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ONTOGENETIC MORPHOLOGY AND ALLOMETRY OF THE CRANIUM IN THE COMMON EUROPEAN MOLE (*TALPA EUROPAEA*)

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The common European mole (*Talpa europaea*) has been the focus of many studies because of its fossorial lifestyle and related sensory and postcranial specializations. However, because of extensive fusion and pneumatization of the adult skull, many aspects of the cranial morphology of *T. europaea* are poorly understood. Here we present the 1st detailed study of cranial development in *T. europaea*, using an ontogenetic series of cleared and stained prenatal specimens to examine bone homologies, sequence of ossification, and prenatal allometry. The enigmatic lacrimal, jugal, and mastoid bones are all identified in prenatal specimens. The jugal and lacrimal bones fuse with the maxilla during prenatal growth, explaining previous difficulties with their identification in adults. *T. europaea* is anomalous among placental mammals in delaying the ossification of the alisphenoid and the orbitosphenoid until after birth. Analyses of allometry for 16 measures of individual bones show marked differences when postnatal specimens are included or excluded. Coefficients of allometry based on prenatal specimens are nearly twice those of analyses including subadult specimens. Comparisons with other taxa are limited by the lack of similar prenatal data, but the pattern exhibited by *T. europaea* differs significantly from those observed in studies of postnatal allometry in other mammals. These results may reflect differences among taxa or between prenatal and postnatal stages.

Key words: allometry, development, Eulipotyphla, homology, ontogeny, ossification, Talpidae

Talpa europaea, the common European mole, is an entirely fossorial, vermivorous, and insectivorous mole, with highly derived forelimbs adapted for digging. Because of their distinctive lifestyle and anatomy, moles have attracted much attention from researchers. There is a wealth of detailed studies on moles, from anatomical descriptions (Giere 2002; Jacobs 1816; Koppers 1990) to more recent studies of phylogenetic relationships (Cabria et al. 2006; Motokawa 2004; Sánchez-Villagra et al. 2006; Shinohara et al. 2003; Shinosara et al. 2004), postcranial development and evolution (Prochel 2006; Sánchez-Villagra and Menke 2004; Sánchez-Villagra et al. 2004), life history (Symonds 2005), growth and reproduction (Barrionuevo et al. 2004), sensory specializations (Catania 2005; Kriszat 1940), and biogeography (Loy et al. 2005).

Despite this attention, there is at present a relative dearth of information on the development of the skull in moles and other eulipotyphlans. Although some authorities refer Taplidae to the order Soricomorpha (Wilson and Reeder 2005), we prefer to use the broader Eulipotyphla (Wilson and Reeder 1993), which includes Soricomorpha (shrews and moles) and Erinaceomorpha (hedgehogs) for consistency with relevant recent studies. One study of the development of the orbitotemporal region in eulipotyphlans (Giere 2002) provides data from an embryological specimen, but it is too young to provide data on ossified elements. Other studies of cranial morphology are based on adult specimens (Jacobs 1816; Koppers 1990), but the adult cranium of *T. europaea* is highly fused (Fig. 1). For this reason, several bones (e.g., lacrimal, jugal, and most basicranial bones) are unidentifiable in adults, leading workers to suggest the loss of some elements, such as the jugal (Hutchinson 1976; MacPhee and Novacek 1993; McDowell 1958; McKenna 1975; Parker 1995; Sánchez-Villagra et al. 2006).

In addition, the heads of subterranean animals often bear interesting apomorphies, such as the lack of external ears, small eyes, and unique sensory systems, such as the Eimer's organs (Eimer 1871). For this reason, studying the cranial development of fossorial animals may offer insight into the evolution of their unique cranial morphology. Here, we present detailed descriptions of the ontogenetic morphology and allometry of the cranial bones in *T. europaea*. To address the issues of

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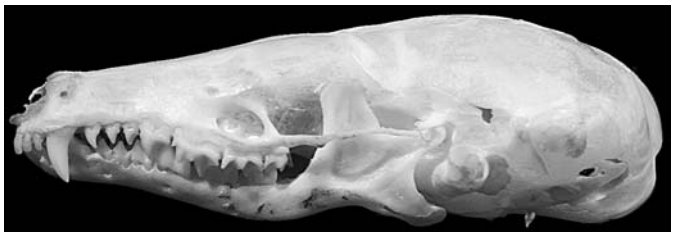

Fig. 1.—Skull of adult *Talpa europaea* in lateral view.

element identity, we pay particular attention to the morphology and suturing of independent centers of ossification for the problematic regions of the skull mentioned above.

Timing of suturing has been established as phylogenetically and functionally important (Chopra 1957; Giannini et al. 2006; Herring 1972; Krogman 1930). Likewise, order of ossification of cranial bones has been studied extensively in mammals in relation to reproductive mode, phylogeny, and functional morphology (Jeffery et al. 2002, 2005; Nunn and Smith 1998; Smith 1996, 1997, 2001, 2002, 2006; Zeller 1987). Comparative studies of the development of bones are often limited to the 1st site of ossification for any single bone. However, many bones form from multiple independent centers of ossification, which fuse during the course of prenatal development to form a single structure (Arey 1924; Curgy 1965; Johnson 1933; Zeller 1987). This facet of development is imperative to understand, because the relationships among different parts of a single bone may be as complex as those among different bones. Heterochronic shifts among bones are often discussed as a major source of morphological variation. However, heterochronic shifts among individual ossification centers within a single bone and rate of bone growth from individual ossification centers are rarely considered, although they may well contribute as sources of variation and provide phylogenetic and functional information (Girgis and Pritchard 1958). Here, we discuss all of these aspects of ossification sequence, number and relationships of ossification centers, timing of contact between centers and elements, and rate of bone growth.

