habits, appearance and structure of the postcranial skeleton (except for the pelvis).

Primitive galliforms are also very likely to have occurred in the Cretaceous. Cracraft (1973a, 1980) argues for the Gondwanian dispersal of the megapodiids and cracids, but Rich (1975) concluded that the Indomalayan and Antarctic routes are equally likely for the megapodes. Now the primitive position of the megapodes appears to be better substantiated (Prager and Wilson 1976), and especially their biology of reproduction, in spite of some specialized features, may have ancient origins (Elżanowski in prep.). If the megapodes are considerably older than the

phasiands which appeared in the Eocene, the Antarctic route remains the only plausible possibility, since Australia approached Asia only during the Eocene. Bearing in mind the galliform similarities of the tinamous, it is perhaps worth noting that Prager and Wilson (1976) suggested the galliform "phenotype" as one of the most primitive types among the neognathous terrestrial birds.

Birds of unquestionable gruiform-ralliform affinities are not known before the early Eocene, but they appear then in such a great diversity that Cracraft (1973b) was probably right in extending their ancestry to the Cretaceous. In any case the small cursorial ancestors of diatrymas, known from the Paleocene and commonly thought to be of gruiform affinities, have been in all probability present in the Cretaceous.

Ostrom (1974, 1976) has convincingly shown that there is no evidence for the arboreal habits of *Archaeopteryx* and all other premises suggest, though indirectly, that the terrestrial habits are primitive for birds: (1) Almost all avian taxa that may be reasonably supposed to be primitive include either terrestrial or water birds. Cracids are a major exception but they do not appear to be highly specialized in the arboreal life either in morphology or in nesting habits; they have strong legs and feed partly on the ground. (2) The Cretaceous embryos (Elżanowski 1981) confirmed a generally accepted view that the precocial/nidifugous mode of development is primitive for birds. Moreover, most primitive among modern birds are predominantly ground nesters (the cracids excepted) and have precocial chicks; both of these premises strongly suggest that the arboreal nesting appeared rather late in the avian evolution. (3) Paradoxically, the Albian record of the foot-propelled divers (*Enaliornis*) constitutes the best evidence for an early radiation of terrestrial birds since the foot-propelled divers are likely to originate only from birds that had once walked on land, then began to do it in water, and finally adapted to swimming.

SCAVENGING REPTILES AND TAPHONOMIC IMPLICATIONS

The strong dominance of water-dependent birds in the Cretaceous record certainly represents a bias which results from (1) the higher fossilisation potential of aquatic organisms, a point that requires no further comments, (2) the poor knowledge of truly continental assemblages, and possibly also (3) a specific taphonomic factor acting against the preservation of terrestrial birds.

In those early Cretaceous formations that are well studied, the remains of land vertebrates are scanty and mostly fragmentary (Ostrom 1970) with the major exception of Bernissart in Belgium, whereas the most promising vertebrate assemblages, especially those of central Asia, are as yet poorly known.

Late Cretaceous assemblages of land vertebrates are mostly recovered from coastal plain deposits, where the dominance of the water-dependent birds is to be expected. The major exception are the Mongolian formations, and one of them (Barun Goyot) yielded *Gobipteryx*, in all probability a true terrestrial bird. If, however, terrestrial birds were as diversified as implied above, the puzzling question is, why only one bird species was found in Mongolia, while other small vertebrates as, lizards and mammals are represented by numerous taxa (see Osmólska 1980)?

A remarkable feature of the Cretaceous record is the rarity of medium sized vertebrates, especially those of less than 10 kg in weight. This applies both to the medium sized species and the juvenile specimens of larger animals, especially dinosaurs. The lack of small dinosaurs led Bakker (1971, 1972) to the known conclusion that the small dinosaurs could not exist because of the thermic requirements. Aside from the controversy about the homeothermy of dinosaurs, this explanation does not account for the known scarcity of juvenile dinosaurs, which is believed by Richmond (1965) to result from the high mortality of juveniles and the dominance of adults in the dinosaurian populations. This however raises the question of why there is no abundant fossil evidence of such a high juvenile mortality (unless it is assumed that death occurred mostly at earlier embryonic stages where the skeletons are little ossified). Smaller vertebrates may be underrepresented in the skeletal remains as shown by Behrensmeyer *et al.* (1979) for the African savanna. However, the microvertebrates (lizards, mammals) are well represented in the Cretaceous record whereas the smaller among medium-sized specimens are unexpectedly rare.

