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Skeletal Development of *Pelobates cultripes* and a Comparison of the Osteogenesis of Pelobatid Frogs (Anura: Pelobatidae)

By

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ABSTRACT The larval skeleton and osteogenesis of *Pelobates cultripes* is described and compared to that of several pelobatoid and non-pelobatoid taxa. Several features of the larval skeleton are of interest, including: absence of a cartilaginous strip between the cornua trabeculae, type of articulation of cornua and suprarostrals, presence of adrostral tissues, and the condition of the otic process. By comparing sequence of ossification events across taxa, several patterns of skeletal development for *Pelobates cultripes* emerge, including: conserved timing of prootic ossification, delayed onset of mentomeckelian ossification, and early formation of vomerine teeth. Several other developmental features, including the absence of a palatine (= neopalatine) bone and the formation of the frontoparietal, also are discussed.

Key Words: Anura, Pelobatoidea, Pelobatidae, desarrollo, osteología, *Pelobates*, *Scaphiopus*, *Spea*.

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RESUMEN Si bien la historia natural y ecología de los pelobátidos son temas que comúnmente se estudian, su osteología y desarrollo son aspectos poco conocidos. En el presente trabajo se describen el esqueleto larval y el desarrollo de *Pelobates cultripes*, y se lo compara con varios taxones tanto pelobatoideos como no pelobatoideos. Varias características del esqueleto larval son interesantes, tales como: la ausencia de una placa etmoidal entre los cuernos trabeculares, el tipo de articulación de los cuernos con los suprarrostrales, la presencia de tejidos adrostrales y la condición del proceso ótico. Cuando se compara la secuencia de los eventos de osificación en diferentes taxones, varios patrones resultan aparentes, incluyendo momento de osificación del prootico conservativo, retardo en el inicio de osificación del mentomekeliano y temprana formación de los dientes del vómer. Otras características del desarrollo, por ejemplo la ausencia de palatino (= neopalatino) y la formación del frontoparietal, también se discuten.

Palabras Claves: Anura, Pelobatoidea, Pelobatidae, development, osteology, *Pelobates*, *Scaphiopus*, *Spea*.

INTRODUCTION

The Pelobatoidea comprises about 95 extant frog species in three families (Pelobatidae, Megophryidae, and Pelodytidae; Frost, 1985; Lathrop et al., 1998), and are distributed throughout the Holarctic and extend into the Old World tropics (Duellman and Trueb, 1986). Within Europe, pelobatoids are represented by at least seven species in two genera (*Pelobates*, *Pelodytes*) and range from southern Sweden and the Iberian Peninsula, east to the Ural Mountains (Frost, 2002). In North America, pelobatoids comprise seven species in two genera (*Scaphiopus*, *Spea*) and range in western North America from southern Canada to southern Mexico (Frost, 2002). Pelobatoids have been the subject of numerous life history and ecological studies (e.g., Driver, 1936; Axtell, 1958; Pfennig, 1990), and have been studied often by morphologists and anatomists (e.g., Sewertzow, 1891; Smirnov, 1992). Unfortunately, most of the works on the group are rarely considered by contemporary authors because they were published in the early part of last century and/or were published in German or Russian. Therefore, works are disparate, and the adult morphology and developmental anatomy of pelobatoids remains poorly understood.

Only a limited number of works describe the morphology of pelobatoids, and few of those have considered their skeletal development. Rodríguez Talavera (1990) described the ossification sequence of *Pelobates cultripes* and *Pelodytes*

punctatus. Wiens (1989) described the larval cranium and skeletal development of *Spea bombifrons*, and Hall and Larsen (1998) described the osteogenesis of *Scaphiopus* (= *Spea*) *intermontana*. Sokol (1981) described the larval cranium of *Pelodytes punctatus* and mentioned several developmental features of *Scaphiopus* (= *Spea*) *bombifrons* and *Pelobates syriacus* (Sokol, 1975; 1981). Ramaswami (1943) described the chondrocranium of *Megophrys parva* and *M. robusta* based on serial sections. Within the genus *Pelobates*, the larval cranium and frontoparietal development of *Pelobates fuscus* have been described (Plasota, 1974; Rocek, 1980; 1988).

Herein, I provide a detailed description of the larval skeleton and osteogenesis of *Pelobates cultripes*, a species for which the development is poorly known, and compare its skeleton to those of several other frogs.

ACKNOWLEDGMENTS

I thank Linda Trueb and Chris Sheil for their comments and Analía Púgener for comments and translation of the Resumen. Miguel Lizana provided the ontogenetic series of *Pelobates cultripes* and José E. González, Museo Nacional de Ciencias Naturales (Madrid), allowed for the loan of adult *P. cultripes*. This work was supported by NSF Grant # DEB 95-21691 (to Linda Trueb), the Natural History Museum of The University of Kansas Panorama Society, and the Colorado Herpetological Society.

MATERIALS AND METHODS

Twenty-one tadpoles of *Pelobates cultripes* from Montalvo, Salamanca, Spain were staged according to the developmental table of Gosner (1960), and were examined for larval cranial and osteological development. These specimens were cleared and double-stained for bone and cartilage following the technique of Taylor and Van Dyke (1985), and were deposited in the herpetological collection of The University of Kansas Natural History Museum (Table 1). The sample represents tadpoles between Gosner Stages 28 and 46. Also, one cleared- and double-stained

adult, two skeletons, and one formalin-preserved *Pelobates cultripes* tadpole, as well as cleared-and-stained developmental series of *Spea multiplicata* and *Spea bombifrons*, were examined (Table 1). Osteological terminology is that of Púgener and Maglia (1997). Terminology of Rocek (1988) was followed for the frontoparietal complex (including the median and lateral extrascapular bones). Descriptions and illustrations were made with the aid of a stereo microscope equipped with a camera lucida.