Studies of allometry have been a primary method of understanding developmental variation for decades (see Klingenberg [1998] for review). Allometry has been a useful tool for examination of heterochrony, for studying the relationship between size and shape, for determining deviations from expected patterns of growth among species, and for highlighting the developmental roots of functional differences among species and higher taxa. Studies of postnatal allometry of mammalian crania are abundant, and a complete review is beyond the scope of this paper, but it should be noted that allometry and the closely related topic of heterochrony are strongly implicated in the generation of morphological diversity (Klingenberg 1998). Prenatal allometry is surprisingly poorly studied in mammals, although this component of growth also must offer important information on the evolution of morphological variation. The few studies of prenatal allometry in mammals are confined to humans and their close relatives and are relatively limited in focus (Mandarim-de-Lacerda and Alves 1992; Vinicius 2005). Our study of prenatal allometry in *T. europaea* thus represents an important contribution to this understudied topic, providing new evidence on the linearity of ontogenetic allometry (Zelditch et al. 2003 and references therein) and a foundation for future comparative studies of prenatal allometry.

Table 1.—Specimen numbers, estimated age, relative developmental stage, skull length, and crown–rump length (CRL) for specimens of *Talpa europaea* included in this study. Relative stage refers to the order of specimens as determined by postcranial ossification sequence (see text for further explanation).

Relative stage	Specimen no.	Age (days)	Developmental stage	Skull length (mm)	CRL (mm)
1	TE-156c	24.7	8	7.81	26.9
2	TE-330d	24.8	8	7.67	27.0
3	TE-127b	25.6	8	8.95	29.8
4	TE-166p	25.5	8	9.35	29.6
5	TE-317a	25.2	8	9.84	28.3
6	TE-137e	26.0	8	10.41	31.0
7	TE-105a	25.2	8	8.60	28.3
8	TE-121e	26.6	9	10.25	33.3
9	TE-318a	26.8	9	9.76	34.0
Subadult 1	NHM 67.287	Subadult		29.90	
Subadult 2	NHM 67.283	Subadult		30.20	

Materials and Methods

Specimens.—An ontogenetic series of 22 prenatal specimens was obtained from the Hubrecht Collection in Utrecht, Netherlands, currently in Berlin (Table 1). Body size (crown–rump length [CRL]) for these specimens ranges from 14 to 34 mm, corresponding to developmental stages 5 to 9 (Barrionuevo et al. 2004; Sterba 1977; Table 1), with the average size at birth being 40–42 mm (Mohr 1933). CRL was measured from digital photographs of whole, unprepared specimens. These specimens were collected in the 1st half of the 20th century and fixed in ethanol. We cleared and double-stained for bone and cartilage following the protocol described in Prochel (2006). Specimens were ordered by postcranial ossification sequence (J. Prochel, in litt.), which generally agrees with the order of body sizes. Only the last 9 specimens showed evidence of bone ossification (visible staining by alizarin red), and, therefore, of the full set of 22 specimens, only 9 specimens were studied in detail here. There is a gap of 3.9 mm CRL between the oldest specimen without any ossified cranial elements and the youngest specimen with ossified elements (relative stage 1), corresponding to a 1.3-day gap in post-conception age (Sterba 1975). Details for the 9 specimens displaying ossified elements are listed in Table 1. Approximate ages for specimens were estimated using the growth curve determined by Sterba (1975) based on an extensive series of embryological specimens of known developmental stage and measured CRL (Table 1).

In addition 2 subadult specimens (sutures not completely fused) from the osteological collection at the Natural History Museum (London) were measured for comparison in the study

TABLE 2.—Measurements (in mm) for each of the variables used in the analyses of allometry of *Talpa europaea*. Relative stages are as in Table 1. Sub = subadult.

Variable	Relative stage										
	1	2	3	4	5	6	7	8	9	Sub 1	Sub 2
Premaxilla length	1.39	1.11	1.31	1.50	1.50	1.57	1.13	1.26	1.58	4.73	4.00
Premaxilla width	2.22	—	2.26	2.88	2.90	2.95	—	3.19	2.76	4.80	5.08
Maxilla length	1.30	1.81	2.16	2.38	2.43	2.68	2.39	2.72	2.21	12.38	12.95
Nasal length	0.55	—	1.07	1.47	1.49	1.65	1.26	1.69	1.39	9.65	10.65
Nasal width	0.85	1.20	1.31	1.46	1.69	1.78	1.54	1.82	1.56	2.45	2.53
Frontal length	0.51	—	1.34	1.42	1.86	1.87	1.15	1.99	2.01	4.58	5.10
Parietal length	4.42	4.19	4.00	4.21	4.55	5.08	4.65	4.89	4.55	11.38	11.40
Squamosal length	1.31	1.91	2.10	2.86	2.96	3.00	2.08	3.42	3.28	8.35	9.13
Supraoccipital width	3.47	4.24	4.05	4.56	4.71	4.75	3.89	4.55	4.64	14.30	13.85
Supraoccipital height	—	0.78	1.00	1.10	1.40	1.54	0.91	2.53	2.20	9.73	10.08
Palatine length	1.11	—	1.50	1.40	1.61	1.63	1.26	1.80	1.67	5.65	5.13
Palatine width	0.95	—	—	0.98	1.10	1.31	1.06	1.20	1.07	5.13	5.08
Basioccipital length	—	0.97	1.33	1.30	1.50	1.54	1.19	1.36	1.30	—	—
Basioccipital width	0.44	0.62	0.49	0.88	0.82	0.75	0.57	0.59	0.88	—	—
Basisphenoid length	—	0.40	—	0.60	0.79	0.80	—	0.89	0.95	—	—
Basisphenoid width	—	0.50	—	0.77	1.03	0.84	0.58	0.96	1.16	—	—

of cranial allometry (Table 1). Digital images of specimens were taken with an AxioCamHRc camera and a Zeiss stereomicroscope for qualitative analysis.

