importance of the astragalus in highly neotenic birds. Despite McGowan's statements, the pretibial bone seems to represent both a separate chondrification and ossification in carinates; we believe that this is also the case in ratites and that the difference (if it exists) between ratites and carinates is the result of varying amounts of overlap with the calcaneum and the astragalus. Because of the extreme lateral placement of the pretibial bone in some carinates, it may be confined to the region above the calcaneum (see Fig. 11 of Martin *et al.*[2]), and after the chondrification has fused with the calcaneum it may resemble a 'spur' of that bone. On the other hand, falcons have the pretibial bone very centrally situated as in the ostrich, and most, if not all, of the fusion of the distal end of the pretibial bone is with the astragalus (Fig. 179 of ref. 3). A juvenile swan, *Cygnus buccinator* [Kansas University 79260], shows a pretibial bone ossifying separately from the calcaneum and partially overlapping the astragalus; except for its slightly more lateral position, it corresponds to McGowan's description of the "astragalar process of the ostrich" which is a "well-ossified ascending process, expanding distally into a disk of bone".[1] We believe that the present evidence indicates that ratites and carinates have a homologous ossified ascending process (pretibial bone) separate from both calcaneum and astragalus, but that the position of this process may vary. We believe that, as originally suggested, the pretibial bone is a neomorph ossification providing a derived character for birds. The late chondrification of this element supports such an interpretation. The Mesozoic birds (*Archaeopteryx*, *Enaliornis*, *Baptornis* and *Hesperornis*) have the pretibial bone laterally placed and fused to the calcaneum as in carinates, but not as in theropods (Fig. 1*b* of ref. 1), and we would therefore caution against arguing that the pretibial bone of carinates is a derived character state within the Class Aves.

To view these results as in any way confirming the theropod origin of birds would be to beg the question. The only way McGowan could conclude that the ratite tarsal condition is more primitive than that of the carinates is by already assuming that theropod saurischians are the out-group most proximate to birds; this approach does not address the fact that pseudosuchians and crocodilians are also contested nearest out-groups[4-7]. McGowan's own interpretation of his material would indicate that the bulk of the known birds (the carinates) do not have a theropod-like ascending process.

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MCGOWAN REPLIES—According to Martin and Stewart, the ascending process of the carinate tarsus commences as a chondrification independent of the cartilaginous astragalus and calcaneum. This subsequently ossifies as a separate element, and a similar ontogeny is believed to occur in ratitites. The pretibial bone thus formed, a new element which is not homologous with the ascending process of theropods, provides a shared derived character for birds.

My X rays of juvenile ostriches (ref. 1, Fig. 3*b-c*) confirmed Huxley's[2] belief that ratites, like theropods, have an ascending process that is continuous with the bony astragalus. Whether this process develops in ratites as an integral part of the astragalus, or, as Martin and Stewart contend, as an independent chondrification, and ossification, can only be determined embryonically. The earliest ratite embryos available to me were close to hatching, at which stage there is a prominent bony ascending process expanded distally into a disk of bone embedded in cartilage. That this entire structure is the astragalus, and not an independent ossification, is confirmed by examining early ostrich and emu embryos[3]; these show that the cartilaginous astragalus is drawn up into an ascending process, as Parker[4] described for the kiwi, and this subsequently ossifies to give the bony ascending process. Ossification commences at the tip of the cartilaginous process, spreads distally and eventually extends across the entire width of the cartilaginous astragalus, as shown in my X rays of juveniles. Ossification of the corresponding process in carinates is confined to the process itself (ref. 1, fig. 2*b-e*).

I have examined swan embryos (*Cygnus olor*), and find that the pretibial bone develops as an ossification of a cartilaginous spur, as described for other carinates[1]. Inasmuch as the pretibial bone ossifies separately from the bony calcaneum, my observations[1] do not conflict with those of Martin and Stewart, and I believe that if they examined later stages of swan development they would find that the pretibial bone eventually fused with the calcaneum, as it does in the chicken (ref. 1 fig. 2*f*).

One area of common ground I now share with Martin and Stewart pertains to the homology of the ascending process in ratites and carinates, but our conclusions differ radically. An examination of early duck embryos (days 8-11 of incubation) revealed a dorsal cartilaginous process from the lateral aspect of the astragalus, similar to that seen in early emu embryos (15-20 days)[3]. This early association with the astragalus is soon obscured by the fusion of the cartilaginous astragalus and calcaneum, and from then on the process develops in close association with the calcaneum, as described previously[1]. Similar observations for gulls lead me to believe that the carinate pretibial bone is an astragalar derivative, supporting its homology with the ascending process of ratites.

Ratites, like theropods, have a bony ascending process that is continuous with the astragalus, but carinates have a derived condition where the process fuses with the bony calcaneum. Martin and Stewart deny that the (predominently lateral) carinate pretibial bone is a derived character within birds, noting that the ascending process is laterally placed in the earliest bird, *Archaeopteryx*, but this is the case in theropods[1]; the significant point is not its orientation but whether it is continuous with the astragalus or the calcaneum.

My conclusion that the ratite tarsus is more primitive than that of carinates does, of course, hinge upon theropods being phylogenetically closest to birds, a position I took at the outset with my reference to Ostrom's work[5]. Citing a review by Benton[6], Martin and Stewart point out that pseudosuchians and crocodilians have also been proposed as the nearest avian out-groups. Their own bias for the crocodilian hypothesis is contained in a paper by Martin *et al.*[7]. Note, however, that Walker[8], the leading proponent of the crocodilian hypothesis, has recently reassessed the evidence, concluding that the hypothesis for a common ancestry of crocodiles and birds (above the thecodont level) should be rejected.

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