RESULTS

CRANIAL DEVELOPMENT

Larval cranium.—Description of the larval cranium is based on one Stage 30 specimen, the last stage before ossification of the cranium commences (Fig. 1). The cranium is relatively shallow, with the width (across the posterior margins of the palatoquadrates) about 80% of the length (midline), and the depth (at the level of the processus muscularis quadrati of the palatoquadrate) is only about one-third the length (Fig. 1).

The floor of the braincase is formed by the basal plate (= basis cranii). At the level of the subocular fenestra, the basal plate is pierced by a pair of carotid foramina posteriorly and a pair of craniopalatine foramina anteriorly. Posteroventrally, the notochord is present between the otic capsules. The otic capsules are about one-fourth the length of the cranium and each is pierced ventrolaterally by a large fenestra ovalis. Posteriorly, the jugular foramina exit the

skull at the level of the occipital arch (visible in dorsal and ventral view).

The lateral wall of the braincase is pierced by five foramina (Fig. 1). The most posterior is the large prootic foramen, bordered by the pila antotica anteriorly and the medial wall of the otic capsule posteriorly. The small oculomotor foramen is anterior to the pila antotica and bordered anteriorly by the pila metoptica. A relatively large, ovoid optic foramen is anterior to the pila metoptica and is bordered anteriorly by the pila preoptica. The trochlear foramen is small and pierces the dorsal margin of the pila preoptica, slightly anterior to the level of optic foramen. A small foramen of which the homology is uncertain (Pügener and Maglia, 1997) pierces the dorsal margin of the pila metoptica just posterior to the trochlear foramen. The pilae preoptica, metoptica, and antotica are united dorsally by the orbital cartilage; this cartilage forms the taenia tecti marginalis, the lateral margin of the frontoparietal fenestra. The posterior margin of the frontoparietal fenestra is formed by the tectum synoticum.

The palatoquadrate is broad and C-shaped in dorsal aspect. Posteriorly, it attaches to the braincase via the processus ascendens, just anterior to the otic capsule. The medial end of the processus ascendens lies dorsal to the oculomotor foramen. A flattened otic process (sensu Sokol, 1981) is present. A chondrified otic ligament (= larval otic process of Sokol, 1981) extends from this process to articulate with the lateral margin of the otic capsule. Anteriorly, the commissura quadratocranialis anterior articulates with the lateral margin of the ethmoid plate. The lateral portion, or body, of the palatoquadrate is composed of the arcus subocularis. This wide band of cartilage (width = length) is separated from the braincase by the ovoid subocular fenestra. The processus muscularis quadrati is a broad vertical ridge on the lateral edge of the palatoquadrate, anterior to the orbit. The hyoquadrate process is ventral to the processus muscularis quadrati, which bears a cotyle for articulation with the ceratohyal. Medial to the hyoquadrate process, on the ventral surface of the commissura quadratocranialis anterior, is the anteromedially directed processus quadratoethmoidale, which serves as an attachment for the quadratoethmoidal ligament from the cornu trabeculum. Anterior to the processus muscularis quadrati is the processus articularis quadrati, which articulates with the pars articularis of Meckel's cartilage. Meckel's cartilage articulates posteriorly with the processus anterior quadrati of the palatoquadrate. Dorsomedially, each Meckel's cartilage fuses with the infrarostral cartilages, the paired elements that support the lower beak of the tadpole.

The suprarostal cartilages, the arcuate elements supporting the upper beak of the tadpole, are separated me-

Table 1. Specimens examined. All specimens are deposited in the herpetological collections at the University of Kansas Natural History Museum, except adult *Pelobates cultripes* from the Museo Nacional de Ciencias Naturales, Madrid (MNCN). Stages are after Gosner (1960).

<i>Pelobates cultripes</i>		<i>Spea multiplicata</i>		<i>Spea bombifrons</i>	
Number	Stage	Number	Stage	Number	Stage
288642	28	110109	33	209862	30
288643	28	110109	33	209863	31
288644	29	110109	34	209865	32
288645	29	110109	35	209867	33
288646	30	110109	36	209870	34
288647	31	110109	36	209872	35
288648	31	110109	37	209873	35
288649	31	110106	38	209879	36
288650	32	110106	39	209880	37
288651	32	110107	41	209844	38
288652	33	110107	42	209886	38
288653	35	110108	43	209887	39
288654	38	110108	44	209888	39
288655	39	110121	45	209890	40
288656	40	110123	46	209893	40
288657	40	39776	46	209904	41
288658	41	39776	46	209898	41
288659	41	97355	subad	209908	42
288660	42	49468	Subad	209909	42
288661	43	106225	subad	209913	43
288662	43	86662	adult	209917	44
288663	44	86664	adult	209918	44
288664	44			209921	45
288665	44			209922	46
288666	44			209929	46
288667	45			209936	46
288668	45			209941	adult
288669	45			209942	adult
288670	45				
288671	46				
288672	46				
288673	46				
288674	46				
MNCN					
20241	adult				