Allometry.—Three-dimensional landmark data were gathered from prenatal specimens using a reflex microscope. Reflex microscopy is a very high precision method of gathering 3-dimensional data, and it is usually used in paleontological, orthodontic, medical, and engineering applications. It has a reported resolution of 1 μm, allowing for high-accuracy measurements of extremely small specimens, such as embryos. This is the 1st use of reflex microscopy for gathering 3-dimensional data from cleared and stained embryological specimens, and it represents a powerful new tool for morphometric studies of development. Specimens were oriented in dorsal, ventral, and lateral view, and 90–152 total landmarks were digitized, including some landmarks that were repeated in multiple views. Three repetitions of each landmark were conducted, and the averages of these repetitions were used in analyses. The measured standard deviation for coordinates is 0.028 mm. Seventeen length measurements (Table 2) were derived from 3-dimensional coordinates. Subadult specimens were measured with calipers for 13 measurements, and the averages of 3 repetitions were used in analyses. Measured error for caliper measurements is 0.12 mm. Basioccipital and basisphenoid length and width were not measured in osteological specimens, because of fusion with neighboring bones obscuring the sutures. Although most studies of allometry use length measurements that span multiple bones, we only analyzed measurements for individual bones. The reason for this choice is simply that measurements incorporating multiple bones cannot distinguish if all of the bones in the measure display the same allometry, or a combination of allometries. This is especially a problem with incompletely ossified skulls, such as in embryological specimens, because there are often large unossified regions between adjacent bones.

Allometry was assessed using bivariate methods. Although multivariate analysis of allometry is perhaps more rigorous (Giannini et al. 2004; Zelditch et al. 2003), it requires large sample sizes, and prenatal specimens for most species are difficult to obtain. Two body size proxies were used: skull length (basion to anterior interpremaxillary suture); and CRL (for prenatal specimens only). Because there is a large size gap between the prenatal and subadult specimens, we conducted 2 analyses using skull length, 1 with all specimens and 1 with only prenatal specimens. We follow the methodology described in Abdala et al. (2001) and Giannini et al. (2004) to assess bivariate allometry. The allometry of variables was assessed with the equation $\log y = \log b_0 + b_1 \log x + \log e$, where y is the dependent variable, x is the body size proxy, b_1 is the coefficient of allometry (slope of the regression line), b_0 is the y-intercept, and e represents the error of the fit. Two methods were used to identify the line of best fit: least-squares regression (LSR), which assumes all error is on the y axis, and reduced major axis regression (RMA), which assumes and minimizes variation on both axes. RMA is better suited to this study, because skull length is measured by the same methods, and with comparable error, as all other variables. A 2-tailed t-test was used to determine if the coefficient of allometry differs significantly from the null hypothesis of isometry ($b_1 = 1$), using a significance value of $P = 0.01$. All analyses were conducted with PAST 1.48 (Hammer et al. 2001)

Because prenatal specimens of all but a few species are difficult to obtain, this study lacks the large sample sizes of many studies of postnatal allometry. The specimens represent a developmental sequence, which is beneficial for qualitative study, but they do not provide multiple specimens of the same age. Thus, statistical analyses may be less robust than in most studies of allometry. However, because bone growth occurs rapidly in prenatal development, it is imperative to consider

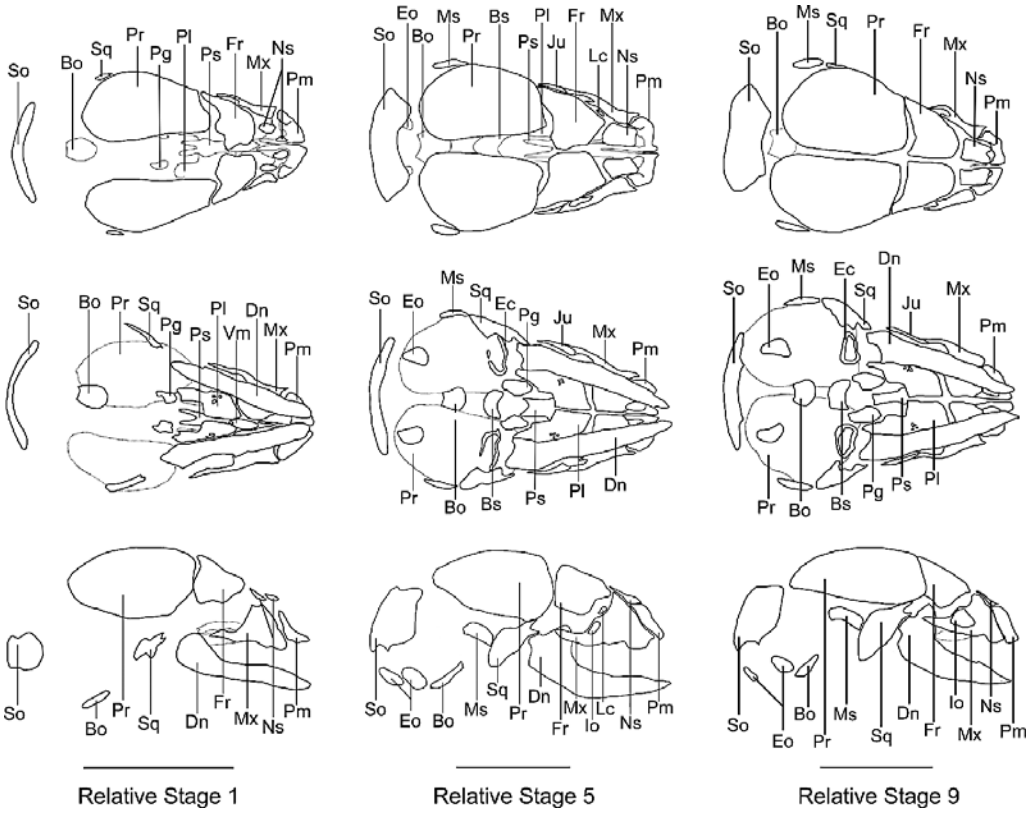

Fig. 2.—Line drawings of relative stage 1, relative stage 5, and relative stage 9 of the skulls of *Talpa europaea* showing ossified elements. Dashed lines refer to ossified elements visible under surface structures. Bo, basioccipital; Bs, basisphenoid; Dn, dentary; Ec, ectotympanic; Eo, exoccipital; Fr, frontal; Io, infraorbital foramen; Ju, jugal; Lc, lacrimal; Ms, mastoid; Mx, maxilla; Ns, nasal; Pg, pterygoid; Pl, palatine; Pm, premaxilla; Pr, parietal; Ps, presphenoid; Sq, squamosal; So, supraoccipital; Vm, vomer. Scale bar is 5 mm.

this period, despite the paucity of specimens. For this reason, we also discuss coefficients of allometry that are marginally significant ($0.05 > P > 0.01$).

