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DERIVED FEATURES OF GIRAFFID OSSICONES

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In a recent paper (Geraads, 1986) regarding the systematics of Recent and fossil Giraffidae, I discussed the types of cranial appendages in this family and their relevance for a cladistic classification. I proposed that the term ossicone be restricted to horns of the living species, *Giraffa camelopardalis* and *Okapia johnstoni*, because there is no evidence that it is legitimate to apply this term to the horns of fossil giraffids. I used presence of ossicones as a synapomorphy uniting living giraffids, which in my cladogram (Geraads, 1986: 475, fig. 2) compose, together with the fossil genus *Palaeotragus* (including *Samotherium*), the tribe Giraffini. I hypothesized that this tribe might best be defined by presence of ossicones, but I refrained from using them as a synapomorphy of the whole tribe, because occurrence of this type of appendage in *Palaeotragus* is doubtful (Geraads, 1986:473). I was more positive about the nature of horns in some other fossil genera, stating that *Climacoceras* and *Sivatherium*, for instance, do not have ossicones.

Solounias (1988) claimed that true ossicones occur in several fossil giraffids, thereby demonstrating that my cladistic analysis was not well founded. However, presence of ossicones in *Palaeotragus* would not necessarily alter my cladogram, because I surmised that they might be present in this genus; it would only shift this synapomorphy to define the whole tribe Giraffini. More fundamental, however, the meaning of the term ossicone seems to have been incompletely understood by Solounias (1988). It is necessary, therefore, to state precisely the characteristics of the ossicone, as defined in Recent giraffids: an ossicone is a bone originally independent from those of the cranial roof, ossifying from a cartilaginous matrix. Other researchers agree upon this point (Janis and Scott, 1987). The term epiphyseal, as used by Solounias (1988), should be used with caution; an ossicone is not homologous to the epiphysis of a long-bone, whose epiphyseal cartilage causes lengthening of the diaphysis, not of the epiphysis.

An ossicone grows from the basal cartilage upward, whereas "ossification proceeds from the tip of the ossicone ventrally toward the skull" (Janis and Scott, 1987:17) until the ossicone almost reaches its adult length. The cartilage then ossifies, therefore preventing growth in length, except as follows: subsequent ossification proceeds both externally and internally, external ossification slightly increases the length and more strongly increases the diameter, and internal ossification yields extremely compact ossicones as found in old males. A fourth characteristic common to both living giraffids is the shift of the ossicones posteromedially, away from their primitive supraorbital position. The latter two points probably are linked with the peculiar mode of intraspecific fighting by both Recent species; during fighting, the robust ossicones endure great stresses transmitted to cranial bones. The weak horns and supraorbital roof of *Samotherium*, for instance, were unable to withstand such stresses, and the mode of fighting in this genus was probably different.

All four characters mentioned are present in the living species, therefore, may be used to define a "true ossicone." From a cladistic point-of-view, the question is to determine whether these derived features, shared by the giraffe and okapi, also are present in the fossil genera. Those features that cannot be found elsewhere become synapomorphies of the Recent species, supporting the monophyly of the Recent Giraffidae.

Neither the hyper-ossification of the horns, nor their location posteromedial to the orbits have been recognized in any genera other than *Giraffa*, its close relative *Bohlinia*, and *Okapia*. However, Solounias (1988) only incidentally addressed these points. The discovery of long, unfused cranial appendages in other genera would weaken my hypothesis of monophyly of the group *Giraffa* (+*Bohlinia*)–*Okapia*.

Solounias (1988) referred to two skulls figured by Bohlin (1926) and contended there was a suture between the "ossicone" and the cranial roof, but Solounias (1988) may have confused a limit or border with a suture, as he did elsewhere: "In . . . *Giraffa* the suture remains and actually is accentuated by additional secondary-bone deposits . . ." and "The ossicone has a slightly rugose surface thus the suture at its base can be observed clearly" (Solounias, 1988:846).The surface of the cranial appendage has an aspect different from that of the cranial roof; this also is found in bovids and cervids. The limit might well be emphasized by minimal outgrowth at the base of the appendage. The same may be true of the sutures said to be present on the skull

of *Giraffokeryx punjabiensis* (AMNH 19475) by Solounias (1988), but not mentioned by Colbert (1933) although Colbert (1933:5) clearly sought evidence of independence of the horns in this species. Further, the *Palaeotragus* skull figured by Bohlin (1926:pl. 1, fig. 1) and mentioned by Solounias (1988) is that of an old male. If the supposed ossicone were still unfused on such an old specimen, as Solounias (1988) claimed, then the ossicones certainly would be too loose on young specimens to be preserved still attached to the skull; many such young specimens are known, however. The relatively young type specimen of *P. rouenii*, for instance, shows no trace of a suture.

Solounias (1988:846) also referred to "two ossicones of *P. rouenii* from Russia that show a suture at the base and are detached from the skulls (Godina, 1979:107, pl. 3, figs. 3, 4)." However, if a suture is visible, it means that the appendage was broken away with part of the skull, not just detached. The line visible near the base of the appendage figured by Godina (1979:107, pl. 3, fig. 3) probably is only a break, likely to occur (and, indeed, often observed) in this area of minor strength, between a pneumatized skull and a more-solid cranial appendage.

Solounias (1988) chief evidence for the ossicone nature of the *Samotherium* "horns" are two orbital roofs from the upper Miocene of Samos, numbered 712a and 712b in the Musée Géologique, Lausanne, Switzerland. Solounias (1988) provided a description and some figures of the specimens, but some details are instructive. Sizes of the specimens are difficult to determine precisely. They are not much, if at all, smaller than the other old-aged specimen, (MGL S 202, purportedly a female), thus certainly not young. Nothing need be added to Solounias' (1988) description of the right orbital area, but a major point incorrectly figured and described by him is that the left minute "horn" is in fact already partly fused to the frontal bone, and not surrounded by a "well-marked suture at the base which continues along the entire periphery" (Solounias, 1988:846). This incipient fusion is visible at several points around the appendage, especially posteriorly, just in front of the depression mentioned. If this appendage had lengthened further, it could have done so only by terminal elongation, thus in a way different from that of the Recent giraffids. Of course, it also is possible that this minute appendage already had reached its adult length (as in S 202, which is only slightly larger). This specimen (S 712) cannot be used to demonstrate presence of true ossicones in *Samotherium*, because basal growth is not demonstrated.

This leaves only specimen GSP 16274, from the Dhok Pathan of the Siwaliks, an isolated detached ossicone, which might provide strong evidence of occurrence of true ossicones as early as the Miocene. However, it was identified by Solounias (1988) as unknown genus and species, thus, is of no use in the cladistic analysis, despite its potential interest.

Therefore, new evidence does not demonstrate the ossicone nature of the cranial appendages of the extinct giraffids. Rather, it shows that, at least in *Samotherium*, small "horns" already are partly fused to the frontal bone, and that their subsequent growth, if present, was certainly achieved, not by the activity of a basal cartilage, but by external bone apposition. Reading of Solounias' (1988) paper and examination of the Lausanne material reinforced my conviction that *Giraffa, Bohlinia*, and *Okapia* compose a monophyletic group.

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