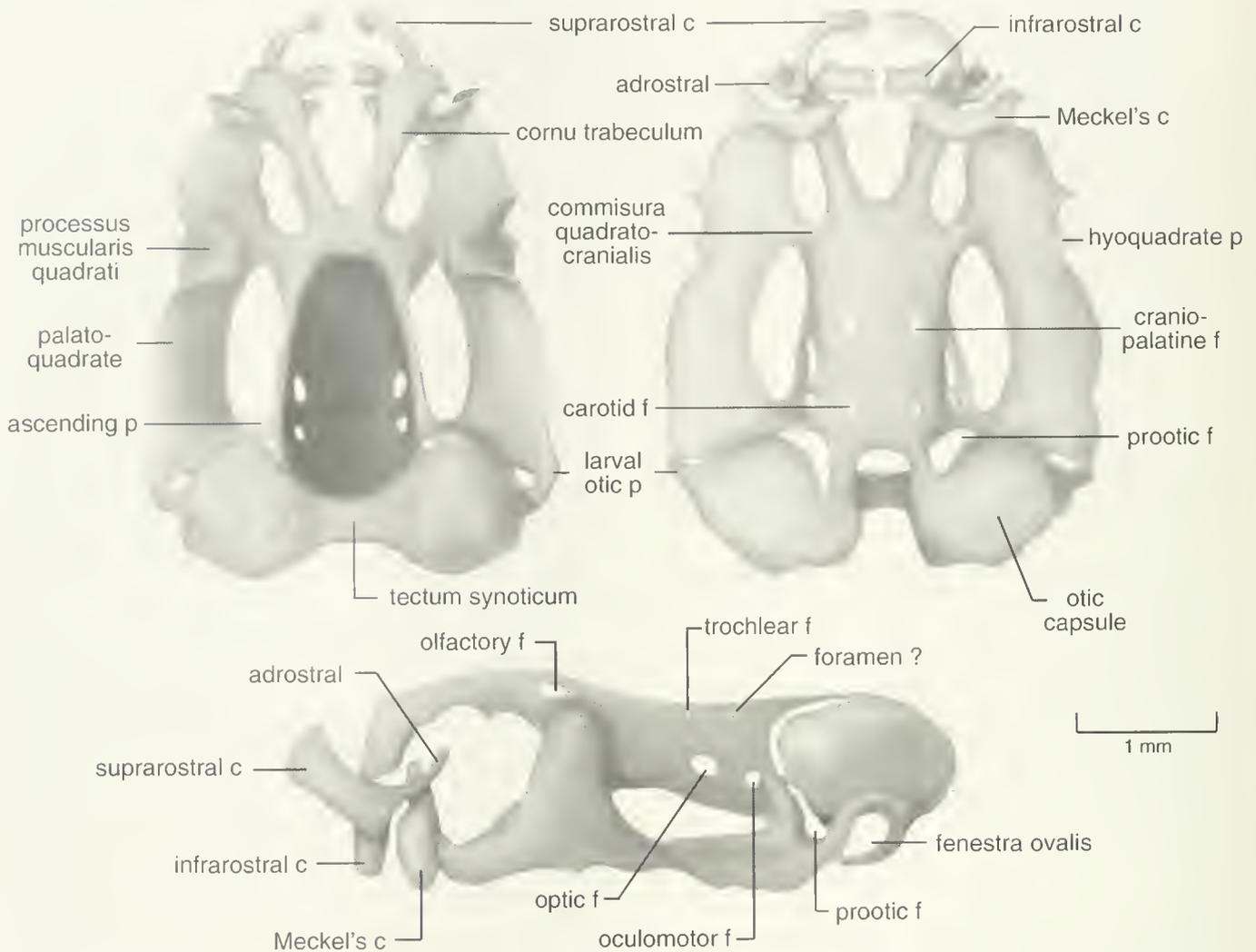


Fig. 1. Larval cranium of *Pelobates cultripes* (Stage 30; KU 288646) in dorsal (left), and ventral (right), and lateral (bottom) view. Gray denotes cartilage; black denotes foramina; c = cartilage, f = foramen, p = process.

dially from one another. Each suprarostrals is composed of a broad corpus and a laterally expanded ala; the corpus fuses ventrolaterally to the ala and bears a processes for attachment to the cornu trabeculum. The suprarostrals are attached to the cornua medially by small ligaments and laterally by what appears to be a synovial joint (similar to that described by Sokol [1981] for *Pelodytes punctatus*). Each suprarostrals ala is directed dorsally and bears a ventral and a dorsal process. Attaching to the dorsal process is a long, thin, dorsally projecting adrostral cartilage (= Suprarostrals 2; Hall and Larsen, 1998; epipraemandibular, Rocek, 1980.)

The planum ethmoidale forms the anterior end of the braincase. Anteriorly, two rodlike cornua trabeculae extend to comprise about 40% the length of the cranium. Throughout their lengths, the cornua diverge from one another anterolaterally. In transverse section, each cornu

is crescentic, with the ventral surface being concave. Ventrally, each cornu bears a short triangular process for the articulation of the quadratoethmoidal ligament. In the proximal lateral wall of each cornu is a large foramen for the lateral nasal ramus of the ophthalmic division of the trigeminal nerve (Gaupp, 1896:131–138).

Ontogeny of larval cranium.—Late in Stage 41, primordia of the alary cartilage, crista subnasalis, and oblique cartilage appear anterior to the planum antorbitale. Metamorphic climax begins around Stage 42, with the start of erosion of the suprarostrals, as well as the commissura quadrato-cranialis anterior and the ascending process of the palatoquadrate cartilage. By Stage 43, the suprarostrals cartilages are absent and the cornua trabeculae are no longer distinct as paired cartilages; instead, they are incorporated into the ethmoid plate and contribute to the solum nasi. Meckel's cartilages and the infrarostral

Table 2. Sequence of skeletal ossification in *Pelobates cultripes* by Gosner (1960) stage at which they first appear.

Stage	Cranial	Postcranial
31	Parasphenoid	Neural arches Centra
32	Frontoparietal	
33	Exoccipital Prootic	
35		Scapula Cleithrum Humerus Radius Ulna Metacarpals Ilium Femur Tibia Fibula Tibiale Fibulare Metatarsals
38		Coracoid Clavicle
39		Hypochord
40		Phalanges of hand Phalanges of foot
41	"Medial extrascapular" "Lateral extrascapular"	
43	Nasals Septomaxilla Premaxilla Maxilla Vomer Vomerine teeth Sphenethmoid Squamosal	Ischium
44	Pterygoid Quadratojugal Dentary Angulosplenic	Sternum Preballux
45	Teeth	Carpal 5
46	Hyoid	

cartilages elongate and articulate at an angle of approximately 180°. By Stage 44, erosion of the commissura quadratocranialis anterior and the ascending process is nearly complete, and the arcus subocularis is absent from the palatoquadrate. Meckel's cartilages fuse to the infrarostrals by this stage. The only remains of the palatoquadrate cartilages, the partes articularis quadrati, migrate posteriorly and slightly ventrally, and lie in a vertical orientation adjacent to the otic capsules.