Results

The estimated ages of specimens showing ossified cranial bones ranged from 24.7 days (relative stage 1) to 26.8 days (relative stage 9). Of the 14 specimens that did not show any ossified structures, the youngest was 19.8 days old (CRL = 14 mm), and the oldest was 23.4 days old (CRL = 23 mm). Birth usually occurs on day 28 at a CRL of 40–42 mm (Mohr 1933; Sterba 1975).

Qualitative description.—Relative stages 1, 5, and 9 are illustrated in Fig. 2. Two separate ossification centers delimited the nasal bone in the earliest stages examined here. These centers, 1 anteromedial and 1 posterolateral, were fused in relative stages 6 and 8, but were in only weak contact in relative stage 9. The nasomaxillary suture began to develop in relative stage 2 and the nasoincisive suture in relative stage 4. Neither the internasal suture nor the frontonasal suture was formed in any prenatal specimen. The rostral cartilages were pronounced and well developed in all prenatal specimens, as described for other eulipotyphylans (Maier 2002).

The premaxilla and maxilla were already well developed in relative stage 1 and experienced mainly anteroposterior expansion in the prenatal specimens. The border of the incisive foramen was defined in relative stage 2 by the closure of the ventral maxilloincisive suture. It decreased in relative size throughout the prenatal stages, primarily due to the anterior expansion of the maxilla, but it was significantly larger than in adult morphology in all of the prenatal specimens. The maxilloincisive suture developed laterally in relative stage 8, whereas the frontomaxillary suture did not form in any prenatal specimen.

The infraorbital canal was partially formed by a single projection off the zygomatic process of the maxilla in relative stage 3. This projection was fused dorsally by relative stage 5, and its shape resembled the adult condition by relative stage 6.

An ossification center was present within the orbit, posterodorsal to the maxilla, in relative stages 5 and 8. We interpret this ossification center to represent the lacrimal bone, which is impossible to identify in adult skulls. In relative stage 5, this element was dorsoventrally elongate and anteroposteriorly short. In contrast, in relative stage 8, it was curved and longer in the anteroposterior direction. By relative stage 9, the lacrimomaxillary suture had fused completely. No other mammals display ossifications centers for the frontal or maxilla in this position; therefore, it is

TABLE 3.—Results of analyses of allometry in *Talpa europaea*. LSR = least squares regression, RMA = reduced major axis regression, b_1 = coefficient of allometry (slope of the regression line), b_0 = y-intercept of the regression line.

	Skull length (all specimens)					Skull length (prenatal only)					Crown–rump length (prenatal only)				
	LSR		RMA			LSR		RMA			LSR		RMA		
Variables	b_1	b_0	b_1	b_0	R^2	b_1	b_0	b_1	b_0	R^2	b_1	b_0	b_1	b_0	R^2
Premaxilla length	0.96	−0.79	0.99	−0.82	0.98**	0.74	−0.57	1.21	−1.30	0.61	0.68	−0.87	1.60	−2.20	0.43
Premaxilla width	0.54**	−0.09	0.56**	−0.12	0.96**	1.24	−0.78	1.41	−0.94	0.88**	0.95	−0.97	1.65	−2.00	0.57
Maxilla length	1.49**	−1.10	1.50**	−1.11	0.99**	1.72	−1.31	2.05*	−1.63	0.84**	1.67	−2.12	2.73*	−3.67	0.61
Nasal length	1.83**	−1.68	1.87**	−1.73	0.98**	3.43**	−3.22	3.77**	−3.56	0.91**	2.83	−4.08	4.48*	−6.52	0.63
Nasal width	0.52**	−0.35	0.63**	−0.46	0.83**	1.85	−1.62	2.14*	−1.90	0.86**	1.85	−2.57	2.84*	−4.02	0.65
Frontal length	1.15	−0.98	1.32	−1.16	0.88**	4.47**	−4.19	4.75**	−4.45	0.94**	4.22	−6.09	5.64**	−8.19	0.75*
Parietal length	0.77**	−0.08	0.78**	−0.09	0.99**	0.41*	−0.26	0.68	0.00	0.60	0.40	0.07	0.91	−0.68	0.44
Squamosal length	1.13	−0.70	1.19	−0.77	0.95**	2.57**	−2.08	2.83**	−2.33	0.91**	2.99*	−4.01	3.76**	−5.15	0.80**
Supraoccipital width	0.99	−0.31	0.99	−0.32	0.99**	0.76	−0.10	0.95	−0.28	0.80**	0.77	−0.50	1.26	−1.23	0.61
Supraoccipital height	1.77**	−1.60	1.84**	−1.68	0.96**	3.43*	−3.20	4.13**	−3.88	0.83**	4.70**	−6.83	5.20**	−7.57	0.90**
Palatine length	1.12*	−0.91	1.12*	−0.92	0.99**	1.56*	−1.34	1.66*	−1.44	0.94**	1.62	−2.22	1.97*	−2.75	0.82**
Palatine width	1.31**	−1.24	1.32**	−1.25	1.00**	0.87	−0.81	1.08	−1.01	0.80*	0.67	−0.96	1.27	−1.83	0.53
Basioccipital length						1.29	−2.62	1.41	−2.87	0.92**	0.82	−2.53	1.77	−5.77	0.46
Basioccipital width						1.35	−3.41	2.27	−5.45	0.59	1.25	−4.69	3.02	−10.65	0.42
Basisphenoid length						2.62*	−6.25	2.87*	−6.79	0.92**	2.91	−10.28	3.52*	−12.37	0.83*
Basisphenoid width						2.42	−5.64	2.83*	−6.56	0.86**	2.66	−9.29	3.53*	−12.24	0.76*

* $0.05 > P > 0.01$, ** $P < 0.01$.

unlikely that this element represents any other bone than the lacrimal.

