

SHORT COMMUNICATION

Ossification sequence in the mole *Talpa occidentalis* (Eulipotyphla, Talpidae) and comparison with other mammals

Jan Prochel^{a,*}, Anjali Goswami^b, F. David Carmona^c, Rafael Jimenéz^c

^aZoologisches Institut, Spezielle Zoologie, Universität Tübingen, Auf der Morgenstelle 28, 72076 Tübingen, Germany

^bDepartment of Earth Sciences, University of Cambridge Downing Street, Cambridge, CB2 3EQ, UK

^cDepartamento de Genética e Instituto de Biotecnología, Facultad de Ciencias, Universidad de Granada, 18071 Granada, Spain

Received 28 February 2007; accepted 21 May 2007

Keywords: Mammalia; Phylogeny; Cranium; Skeleton; Heterochrony

The skeleton of mammals has been the subject of detailed anatomical and functional studies for centuries, and investigations of its ontogeny enjoy a long tradition (Starck 1995). However, knowledge of the timing of ossification is restricted to few species. Most available data of this kind pertain to species used in the lab or domesticated animals (e.g., Cury 1965). Here we report on the ossification timing in the Iberian mole *Talpa occidentalis* (Fig. 1), based on the study of a developmental series obtained in studies of reproductive biology and growth in this species (e.g., Barrionuevo et al. 2004). This study complements those on the ossification patterns in the European mole *Talpa europaea* (Prochel 2006; Goswami and Prochel 2007) and in other eulipotyphlans (Prochel et al. 2004).

The sequence of developmental events in mammalian evolution has been subject of some attention in recent years (e.g., Bininda-Emonds et al. 2003), correlated with the development of analytical techniques to study sequence heterochrony (Richardson et al. 2001). Relatedly, studies of ossification timing have been conducted, concentrating on heterochrony (Smith 1997; Sánchez-Villagra 2002; Schoch 2006) and modularity (Goswami 2007).

Twenty-nine specimens of *T. occidentalis* (Cabrera, 1907) were cleared and double-stained for bone and

cartilage (Dingerkus and Uhler 1977; Prochel 2006). The onset of ossification, shown by intake of alizarin red, was examined in 25 cranial and 24 postcranial elements and was recorded in (prenatal) stages 7–9 (Barrionuevo et al. 2004). The results were compared with those resulting from previous studies of a similar kind of 22 prenatal stages of *T. europaea* for the cranium (Goswami and Prochel 2007) and the postcranium (Prochel 2006).

Onset of ossification data of 11 selected cranial elements in eight placentals and four marsupials and of postcranial elements in 10 therian and three sauropsid species were compiled in two matrices of pairs of events (i.e., onset of ossification of each element is related to every other one), as described in Smith (1997). Sequence data for the non-talpids species, including the sauropsids used as outgroups, were taken from Sánchez-Villagra (2002 and references therein), Nunn and Smith (1998), and literature cited therein. A similar analysis was performed by Sánchez-Villagra (2002) on the same postcranial data set without the talpids, and by Prochel (2006) without *T. occidentalis*.

The cranial matrix including 12 taxa and 11 elements resulted in 55 event-pairs (characters), whereas the postcranial matrix of 14 taxa and 24 elements resulted in 276 event pairs (characters). These ‘characters’ were mapped on existing cladograms, which include the species examined or close relatives (Fig. 2) using Mesquite (Maddison and Maddison 2006). We coded

*Corresponding author.

E-mail address: jan.prochel@uni-tuebingen.de (J. Prochel).

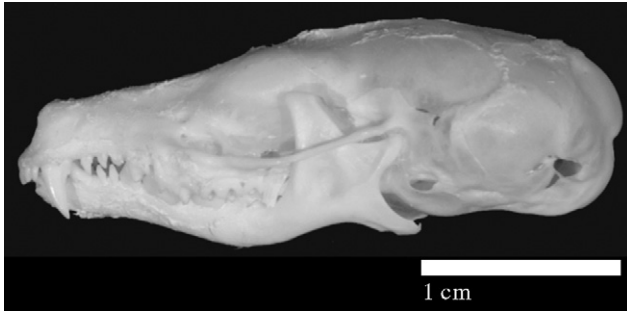


Fig. 1. Lateral view of a macerated skull of an adult *Talpa occidentalis* (TO 506).

in each event-pair (= character) the relative timing of the onset of ossification of the two elements, using 0 = before, 1 = simultaneous, and 2 = after.