Ossification of cranial elements.—Sequence of ossification is listed in Table 2.

Sphenethmoids: During Stage 43, the sphenethmoids ossify and fuse to one another dorso- and ventromedially,

giving the impression of a single element. Ossification of the sphenethmoid proceeds slowly, and there is little modification of this bone through Stage 46.

Exoccipitals: The exoccipitals first appear during Stage 33 as thin slivers of bone along the posterior margins of the jugular foramina. Ossification of these elements proceeds from the dorsal regions of the occipital condyles.

Prootics: The prootics first appear in bone as small patches just posterior to the medial articulation of the pars ascendens of the palatoquadrate during Stage 33. Ossification of these elements proceeds steadily, and by Stage 41, most of the anterior margin of the otic capsule is encased in bone. By Stage 43, the prootics and exoccipitals fuse ventrally, and by Stage 46, each otic capsule is encased in bone.

Septomaxillae: Septomaxillae first appear during Stage 43 as laterally oriented slivers of bone, just posterior to the premaxillae. There is little change to these bones through Stage 46.

Nasals: The paired nasals appear during Stage 43, simultaneously with the appearance of the premaxillae, maxillae, septomaxillae, and vomers. Initially, each nasal is a small, triangular sheet of bone, posterodorsal to the septomaxilla. They enlarge slowly, maintaining their original shape; by Stage 46, they develop thin ventrolateral maxillary processes.

Frontoparietals: The paired frontoparietals are first observed during Stage 32. Each develops as a thin sliver of bone dorsal to the taenia tecti transversalis. In later stages, these bones lengthen and broaden, and by Stage 39, their narrow anterior margins lie approximately at the level of the commissura quadratocranialis anterior. During Stage 41, the posterior margin reaches the level of the tectum synoticum.

"Median Extrascapular:" This bone also has been referred to as the interparietal, the parieto-extrascapular, the dermal supraoccipital, and the postparietal (as discussed by Rojek, 1988). During Stage 41, this element appears as a posteromedial ossification dorsal to the tectum synoticum. By Stage 44, this ossification proceeds anteriorly, fuses with the frontoparietals, and covers the frontoparietal fontanelle.

"Lateral Extrascapular:" These elements also have been termed, among others, supraparietals, tabulars, dermosupraoccipitals, retroparietals, and postparietals (as discussed by Rocek, 1988). During Stage 41, these elements appear as small centers of ossification dorsal to the otic capsule. By Stage 44, these elements, along with the "median extrascapular," fuse with the frontoparietal condensations.

Parasphenoid: The parasphenoid, appearing by Stage 31, is the first element to ossify. It appears as a thin, rectangular sheet of bone ventral to the basal plate. Anteriorly,

bone deposition lengthens the cultriform process; posterolaterally, ossification forms the alae, ventral to the otic capsules. By Stage 33, the parasphenoid achieves its adult inverted T shape.

Vomers: These paired elements appear during Stage 43 as tiny centers of ossification anterior to the rostral tip of the parasphenoid; ossified primordia of vomerine teeth also are present. By Stage 46, the anterior, prechoanal, postchoanal, and dentigerous processes are present.

Premaxillae: The alary process is the first part to ossify, and appears concomitant with the nasals and septomaxillae during Stage 43. Each process forms as a thin, anteriorly directed sliver of bone on each side of the cornu trabeculum. The pars palatina and pars dentalis ossify at Stage 44, and premaxillary teeth are present by Stage 45.

Maxillae: The pars facialis is the first portion of the maxilla to ossify (Stage 43). Each maxilla is visible as an anteriorly directed sliver of bone, lying posterior, lateral, and slightly ventral to the premaxillae. During Stage 44, the pars dentalis begins to ossify ventrally, and the palatine process appears lateral to the pars facialis. Primordia of teeth are present by Stage 45.

Mandibles: The infrarostral and Meckel's cartilages begin to elongate and form a horizontal articulation by Stage 43. By Stage 44, the paired angulosplenials ossify anteriorly from a center medial to Meckel's cartilage. Also by this stage, the dentaries are present as long, thin slivers of bone; these ossify posteriorly, lateral to the infrarostral cartilage and extend onto Meckel's cartilage.

Squamosals: Each squamosal appears during Stage 43 as a thin sliver of bone on the medial side of the palatoquadrate cartilage. This center of ossification gives rise to the ventral ramus of the adult squamosal. Zygomatic and otic rami are well developed by Stage 46.

Pterygoids: The posterior ramus is the first to ossify early in Stage 44; it appears as a small, obliquely vertical plate medial to the palatoquadrate cartilage. By Stage 46, the anterior ramus is present, but poorly ossified. The medial ramus does not ossify until after Stage 46.

Quadratojugals: These elements appear by late Stage 44 as two small centers of ossification on the lateral surface of the posterior end of each palatoquadrate cartilage.