The jugal 1st appeared in relative stage 4, and was already in contact with the maxilla. The zygomaticomaxillary suture was barely discernible by relative stage 6, whereas the jugal and squamosal were distant in all of the prenatal specimens examined.

In relative stage 1, a single small ossification center of the squamosal was present, without any indication of the zygomatic process. An anterolateral projection representing the later zygomatic process of the squamosal was evident by relative stage 2. Subsequent growth of the squamosal was primarily in the dorsoventral direction. The squamous suture developed anteriorly in relative stage 8.

The palatine was well developed in relative stage 1 (Fig. 2). The lateral and posterior portions extended far posterior to the ventral wall of the palatine, approaching the pterygoid in relative stage 1. Minor palatine foramina were present in all prenatal specimens. These ranged from 3 to 4 on each side, and they varied in number and morphology within and between specimens. The pterygoid was roughly trapezoidal and inflected along its shorter ventral edge in relative stage 1. The pterygopalatine suture closed by relative stage 2. The ventral tip of the pterygoid was well developed and posteriorly oriented in relative stage 3.

There was a suture between 2 separate ossification centers of the frontal bone in relative stage 1. The coronal suture was developed along the orbital wall in relative stage 1, with significant overlap of the parietal and frontal in relative stage 2. Neither the interfrontal nor sagittal sutures were formed in any prenatal specimen.

There was a single large ossification center of the supraoccipital dorsal to the foramen magnum in the youngest specimen examined. Two small centers of the exoccipital appeared in relative stage 2, ventrolateral to the foramen magnum. The basioccipital was visible in relative stage 1. These 4 centers did not suture in any prenatal specimen, and there was no evidence of a separate interparietal ossification center.

The posterior extent of the presphenoid was approximately equal to that of the palatine in relative stage 1. The vomersphenoidal suture was well developed in relative stage 1. The presphenoid contacted the palatine laterally in relative stage 3. The intersphenoidalis synchondrosis did not form in any prenatal specimen. There was no evidence of an orbitosphenoid in any prenatal specimen. The basisphenoid was not present in relative stage 1, but appeared as a small, elliptical ossification in relative stage 2. It was kidney-shaped in relative stage 4, and the pterygosphenoid suture is formed by anterolateral projections of the basisphenoid in relative stage 5. There was no evidence of an alisphenoid bone in any prenatal specimens.

In relative stage 2, a slender ossification center, posterodorsal to the squamosal and ventral to the parietal, was visible. We interpret this center to represent the mastoid, the dorsal most extension of the petrosal bone (the ''mastoid process'' of Motokawa [2004]). The mastoid and squamosal are fused in adult specimens, leading to different identifications for this part of the skull in several publications (Koppers 1990), although the squamosomastoid suture is visible in juveniles. This element expanded ventrally through the sequence, but it did not exhibit much total growth. The squamosomastoid suture developed in relative stage 9.

The ectotympanic bone began to ossify immediately ventral to the squamosal in relative stage 4 and was well ossified by relative stage 6 (Fig. 2). It was absent in relative stage 7, but this stage appeared to be out of sequence, as discussed below. Reichert's cartilage and the cartilaginous precursor of the tympanohyal were recognizable in relative stage 1, but no

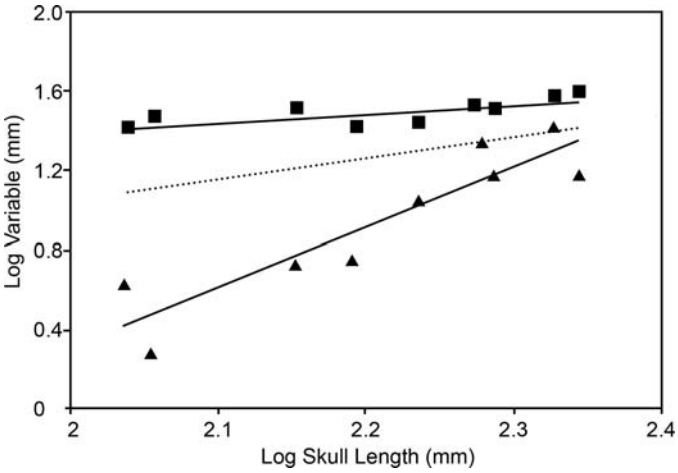

Fig. 3.—Least-squares regression lines for a trait with positive allometry (squamosal length, ▲), and a trait with negative allometry (parietal length, ■), in prenatal specimens of *Talpa europaea*. Dotted line represents perfect isometry.

ossified elements developed from these structures in any prenatal specimen.

In relative stage 1, the Meckel's cartilage spanned the full length of the mandible. By relative stage 6, the Meckel's cartilage was restricted to the most anterior part of the mandible, and was still visible in relative stage 9.

In relative stage 1, the dentary is represented by a partially ossified coronoid process. In relative stage 2, the articular condyle began to ossify, represented initially by a small spike. In relative stage 5, the coronoid process was defined dorsally, but incomplete posteriorly. The mandibular symphysis did not form in any prenatal specimen.

The 1st teeth (1 upper canine and 1 upper and 1 lower premolar) were observed in relative stage 5. Only the upper canine was visible in relative stage 6. No teeth were observed in relative stage 7. The upper canine and 1 upper premolar were visible in relative stages 8 and 9.

Allometry.—When all specimens, prenatal and subadult, were analyzed, LSR and RMA produced similar results (Tables 3 and 4). Skull length was significantly correlated with all 12 variables, with only 2 of 12 correlations falling below 0.90 (Table 3). Across this sample, 4 variables (maxilla length, nasal length, supraoccipital height, and palatine width) displayed significant positive allometry, whereas 1 (palatine length) was marginally significant. Three variables (premaxilla width, nasal width, and parietal length) displayed significant negative allometry. Premaxilla length, frontal length, squamosal length, and supraoccipital width displayed isometric growth.

