SUTURE CLOSURE AS A PARADIGM TO STUDY LATE GROWTH IN RECENT AND FOSSIL MAMMALS: A CASE STUDY WITH GIANT DEER AND DWARF DEER SKULLS

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Sutures are the joints at which bones articulate with one another through intervening fibrous connective tissue (Depew et al., 2008; Rice, 2008). During growth they serve as major sites of bone expansion. In order to accommodate the developing brain, growth in intracranial volume is achieved mostly by bone production at the sutural margins (Morris-Kay and Wilkie, 2005). The numerous sutures in the mammalian skull do not obliterate simultaneously, but in a sequence that is species specific, and largely in postnatal stages (Wilson and Sánchez-Villagra, 2009) that are preserved in good fossil series. In this paper I examine ectocranial sutures in a clade of cetartiodactyl mammals, the deer (Cervidae), and integrate information on two remarkable fossil taxa, Megaloceros and Candiacervus, in order to examine the potential effect of size changes on growth patterns as paleontologically recorded.

Throughout the Quaternary, deer were one of the most ubiquitous and diverse groups of large mammals in the Northern Hemisphere (Groves, 2007). Among them were species that reached very large size, including the giant deer Megaloceros giganteus, named by Cuvier (1812:8) “le plus célèbre de tous les rumins fossiles,” with a distribution across Europe and Western Asia spanning 300,000-400,000 years (Lister, 1994). There are also fossil deer from Mediterranean Islands, including species of Candiacervus, which is probably a Megacerini and thus a member of the same clade as Megaloceros (De Vos, 1979; Capasso Barbato, 1992; but see Kuss, 1975). Most likely Candiacervus evolved small size in short geological time (De Vos, 1979). The species examined here, C. ropalophorus, had in comparison with its hypothesized mainland ancestor shorter limbs, a massive body, and simplified, long antlers, occupying an ecological niche probably similar to that of the Cretan wild goat Capra aegagrus of today (van der Geer et al., 2006).

MATERIALS AND METHODS

I examined the relative timing of suture closure in deer skulls represented by samples of 8 living and two fossil species and three closely related species as outgroups; additional original observations on llama and peccary skulls are also discussed below. A total of 28 suture sites were coded, of which a maximum of 20 were closed in only one of the species examined (Fig. 1). Sutures were primarily scored as either open or closed in each individual and based on this information for all specimens of the same species, the sequence was established. In some cases different degrees of closure were used to provide additional resolution to the closure sequence for two or more suture closures coded otherwise as simultaneous. An open suture is visible in the bone surface, with the two elements involved firmly attached to each other or not. A closed suture has no trace of the suture on the bone surface (Irmis, 2007). Crania were specifically chosen such that the sample for each species resembled a growth series, using size as a proxy for age (Fig. 2). No differences between males and females were detected in the pattern for several species at the beginning of the study, so both sexes were compiled for each species. Presence of antlers or signs of them reveal the male gender of a specimen except for very young individuals in which males can lack these structures and for the reindeer, the only cervid in which females also possess antlers. At least 10 skulls were examined for each species, and at least two individuals with a high degree of tooth-wear were examined for each, to ensure that the ‘maximum’ number of suture obliterations could be recorded (e.g., Moschus moschiferus, NHM-B-5110 and -5112, of condylobasal length 139 and 144 mm, respectively).

Specimens studied are housed at the Zoologisches Museum der Universität Zürich (ZMUZH), Naturhistorisches Museum Basel (NHMB), Naturhistorisches Museum der Burgergemeinde Bern (NMBE), Museum für Naturkunde Berlin (MfNK), Zoologische Staatsammlung München (ZSM), Naturalis, Nationaal Natuurhistorisch Museum, Leiden (RMNH), Naturhistoriska Museet, Stockholm (NRM), Zoologisches Institut (ZICAU) and Zoologisches Museum der Christian-Albrechts-Universität zu Kiel (CAU-ZM), Museum of Zoology Cambridge University (CUMZ), and Bayerische Staatsammlung für Paläontologie und Geologie (BSPG).

RESULTS AND DISCUSSION

Although minor differences in suture closure sequence exist among species, the overall shared sequence is highly conservative for the first five sutures considered across cervids (Fig. 1). The first sutures to obliterate are those contacting the interparietal, exoccipital, and basisciptal bones, followed by those related to the basisphenoid, basioccipital, and presphenoid in the skull base. The overall regional pattern starts with the vault and continues with the base of the skull, as in hominoids and great apes (Krogman, 1930; Schultz, 1941), monkeys (Chopra, 1957), hyenas (Schweikher, 1930), otarid seals (Brunner et al., 2004), manatees (Hoson et al., 2009), pigs (Herring, 1972), and hystrixnognath rodents (Wilson and Sánchez-Villagra, 2009). After the vault and base sutures obliterate, only a few additional ones do so in some living cervid species, as noted by Kierdorf et al. (1995), with some species obliterating a total of eight sutures and the elk, Alces alces, 10 sutures.

The five sutures that obliterate in all cervids examined are the first ones to do so in Megaloceros. After that, the sequence includes up to 15 sutures, whereas only 5 additional sutures obliterate in Alces alces for a total of 10. In fact, of the total of 28 sutures examined, only 8 remain open in all Megaloceros examined (premaxilla-maxillary ventrally; parietal-squamosal; supraoccipital-squamosal; intermaxillary; interpalatine; alisphenoid-squamosal; alisphenoid-orbitsphenoid; interpremaxillary). The greater degree of suture obliteration in Megaloceros is not an artifact of preservation, because among the several individuals recorded (total 18) four have all or almost all the 20 listed sutures obliterated (Fig. 2). Extended growth after maturity resulting in a peramorphic trait, as with antler growth in this species (Gould, 1974), is a potential but unlikely involved mechanism. In fact, the recent study of Chritz et al. (2009) of stable isotopes and cementum analyses indicated a maximum of 14 years of age for a sample of seven Megaloceros, a figure comparable to the maximum longevity of several living cervid species (Grzimek, 1997). This suggests that hypermorphosis is not the mechanism related to the high degree of suture closure in...