

basis of the derived features characterizing the major clades.

We do not consider that the recent description⁴ of an avian dentary symphysis of a supposed psittaciform (parrot-like) bird from the Cretaceous Lance Formation of North America represents such a record. If it did, then this would be not only the oldest record of parrots by some 15 million years, but also the earliest recorded occurrence of a 'terrestrial' modern bird in the Cretaceous. Other reports from this period have been shown to be too fragmentary to be of any taxonomic value^{5,6}, to occur with formations of uncertain Cretaceous age^{7,8}, or to have been incorrectly assigned in the first place⁹.

We therefore recommend that this record be treated with caution until further fossil material of a similar age can be assigned with confidence to the Psittaciformes. This record should not be used to support hypotheses invoking an origin for the modern clades before the Cretaceous/Tertiary boundary^{2,3} for the following reasons.

First, the characters listed by Stidham⁴ to support the referral of this material to the Psittaciformes have a wider distribution among Cretaceous Maniraptoriformes (for example, a 'hook-like' dentary is seen in caenagnathid theropods¹⁰), and are variable within the group in question. Although a K-shaped neurovascular canal pattern is seen in some modern psittacids (such as *Cyanoramphus* sp.), this character is not seen in other taxa (*Polytelis* sp., for example). In a survey of large numbers of skeletal specimens of several modern species, we have observed that a K-shaped neurovascular canal pattern is variable in occurrence within individual psittaciform taxa (for instance, *Psittacula roseata*; G.J.D., personal observation), and that both the putative psittaciform characters cited by Stidham⁴ are seen in other groups of modern birds (such as the Ciconiiformes; G.J.D., personal observation).

Second, the overall morphology of the Lance Formation specimen is markedly different from that of the oldest unequivocal parrots known in the fossil record, including well-preserved and complete skulls from the lower-middle Eocene of the London Clay, England, and Grube Messel, Germany¹¹. These fossil birds, although exhibiting a typically psittaciform postcranial morphology (including the zygodactyl foot, which has the fourth toe directed backwards), lack the parrot-like beak of modern Psittaciformes. Moreover, the mandibular symphysis in Eocene forms is much smaller and narrower than in recent parrots and in the specimen from the Lance Formation^{4,11}.

At present, the monophyly of the Psittaciformes, one of the most homogeneous of modern orders, is supported

exclusively by postcranial characters¹¹, although the single recent family within the order, the Psittacidae, does have a single unique skull character: the presence of a 'parrot-like' beak (for example, maxilla broad dorsoventrally, with a sigmoidally curved ventral margin). We argue that, given the benefit of well-preserved and largely complete fossil material from the early Eocene, taxonomic assignments of material such as the Lance Formation specimen must remain tentative at present.

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Stidham replies — I have presented a hypothesis for the identification of a Late Cretaceous fossil as the oldest known parrot¹. The specimen lacks the characters distributed more widely in non-avian maniraptoriforms, such as abundant teeth and unfused dentaries. It has many characters¹, including the absence of an internal pillar of bone supporting a midline ridge, that are not present in oviraptoroids². To assign the specimen to a non-avian clade requires a less parsimonious hypothesis of character evolution. The K-shaped neurovascular canal pattern character¹, mapped onto various phylogenetic hypotheses of the relationships of crown group parrots^{3–5}, is primitive for that clade. Like most characters, the K-shaped neurovascular canal pattern exhibits homoplasy and variation within natural populations. The complete absence of this character from some extant parrots seems to be the result of secondary loss due to the relative shortening of the jaw symphysis in some parrots (*Neophema*, for example). However, this character, as figured and described¹, is not found outside crown-group parrots, although it superficially resembles the state in extant cathartid vultures. Although individual characters seen in the fossil can occur in other taxa, the combination of characters seen in the fossil

is not present outside crown-group parrots, and Dyke and Mayr have not demonstrated what clade, other than parrots, has this combination of characters.

It seems less than defensible to propose that we cannot have Cretaceous parrots because the oldest well-preserved fossils known so far are Eocene⁶. Previously proposed sister groups to parrots (reviewed in ref. 7), and the known fossil record of these sister taxa^{8,9}, show that the parrot lineage should have been present at least 5 to 10 million years before the (middle Eocene) Messel and London Clay parrots⁶. This is the same amount of missing fossil record required by both my hypothesis of a latest Cretaceous parrot and Mayr and Daniels' suggestion⁶ (made during their study of the Eocene parrots) of a Cretaceous origin of parrots.

The other known Cretaceous neornithines (listed earlier¹: in contradiction with Dyke and Mayr, the New Jersey fossil birds are Cretaceous in age¹⁰) placed in various phylogenetic hypotheses of the ordinal level relationships of neognaths, including parrots^{7,11}, show that parrots and most other neognath ordinal level clades are constrained to have diverged from other orders of modern birds in the Cretaceous or early Palaeocene.

If non-crown-group parrots are present in the Eocene⁶, then the sister group to those taxa (the stem leading to the crown group or the crown group itself, possibly with a modern-looking jaw) must have been present by the middle Eocene as well. The identification of the Cretaceous jaw as a parrot is subject to test and refutation, like any hypothesis. However, the accepted methods of the field, not statements about gaps in our current knowledge and preconceived notions of character evolution, must be used to falsify hypotheses and generate alternatives.

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