When only prenatal specimens are examined, with skull length as the body size proxy, most variables were significantly or marginally significantly correlated with skull length (Table 3), with the exceptions of premaxilla lateral length, parietal midline length, and basioccipital width. LSR and RMA results were less consistent in this reduced sample (Tables 3 and 4). With LSR, 3 variables (nasal length, frontal length, and squamosal length) displayed significant positive allometry (Fig. 3; Tables 3 and 4), whereas 3 (supraoccipital height, palatine length, and basisphenoid length) were marginally significant. Only 1 variable (parietal length) showed significant negative allometry (Fig. 3). With RMA, supraoccipital height was added to the variables showing significant positive allometry, whereas 3 more variables showed marginally significant positive allometry (maxilla length, nasal width, and basisphenoid width) than in LSR. No variables display significant negative allometry in the RMA analyses.

Table 4.—Gross results of analyses of allometry in *Talpa europaea*, comparing prenatal and all specimen analysis (skull length only): +, positive allometry; =, isometry; −, negative allometry. LSR = least squares regression, RMA = reduced major axis regression.

	All specimens		Prenatal only	
Variable	LSR	RMA	LSR	RMA
Premaxilla length	=	=	=	=
Premaxilla width	−	−	=	=
Maxilla length	+	+	=	+
Nasal length	+	+	+	+
Nasal width	−	−	=	+
Frontal length	=	=	+	+
Parietal length	−	−	−	=
Squamosal length	=	=	+	+
Supraoccipital width	=	=	=	=
Supraoccipital height	+	+	+	+
Palatine length	+	+	+	+
Palatine width	+	+	=	=
Basioccipital length			=	=
Basioccipital width			=	=
Basisphenoid length			+	+
Basisphenoid width			=	+

The analyses using CRL as a proxy for body size were restricted to prenatal specimens and were markedly different than the analyses using skull length (Table 3). With LSR, only 1 variable (supraoccipital height) showed significant positive allometry, with squamosal length marginally significant. In contrast, with RMA, 3 variables (frontal length, squamosal length, and supraoccipital height) were significantly, positively allometric, and 6 variables (maxilla length, nasal length, nasal width, palatine length, basisphenoid length, and basisphenoid width) showed marginally significant positive allometry. Only 6 variables (frontal length, squamosal length, supraoccipital height, palatine length, basisphenoid length, and basisphenoid width) were significantly or marginally significantly correlated with CRL, and only 1 correlation was greater than 0.90.

Bivariate methods assume that the variable used to estimate size is isometric with size (Giannini et al. 2004). However, skull length may scale allometrically with true body size. CRL is a more established body size metric for embryological specimens, but it is not applicable to subadult osteological specimens. Although there is no obvious independent and isometric variable that can be applied to both prenatal embryological specimens and subadult osteological specimens, we can estimate the potential effect of skull length allometry on these results using the data for skull length and CRL in prenatal specimens. We assessed the isometry of skull length relative to CRL for prenatal specimens. Skull length and CRL were significantly correlated ($R^2 = 0.78$, $P = 0.01$). When skull length

is regressed against CRL, it is not significantly different from isometry using LSR ($b_1 = 1.63$, $P > 0.05$), but it is marginally significantly allometric using RMA ($b_1 = 2.07$, $P = 0.04$). The true coeffiecient of allometry for any variable in analyses using skull length as the proxy for body size is the product of the coefficients of allometry for both variables. Thus, the net effect for analyses using skull length as a proxy for body size is that positive allometries will be underestimated and negative allometries will be overestimated and are actually closer to isometry. This assessment of skull length allometry is not applicable to subadult specimens, as it is unlikely that skull length allometry is linear across this sample. It is possible that skull length is allometric in postnatal development, but it cannot be estimated with the available specimens. Therefore, data tables report the original, uncorrected results of all analyses, for consistency among analyses, but the effect of prenatal skull length allometry will be considered in the discussion.

Discussion

Ages.—The age estimates, based on CRL, suggest that cranial ossification, as recorded by intake of alizarin red, initiated around days 23–24, and progressed rapidly (Table 1). Several cranial bones appeared in relative stage 1 and most were at least in contact with neighboring bones by relative stage 9, representing a time span of 2 days. Unfortunately, there were no specimens for the 27th day of development. Several bones, particularly the dentary, basioccipital, and exoccipital bones, were poorly developed in relative stage 9 and must undergo extensive growth before birth on the 27th day, or extensive postnatal development.

The postcranial ossification order (Prochel 2006) of the prenatal specimens, relative stages 1–9, corresponds to the development of the cranial bones relatively well, with exception of relative stage 7. The developmental morphology of several cranial bones (presence of multiple ossification centers, lack of teeth, lack of ectotympanic, and relative sizes of bones) suggests that it is a younger specimen, perhaps corresponding to relative stages 2–3. The development of the cranium in relative stage 7 matches its size order as well, as it falls between relative stages 2 and 3 in CRL (Table 1). Relative stage 5 is the same size as relative stage 7, and according to the Mohr (1933) and Sterba (1975) methods of age estimation by CRL, the same age. Relative stage 5 appears younger than relative stage 7 in terms of postcranial ossification, but it appears in the correct order, between relative stages 4 and 6, in terms of both cranial and postcranial ossification. This combination of staging methods suggests an anomalous acceleration of postcranial development in the specimen of relative stage 7, independent of its cranial development and overall growth.

Ontogenetic morphology.—Because these specimens reflect the earliest ossification of cranial bones in *T. europaea*, a number of noteworthy morphological changes were described. Among the most useful for phylogenetics is the identification of a number of bones that are undetectable in adults, including the lacrimal, jugal, and mastoid.

The boundaries of the lacrimal bone have not been convincingly identified in any study of talpids (Giere 2002; Jacobs 1816; Koppers 1990), and this study is the 1st known to the authors to identify this structure in *T. europaea*. Indeed, the reason for this lack of certainty about its position becomes obvious in the prenatal specimens, because it was visible only in 2 specimens (Fig. 2), and is presumed to have fused completely with the maxilla by relative stage 9. As noted above, the morphology of the lacrimal varied markedly during its brief appearance, and more specimens bridging this period are needed to assess these changes and its fusion with the maxilla in more detail.