Cranial ossification began in stage 8 and proceeded quickly. The first specimens with ossified cranial elements display 16 cranial elements in which ossification has started (Tables 1 and 2). This lack of resolution is due to a lack of early stage 8 specimens. The basisphenoid was visible only as a small centre of ossification in the most advanced stage 8 specimen. The lacrimal was anteroposteriorly elongate in stage 8, but in later stages, it was ovoid and bore a well-defined lacrimal canal. The infraorbital canal was complete by stages 8–9. The mastoid was only weakly ossified at its dorsal boundary, near the parietal, in stages 8 and 9, but it was well ossified by stage 10. The jugal was not discernable in any specimens, potentially due to early closure of the zygomaticomaxillary suture. This suture fused soon after the first appearance of the jugal in stage 8 specimens of *T. europaea* (Goswami and Prochel 2007), and this period was poorly resolved in *T. occidentalis*, as noted above. Canines and premolars were first observed by staining of the enamel by alizarin red in specimens of stages 8–9, and incisors appeared in stage 9. The alisphenoid was visible as a small ossification centre in stages 8–9, and was well ossified in stage 10. The orbitosphenoid was visible for the first time in stage 10. The ethmoid appeared as a small ossification centre in stage 10.

The first eight postcranial elements to start ossification in stage 8 are elements in the upper part of the body (clavicle, scapula, humerus, radius, ulna, ribs, and cervical vertebrae, in addition to calcified tendons disto-palmar to the third phalanx). Elements of the lower appendicular skeleton, including the femur, tibia, and fibula, as well as the thoracic vertebrae, are next to begin ossification, in early stages 8–9. Later in stages 8–9, the ilium begins ossification, followed closely by the lumbar vertebrae. The sacral and caudal vertebrae, sternum, pubis, and ischium begin ossification by stage 10. The distal elements of the appendicular skeleton are last to ossify, starting with the phalanges of the hand

starting later in stage 10. These are followed by the tarsals and the phalanges of the foot. In the latest stage 10 specimens, the metatarsals begin ossification. The carpals do not begin ossification in any specimens examined in this study, and are thus presumably the last postcranial elements to ossify.

The cranial ossification sequence of *T. occidentalis* broadly resembles that of *T. europaea*, with the main differences being that the lacrimal and alisphenoid ossify later and the basisphenoid ossifies earlier in *T. europaea* than in *T. occidentalis*. The delay of the alisphenoid is also evident in raw timing of ossification, as the alisphenoid is not visible in stages 8 or 9 of *T. europaea*, but appears in stages 8–9 in *T. occidentalis*. Other differences in relative timing of ossification are probably due to differences in resolution, as *T. europaea* specimens include more early and intermediate stages, whereas later stages are better represented in *T. occidentalis*.

As reported for *T. europaea* (Goswami and Prochel 2007) and shown here for *T. occidentalis*, the cranial elements in these moles appear in a very short period during prenatal development. Therefore it is a well-resolved sequence of ossification for most cranial elements difficult to obtain. However, we found that there is at least one unequivocal autapomorphy for the talpids in the onset of cranial ossification: talpids are the only mammals included in this study in which the alisphenoid appears after the basisphenoid. This character is not resolved in *Mus*, but is well resolved in all other taxa. Another potential autapomorphy is that the basisphenoid starts to ossify before the exoccipital in *T. occidentalis*. The exoccipital ossifies before the basisphenoid in all of the other mammals considered here, with the possible exception of the other talpid, *T. europaea*, in which it is unresolved. Thirteen other changes in the cranial onset of ossification sequence appear as unequivocal autapomorphies of talpids, six of which are unique for talpids. However, in all but two of these cases, the two *Talpa* species show the ‘simultaneous’ ossification condition. Thus, it is possible that these features reflect of lack of resolution of the data, and these autapomorphies require analysis when more detailed sequence data become available.

Several clades other than talpids show cranial sequence synapomorphies. In *Tupaia* and *Tarsius* and in *Manis* and *Felis* the jugal starts to ossify before the exoccipital, which is possibly a derived condition among the placentals. In *Manis* and *Felis* the jugal starts to ossify before the squamosal. This character is unresolved in two of the marsupials, *Dasyurus* and *Perameles* and is opposite in all other mammals. The parietal ossifying before the exoccipital appears to be a marsupial synapomorphy.

The postcranial changes in the onset of ossification that characterize the two talpids concern vertebrae, the

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