HYOBRANCHIAL DEVELOPMENT

Larval hyobranchial skeleton.—At Stage 30, the visceral skeleton consists of Copulae I and II, two ceratohyals, and four pairs of ceratobranchials (Fig. 2). The ceratohyals are robust plates of cartilage connected medially by the pars reuniens to form an elongated transverse bar. Each ceratohyal possesses a broad anterior process, a larger posterior process, a rhomboid hyoquadrate process (= articularis process of de Sá, 1988), and a distally rounded

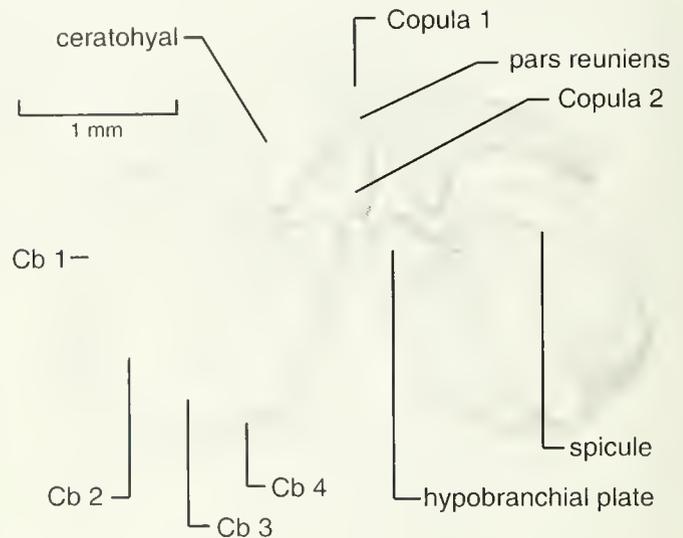


Fig. 2. Hyobranchial apparatus of *Pelobates cultripes* larva (Stage 30; KU 288646) in ventral view; Cb I-IV = Ceratobranchials I-IV.

lateral process. The posterior process unites with the hypobranchial plate via a cartilaginous bridge. Copula I is a well-developed, reniform cartilage. Anteriorly, Copula II fuses to the pars reuniens; laterally it is fused to the hypobranchial plates. Ventrally, Copula II possesses an ovoid urobranchial. Distally, the ceratobranchials articulate via the commissurae terminales and are continuous with the hypobranchial plates. Ceratobranchial I is the widest of the ceratobranchials, but is not well chondrified; Ceratobranchial IV is the most narrow and best chondrified. Long spiculae arise dorsally from the proximal ends of the ceratobranchials and the commissurae terminales.

Ontogeny of hyobranchium.—The hyobranchial apparatus begins to erode by Stage 43 when the ceratohyals lengthen and the ceratobranchials begin to condense and fold over themselves. By Stage 44, the branchial arches are absent and the ceratohyals form elongate hyalia. The hypohyal plates condense at the midline and form rudimentary posteromedial processes by Stage 45. By Stage 46, the laryngeal cartilages are present and well developed, and small posterolateral processes form on the lateral margin of the small hyoid plate. Also by this stage the posteromedial processes begin to ossify.

POSTCRANIAL DEVELOPMENT

Axial skeleton.—By Stage 28, the earliest stage in this series, neural arches of Vertebrae I-IX are present as small, cartilaginous semicircles lateral to the notochord (Fig. 3). Free ribs are absent. By Stage 31, the neural arches of the first seven vertebrae begin to ossify. Also during this stage ossification of the centrum of Vertebra I is faintly visible as a small bifurcated plate dorsal to the notochord, form-

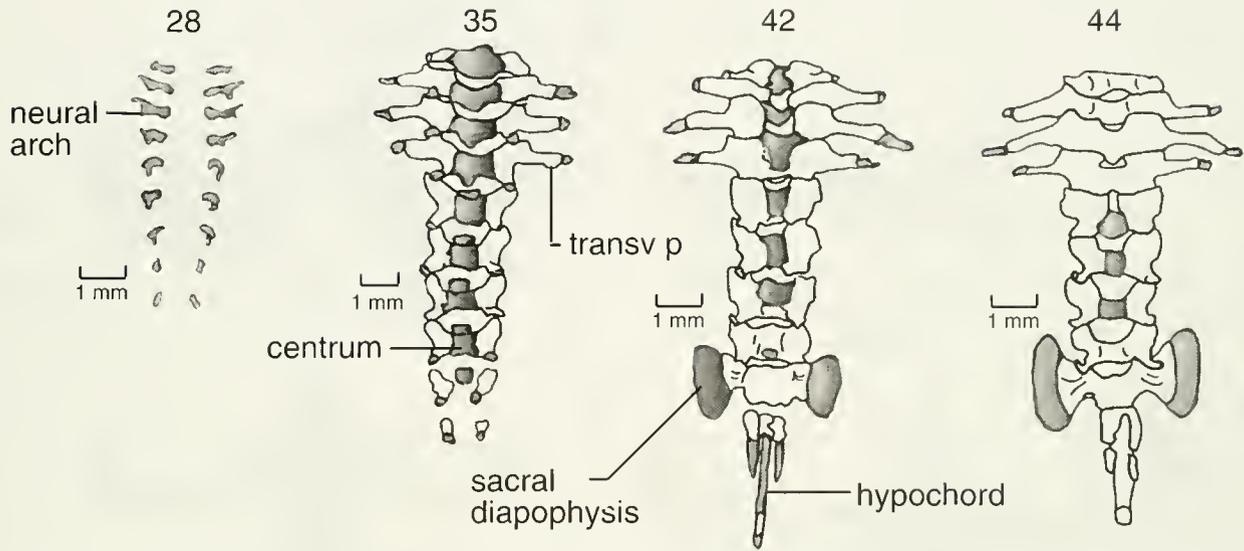


Fig. 3. Development of the axial skeleton of *Pelobates cultripes*. Numbers refer to Gosner (1960) stage. White denotes ossification; gray denotes cartilage; transv p = transverse process.

ing in a typical epichordal condition (Duellman and Trueb, 1986).

The neural arches and centra develop steadily, and by Stage 35 the neural arches of Vertebrae I–X have begun to ossify. Also during this stage, most of the neural arches of the presacral vertebrae (= I–VIII) meet dorsally via a cartilaginous bridge. By Stage 38, the hypochord is present ventral to the notochord; it begins to ossify by Stage 39 (Fig. 3). The vertebral centra all show some ossification by Stage 39.