The jugal bone has been a topic of debate among lipotyphlan researchers for decades, with some researchers suggesting that it is absent in talpids (Hutchinson 1976; McKenna 1975), whereas others recognize it in young specimens (McDowell 1958; Parker 1995). We were able to identify the jugal in 2 prenatal specimens (relative stages 4 and 5; Fig. 2), thus confirming that the zygomatic arch in talpids is tripartite. This element was indistinguishable from the maxilla by relative stage 6, again demonstrating the difficulties that workers have encountered with identifying cranial element in adult specimens.

The mastoid, or petromastoid, bone appeared at its dorsal boundary, adjacent to the squamosal and near the parietal, and gradually expanded in the ventral direction in the stages examined here. It is possible that this bone is instead a 2nd ossification center of the squamosal, but a suture between these elements is still visible in juvenile specimens, suggesting that it is a separate bone. This element is fused with the squamosal in adult specimens, and thus is usually referred to as the squamosal in most figures (Jacobs 1816; Koppers 1990; but see Motokawa 2004). It is unusual that the mastoid is the only portion of the petrosal that is ossified in these specimens, because it is the last part to ossify in other placentals, such as the laboratory mouse (Johnson 1933).

The basicranium is another area that is completely fused and pneumatized in adult skulls, with no identifiable sutures between the basioccipital, basisphenoid, presphenoid, and alisphenoid bones. In contrast, these bones were not in contact in any prenatal specimen, and the alisphenoid was not visibly ossified. The late development of these sutures, particularly considering their complete fusion in the subadult specimens we examined, may be of phylogenetic importance, because some of the sphenoid sutures are among the 1st to develop in other placental mammals (Chopra 1957; Giannini et al. 2006; Krogman 1930).

Another character of phylogenetic importance is the absence of a frontopalatine suture, which has been suggested to be a synapomorphy for Eulipotyphla (Asher 2005; Giere 2002; MacPhee and Novacek 1993). In the specimens studied here, the frontal and palatine were distant throughout the prenatal stages, and no other element occupied this space. MacPhee and Novacek (1993) discussed the disruption of the frontopalatine contact by the intrusion of the maxilla, possibly to allow for the rapid postnatal development of permanent dentition in this species, discussed below. This hypothesis of timing of maxilla growth is supported in this study, because there is no expansion

of the maxilla into the orbital region in any of the prenatal specimens. Adult specimens of *T. europaea* clearly display this orbital extension of the maxilla (Giere 2002), thereby limiting the possible growth phase to juveniles.

Talpa europaea is one of many eulipotyphlans to reduce or lose their functional deciduous dentition (Misek and Sterba 1989; Van Nievelt and Smith 2005). Although enamel formation is completed in a full complement of deciduous teeth by birth, these teeth, with the exception of the unreplaced 1st premolar, are resorbed completely within 2 weeks of birth (Misek and Sterba 1989). Juvenile *T. europaea* are weaned at 33 days, by which time they have achieved adult body size (Nowak 1999; Sterba 1980). Therefore, the permanent dentition must erupt within the few weeks between deciduous tooth resorption and weaning. In the prenatal specimens studied here, only canines and premolars were observed. However, previous studies suggest that most of the deciduous teeth develop at approximately the same time (Misek and Sterba 1989). The difference in these studies may reflect the differences among serial sections and alizarin-stained specimens, because histological sections tend to record the onset of events earlier than alizarin staining does (Vogel 1972). Given the poor development of the deciduous dentition, as even the observed teeth do not extend beyond their alveoli, it is possible that other teeth are present but undetectable without sectioning.

Ossification sequence.—Only a few bones appear after relative stage 1, despite the high resolution of this critical period of cranial development offered by these specimens. This demonstrates a large degree of concurrent ossification in the talpid skull. However, a number of elements of note are missing or poorly developed in the prenatal specimens. Most strikingly, we were unable to identify an orbitosphenoid or alisphenoid in any specimen. The alisphenoid ossifies before the basisphenoid and presphenoid in most placental mammals, and often ossifies before or at the same time as the basioccipital (Nunn and Smith 1998; Zeller 1987). Likewise, the orbitosphenoid often ossifies at the same time or before the basisphenoid (Goswami 2007; Zeller 1987). Because the basioccipital, basisphenoid, and presphenoid are all ossified within the first 2 stages examined here, the lack of an alisphenoid or orbitosphenoid represents a marked departure from the ossification sequence pattern observed in other placental mammals. The gap in the orbital and anterior basicranial regions due to these missing bones is conspicuous in all prenatal specimens (Fig. 2). In combination with the weak development of the basisphenoid, basioccipital, and petrosal (mastoid portion) in these prenatal specimens, it appears that much basicranial and orbital development is relegated to the postnatal period in *T. europaea*. These deviations from the typical placental pattern should be considered in future studies of sequence heterochrony, life history, and phylogenetic relationships of talpids.

Allometry.—Studies of allometry are also commonly used to identify possible heterochronic differences among taxa, and there were several interesting allometric patterns noted in this study of *T. europaea*. Because of an insufficient number of juvenile specimens of *T. europaea*, direct comparisons among prenatal and postnatal specimens were not possible. We used a combined set of prenatal + postnatal specimens, in comparison to the prenatal set, as an approximation of differences in allometry between prenatal and postnatal specimens. The combined data set most likely obscures the differences between higher prenatal and lower postnatal allometry, and it is discussed here only as a 1st estimate of these differences. However, it should be noted that the coefficients of allometry for analyses of the combined data set were similar to those observed in studies of postnatal specimens of other mammalian taxa (0.5–2.0—Abdala et al. 2001; Flores et al. 2003; Giannini et al. 2004).