A major factor, possibly responsible for the lack of medium sized vertebrates in the fossil record, is scavenging and predation by carnivorous reptiles, mainly theropod dinosaurs. The feeding method of large reptilian carnivores is essentially different from that of mammalian predators. Both crocodiles and large lizards (monitors) swallow the items as large as can pass through their gullets. Auffenberg (1972) noticed that the Komodo dragons (*Varanus komodoensis*) swallow bones even when cleaned of flesh (but not too dry) and the skeletal remains of dragons are said to be rare on the island because of scavenging by their conspecifics (Peters 1963).

To the contrary, the carnivorous mammals, including the largest (as the lion) tend to disarticulate the larger prey and eat only the selected parts, discarding the others, as heads or distal parts of the legs (or wings). That is why skeletal remains are very common in the wild areas of open country as the central Asiatic steppes or the African savanna. Moreover, the mammalian carnivores commonly cache the remaining parts of prey, mainly in the ground, and bring the prey to their young. Both habits may largely contribute to the dispersion of bones.

The large reptilian carnivores, both the crocodiles and monitors, are very fond of carrion in any stage of decay. Similar feeding habits may be safely assumed for the carnivorous theropods. In contrast to predation which is size selective, scavenging is largely non-selective with respect to size, i.e. scavengers take any carrion they perceive. Therefore, assuming the same detectability by scavengers, smaller carrion has a greater chance than the larger one to be swallowed whole, since both smaller and greater scavenger can do it. In fact, the detectability of carrion may strongly depend on its size and the cadavers of microvertebrates, lying in vegetation or various natural crevices, are certainly less detectable than those of larger animals especially when sight-directed scavengers are active. The greater chance for the smaller carrion to be swallowed whole and the smaller chance to be detected are two conflicting factors acting jointly against preservation of medium sized animals. I would predict that there is a critical medium size range of animals, small enough to be swallowed whole, and large enough to be well detectable and/or accessible. The detectability of carrion will be also influenced by the behaviour of living animals e.g. by burrowing habits which will increase the chance of preservation of skeletons among fossorial forms.

A few records of specimens approaching the critical medium size may confirm the presented hypothesis after careful palaeoecological consideration. For instance, juvenile dinosaurs (protoceratopsians), represented by nearly all growth stages, are known to be abundant only in Bayn Dzak, Djadokhta Formation, Mongolia and the same locality yielded also the smallest specimen of a theropod (ZPAL MgD-II/29, under study by the author) with the skull length of about 5 cm. In accordance with the proposed hypothesis, larger carnivores are scanty in the Djadokhta Formation, especially in Bayn Dzak (Osmólska 1980). Aside from dinosaurs, other Cretaceous medium sized land vertebrates are large lizards from the families Varanidae, Polyglyphanodontidae and Macrocephalosauridae, which, however, may have been partially burrow dwellers and/or semiaquatic in habits (Estes 1964) as are the modern varanids (Auffenberg 1980).

Bird cadavers appear to be more conspicuous than those of most other vertebrates of comparable size because of feathers which are often spread out, moved by the wind and, at later stage of decomposition, dispersed around the cadaver. These may be important cues in the searching image of the scavenger. Even when falling in water, the bird cadavers are not immune from scavenging by land or flying vertebrates since, contrary to other vertebrates, they float for a long time at the surface, as shown by Schäfer (1962).