During Stage 41, Vertebra IX (= sacrum) begins to form small, lateral projecting cartilaginous diapophyses. By Stage 42, these sacral diapophyses begin to ossify (Fig. 3). Also during this stage, small cartilaginous processes form on the posterior margins of the neural arches of Vertebra X. These small processes begin to ossify early during Stage 43, and by late Stage 43, they detach from Vertebra X. Also during this stage, Vertebra X begins to fuse, via its ventrolateral margins, to the sacrum. Because the neural arches of this vertebra are not joined dorsally during this stage, and the centrum is not fully formed, the articulation of Vertebra X and the sacrum appears to be a bicondylar articulation.

By Stage 44, the neural arches of Vertebra X join dorsally and form the dorsal articulation with the sacrum (Fig. 3). The urostyle is formed during Stage 46 when the hypochord fuses to both Vertebra X and its posterior processes.

Pectoral girdle.—The earliest appearance of primordia of the pectoral girdle is during Stage 35, in which each half of the pectoral girdle is composed of cartilaginous precursors of the procoracoid, coracoid, and

scapula/suprascapula. The scapula and suprascapula are fused synchondrotically, constituting one cartilaginous unit (Fig. 4).

Ossification of the scapula/suprascapula begins by Stage 35 as a small, barely visible narrowing between the elements. Also at this stage, dermal ossification of the cleithrum begins. During Stage 38, the coracoid and clavicle commence ossification and the epicoracoid cartilages appear. By Stage 39, the epicoracoids form well-developed medial cartilaginous bridges between the procoracoid cartilages and the coracoids (Fig. 4). Ossification of all elements continues steadily, and by Stage 43, the two halves of the pectoral girdle overlap at their ventromedial margins. Early in Stage 44 the sternum appears posterior to the epicoracoid cartilages as an elongate piece of cartilage (Fig. 4); by late Stage 44, the sternum begins to ossify.

Forelimb.—None of the forelimb elements are present by Stage 33, but by Stage 35, the humerus, radius, ulna, metacarpals, Element Y, radiale, ulnare, Carpals 2–5, and several phalanges appear in cartilage (Fig. 5). Also by this stage there are small centers of ossification at the midpoint of the long bones and metacarpals. By Stage 39, the radius and ulna fuse at their medial margins, and Carpal 1, two prepollical elements, and the remaining phalanges appear (Fig. 5). At this stage, all phalanges are present and represent the adult formula of 2-2-3-3. By Stage 43, all metacarpals and phalanges and Carpal 5 have begun to ossify. None of the remaining carpal elements is ossified by Stage 46 (Fig. 5).

Pelvic girdle.—By Stage 35, the ilium, ischium, and pubis are present, although the pubis is thin and transparent (Fig. 6); slight ossification of the ilium is apparent at the midpoint of the shaft. The ilium elongates anteriorly

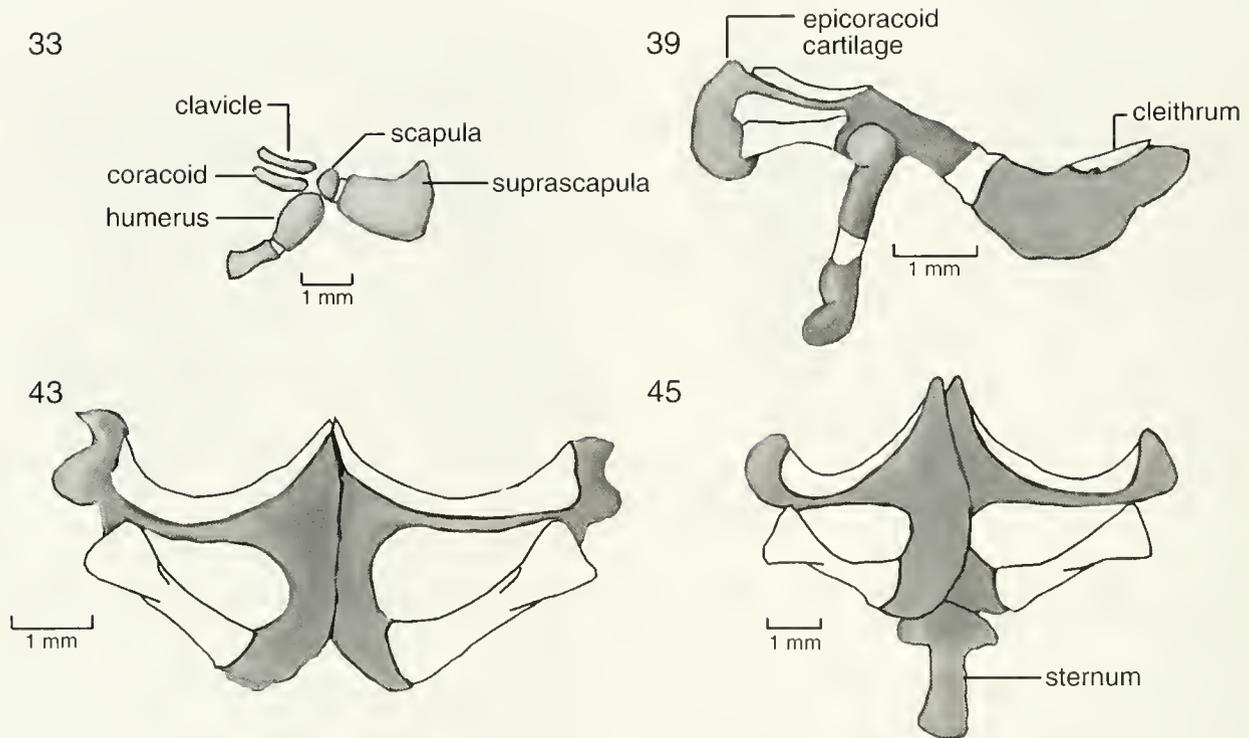


Fig. 4. Development of the pectoral girdle of *Pelobates cultripes*. Numbers refer to Gosner (1960) stage. Top illustrations are shown lateral view; bottom illustrations are shown in ventral view. White denotes ossification; gray denotes cartilage.

as the ventromedial borders of the ischia migrate toward one another. By Stage 42, the two sides of the pelvic girdle fuse at the midline and the ilia attach to the developing sacral diapophyses just anterior to the midpoint of the ilial shaft (Fig. 6). During Stage 43, the ischium begins to ossify, ventral to the acetabulum. The pubis remains cartilaginous through Stage 46.