In analyses restricted to prenatal specimens, there were differences between the analyses using skull length and CRL but many of the bones examined (9 of 16) displayed significant or marginally significant positive allometry in both analyses (Tables 3 and 4; Fig. 3). The parietal bone was the only one to show negative allometry in prenatal specimens (Fig. 3), even after correcting for skull length allometry. In contrast, only 5 variables were positively allometric when all specimens (prenatal + subadult) were considered, while 3 were negatively allometric. Two variables that were positively allometric with only prenatal specimens, were isometric when all specimens are analyzed. One measure, nasal width, shifted from positive allometry in prenatal specimens to negative allometry when all specimens were analyzed, providing the strongest example of nonlinear ontogenetic allometry (Tables 3 and 4). Interestingly, the coefficients of allometry, before to correcting for skull length allometry, were on average twice as large in prenatal specimens as in the entire sample, again suggesting that the rate and allometry of bone growth shifts dramatically during the course of ontogeny (Table 3). As stated above, skull length allometry may influence results. However, skull length allometry in postnatal growth is most likely less than in prenatal growth (i.e., closer to isometry). Therefore, these comparisons among uncorrected results probably underestimate the differences between prenatal only and prenatal + subadult analyses.

This high positive allometry in prenatal specimens is unsurprising, as cranial ossification begins only a few days before birth in *T. europaea*. The change in body size was relatively small (2.8 mm skull length and 7.1 mm CRL) in the prenatal specimens from the 1st ossification of cranial elements to oldest prenatal specimen studied. In contrast, cranial bones certainly developed more quickly, with many facial and vault bones in contact by relative stage 9. The linearity of postnatal ontogenetic allometry has been debated in the mammal literature, with some studies supporting linearity (Monteiro et al. 1999; O'Higgins et al. 2001; O'Higgins and Jones 1998; Singleton 2002) and other rejecting it (Hingst-Zaher et al. 2000; Zelditch et al. 1992, 2003). The data presented here afford some evidence of nonlinearity in cranial allometry, with regard to the birth. Previous studies demonstrating nonlinear postnatal allometry have found that allometries stabilize several weeks after birth in both precocial and altricial species, though it is suggested that highly precocial species may stabilize earlier (Zelditch et al. 2003). Given the altriciality of

T. europaea, we hypothesize that cranial allometry stabilizes relatively late in postnatal development, and that the high coefficients of allometry observed in prenatal specimens may continue well into the postnatal period. The timings of transition and stabilization of ontogenetic trajectories and their relationship to overall level of development remain to be tested, but it is clear that explicit study of prenatal allometry has much to offer the debate on linear ontogenetic allometry.

Positive facial allometry and negative neurocranial allometry is a commonly discussed postnatal pattern in mammals (Singleton 2002; Weston 2003). This general pattern is functionally interpreted as reflecting the rapid prenatal development of the brain, relative to the face, which experiences most of its growth postnatally. Thus, one would expect positive allometry of the neurocranium in prenatal specimens. Five of the 9 neurocranial traits analyzed here, including supraoccipital height, frontal length, squamosal length, basisphenoid length, and basisphenoid width, displayed significant positive allometry in most analyses limited to prenatal specimens. However, 1 neurocranial trait, parietal length, showed negative allometry in prenatal specimens, contradicting the prediction. This may be expected if the ossification of the parietal is more tightly linked to the growth of the brain than other neurocranial bones are, and if the growth of the brain decelerates during this period. However, the data presented here are insufficient to test this hypothesis.

In contrast, analyses incorporating all specimens found only 1 neurocranial measure (supraoccipital height) with positive allometry, but found 4 facial measures with positive allometry. Still, analyses with only prenatal specimens generally showed equal or more positive allometry in facial bones, with the exception of palatine width, than did analyses with all specimens. Our results suggest that neurocranial allometry changes at birth more significantly than does facial allometry. Both regions show much positive allometry in prenatal specimens, and coefficients of allometry are generally greater in prenatal specimens.

Because of differences in the measurements used (individual bones versus combined measures) and differences in focus, there are only a few direct comparisons of allometry for individual bones that can be made with previous studies. A series of papers on postnatal cranial allometry in marsupials (Abdala et al. 2001; Flores et al. 2003, 2006; Giannini et al. 2004) provides the most direct comparisons with the data provided in this study. Two measurements (nasal length and palatal breadth) overlap between those studies and the present one, whereas 2 others are similar (palatal length and occipital height). Nasal length, palatine length, and supraoccipital height all display positive allometry in *T. europaea*, in all analyses. Palatine width shows positive allometry only when all specimens are considered. In contrast, nasal length shows positive allometry only in 2 marsupials, *Didelphis* (Abdala et al. 2001) and *Dromiciops* (Giannini et al. 2004), whereas it shows negative allometry in *Lutreolina* (Flores et al. 2003) and isometry in *Dasyurus* (Flores et al. 2006). Palatal width is negatively allometric in most of the marsupials, except *Dasyurus*, in which it is isometric. Palatal length is isometric in all of these taxa except *Dasyurus*, in which it is negatively allometric. Studies of slow lorises (*Nycticebus coucang*—Ravosa 1998), greater galagos (*Otolemur crassicaudatus*—Kieser 2006), and canids (*Canis familiaris*—Wayne 1986) also include comparable measures of palatal length and breadth. Palatal breadth shows negative allometry in both lorises and galagos, but positive allometry in canids. Palatal length is isometric in lorises and canids and negatively allometric in bushbabies. Lastly, occipital height is negatively isometric in all of the marsupials, whereas it has one of the strongest coefficients of positive allometry of the measures examined for *T. europaea*. *T. europaea* differs from all of these taxa in all comparable measurement, except for the positive allometry of palatine breadth seen in canids and *T. europaea*.

Conclusions

Our results show that *T. europaea* differs from other mammals in several ways. The late development of several cranial bones and structures (alisphenoid, orbitosphenoid, orbital wall, and basicranial sutures) is perhaps the most extreme example, and the relationship between timing of ossification and life history requires further investigation with ecologically convergent, fossorial and altricial species, and with other moles. The study of prenatal cranial allometry has few direct comparisons, but there are significant differences between the patterns observed in *T. europaea* and in other mammal species. Some of these differences, such as in occipital height, probably reflect the prenatal–postnatal comparison, whereas others also may reflect species differences. Future work should focus on comparisons of prenatal and postnatal cranial allometry across a wide range of taxa to better understand the evolutionary significance of prenatal allometry and its relationship to adult morphological variation.

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