Of prime importance for my hypothesis is the ability of reptiles to digest bone. Snakes may digest bone completely, although small fragments of bone sometimes occur in the excrements (Skoczylas 1978). Bo-

nes were also found in the fecal pellets of *Varanus komodoensis* by Auffenberg (1980). Crocodiles are known to decalcify bones and teeth completely although the organic matrices may be left intact (Fisher 1981 and references therein). In contrast, the mammalian digestion of bone is largely incomplete because food passes through the alimentary tract much more rapidly. This is due to the high levels of body temperature and metabolism in mammals. Dinosaurs may be considered as homeotherms, but this does not imply a mammalian level of body temperature and metabolic rate (Skoczylas 1980; Spotila 1980) and therefore the rate of food passage in dinosaurs may have been similar to that of other reptiles. Swinton (1970) remarked upon the absence of any solid materials in dinosaur coprolites and suggested that the digestion of bones was as effective as that of crocodiles.

If the presented explanation of the rarity of medium sized vertebrates in the late Mesozoic is at least partly true, both the mode of feeding and the digestive rates of reptilian predators, which differ from those of mammals, must impose a significant limitation on the actualistic approach to the taphonomy of Mesozoic vertebrate assemblages.

Acknowledgements. — I thank P. Brodkorb (University of Florida), R. Molnar (Queensland Museum, Australia) and C. A. Walker (British Museum) for the comments and unpublished information. M. Brett-Surman (George Washington University), Laurie McDonald (University of California) and D. McInnes (Provincial Museum of Alberta) generously provided locality data for occurrences of *Hesperornis*. J. S. Mellett (New York University), A. Seilacher (Geologisches Institut, Tübingen) and S. Tarsitano (Queens College, Flushing) kindly improved the early drafts. W. Clemens (University of California) and A. Jerzmańska (Uniwersytet Wrocławski) made valuable suggestions concerning taphonomic and palaeoichthyological questions, respectively. P. Currie (Provincial Museum of Alberta) placed at my disposal the manuscript on the footprints of Cretaceous birds. P. Currie, P. Dodson (University of Pennsylvania), R. Marcinowski (Uniwersytet Warszawski) and H. W. Miller (Fort Hays Kansas State College) provided missing literature.

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NOTE ADDED IN PROOF

New record

Lower Cretaceous of Asia. Kurochkin (1982: Dokl. Akad. Nauk SSSR, 262, 2, 452—455) gave a preliminary description of an unquestionable carinate, *Ambiortus dimentjevi*, from Neocomian beds (stage and formation undetermined) of Mongolia (locality: Khurilt-Ulan-Bulak). Moreover he announced a second avian skeleton from another locality of Mongolia and numerous prints of feathers from eight localities of Mongolia and transbaikalian Siberia.

Upper Cretaceous of North America. Lucas and Sullivan (1982: J. Paleont. 56, 2, 545—547) described a humerus of *Ichthyornis* sp. from the late Turonian beds of Mancos Shale, Juana Lopez Member, northwestern New Mexico; this record extends the range of *Ichthyornis* westwards but confirms its southern distribution. However, Martina and Stewart (1982: Can. J. Earth Sci., 19, 2, 324—327) assigned to *Ichthyornithes* a single centrum of vertebra coming from the Campanian Vermilion River Formation, Pembina Member, area of Morden, Manitoba (Canada); if correctly recognized, this vertebra would extend the range of *Ichthyornithes* far northward. Martin and Stewart also declared the record of *Ichthyornis* from the Austin Chalk, Texas (as referred above) to be erroneous.

Terrestrial birds

Mourer-Chauviré (1981: Geobios 14, 5, 637—647, and 1982: Geobios 15, 2, 268—269) came to the conclusion that the Phorusrhacidae must have differentiated as early as the Cretaceous. They originate most probably from South America where they are known since the Oligocene and Mourer-Chauviré has recently discovered one of them, *Ameghinornis minor*, in the Oligocene of Quercy, France. Now, there are only two possible dispersal routes to Europe: either through North America or via Africa. Either of these two continents lost any connection to South America before the beginning of Tertiary and therefore the dispersal must have occurred during the Cretaceous. The same applies to the Idiornithidae and Bathornithidae which all certainly appeared with an old radiation of the ralliforms.