Hind limb.—No hind limb elements are evident before Stage 35. By this stage, the long bones, Tarsal 1, combined Tarsal 2 + 3 + 4, most of the metatarsals, and the

prehallux (= spade) are present (Fig. 7). Also by Stage 35, ossification of the long bones and metatarsals commences. By Stage 38, all of the elements of the adult skeleton are present, with the phalangeal formula of 2-2-3-4-3. Also by this stage the prehallux begins to elongate and broaden into its adult spadelike form. By Stage 41, all of the phalanges have begun to ossify (Fig. 7). The spade ossifies during Stage 44. None of the tarsal elements is ossified by Stage 46.

DISCUSSION

In comparing my results with published observations and the larval skeletons of other pelobatids, I found several features of the larval skeleton and osteogenesis of *Pelobates cultripes* that are of interest. These include: the absence of a cartilaginous strip between the cornua trabeculae, the type and position of the articulation of the cornua trabeculae and suprarostral cartilages, the presence of adrostral tissues, the condition of the otic process, and the formation of the frontoparietal. There are also several differences in the relative timing of ossification events that vary among pelobatoids and/or other frog taxa.

Among pelobatoids, the cornua trabeculae may or may not be joined to one another medially by a cartilaginous strip. In *Pelobates cultripes*, the cornua diverge from one

another at their bases (at the level of the planum antorbitale), and no cartilage is present between them. This is also the condition in *Pelobates fuscus* (Rocek, 1980) and *Megophrys parva* (Ramaswami, 1943). However, in other pelobatoids, such as *Spea intermontana* (Hall and Larsen, 1998), *S. bombifrons* (Wiens, 1989; pers. obs.), and *Pelodytes punctatus* (Sokol, 1981), the cornua are connected to one another medially via a cartilaginous strip.

The type and position of the suprarostral/cornu trabeculum articulation differ among pelobatoid groups. In *Pelobates cultripes*, the cornua articulate laterally with the alae of the suprarostrals. This articulation is both syndesmotomic (via small ligaments at the medial portions of the articulation) and synovial (laterally), but does not appear

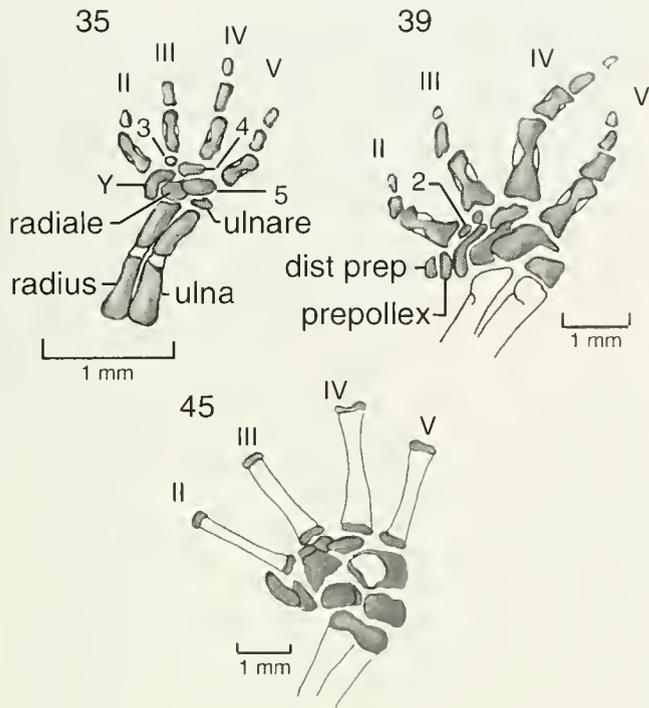


Fig. 5. Development of the right manus of *Pelobates cultripes*. Numbers refer to Gosner (1960) stage. White denotes ossification; gray denotes cartilage. Digits are numbered (Roman numerals) according to Fabrezi (1992); 2-5 = Carpals 2-5; Y = Element Y; dist prep = distal prepollex.

to have a synchondrotic component. In *Pelodytes punctatus*, the cornua articulate with the corpus of the suprarostrals by joints that are synchondrotic medially, synovial laterally, and syndesmotic more laterally (Sokol, 1981). In *Spea intermontana*, the cornua attach to the corpus of the suprarostrals by way of a synchondrotic articulation (Hall and Larsen, 1998). The articulation in *Spea bombifrons* (Wiens, 1989; pers. obs.) and *Spea multiplicata* (pers. obs.) is also via the suprarostal corpus, but it is syndesmotic in these taxa. Although the type of articulation in *Megophrys parva* was not reported by Ramaswami (1943:plate 1; fig. 1), it appears to include the suprarostal ala.

The presence of adrostral cartilages (= Suprarostal 2; Hall and Larsen, 1998) or undifferentiated adrostral connective tissue masses varies among pelobatoids. In *Pelobates cultripes*, there are well-developed, elongate adrostral cartilages present at the posterolateral margins of the suprarostrals. These also are present in *Pelobates fuscus* (Sewertzow, 1891:fig. 1; Rocek, 1980) and in *Megophrys parva* (Ramaswami, 1941). Sokol (1981) suggested that these tissues were present, but unchondrified, in *Pelodytes punctatus* and *Spea bombifrons*. However, neither Hall and Larsen (1998; *Spea intermontana*), Wiens (1989; *S. bombifrons*), nor myself (*S. bombifrons*, *S. multiplicata*)

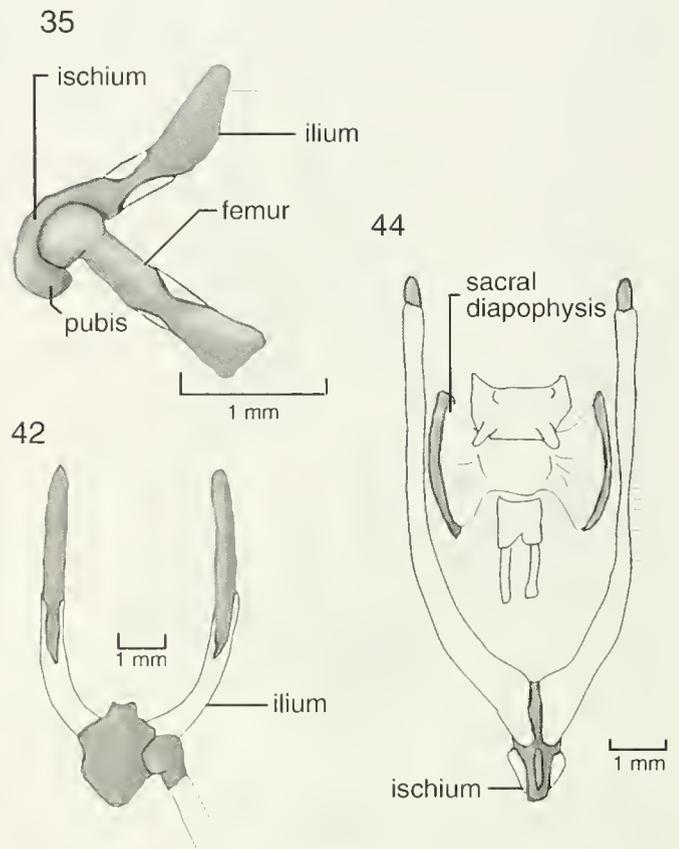


Fig. 6. Development of the pelvic girdle of *Pelobates cultripes*. Numbers refer to Gosner (1960) stage. Top left illustration is shown lateral view, bottom left illustration is shown in ventral view, right illustration is shown in dorsal view. White denotes ossification; gray denotes cartilage.

found these tissues in *Spea*. But, as pointed out by Hall and Larsen (1998), this may be an artifact of the methods by which specimens were prepared.

There is considerable variation in the condition of the posterolateral portion of the palatoquadrate. In *Pelobates cultripes* the palatoquadrate is posterolaterally flattened to form a thin plate called the otic process (Sokol, 1981). Extending from the otic process, to articulate with the otic capsule, is a chondrified otic ligament, which, when chondrified, is referred to as the larval otic process (Sokol, 1981). In *Pelodytes punctatus* and *Megophrys parva*, the otic process resembles that in *Pelobates cultripes* (Sokol, 1981). However, with the exception of some species of *Megophrys* (Sokol, 1981), the otic ligament does not chondrify. In *Spea intermontana* (Hall and Larsen, 1998), *Spea bombifrons* (Wiens, 1989), and *Spea multiplicata* (pers. obs.), the otic process is thick and rounded, and forms a cuplike structure (referred to as the "primitive" condition by [Sokol, 1981:176] and Hall and Larsen [1998:219]). There is a robust, unchondrified otic ligament connecting the otic process and the otic capsule. At the anterolateral margin of

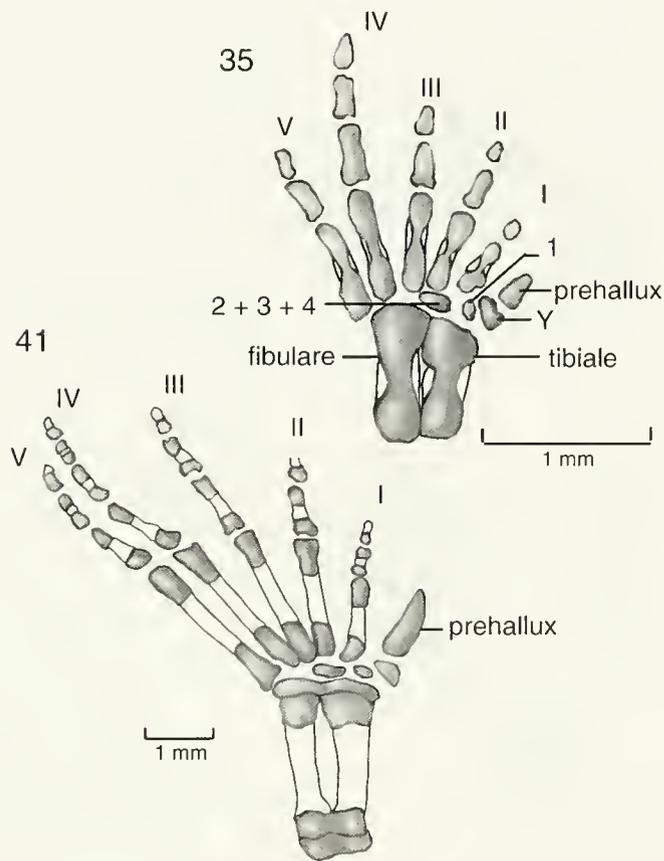


Fig. 7. Development of the right foot of *Pelobates cultripes*. Numbers refer to Gosner (1960) stage. White denotes ossification; gray denotes cartilage. Digits are numbered I-V. Abbreviations: 1 = Tarsal 1; 2+3+4 = combined Tarsal 2+3+4; Y = Element Y.

the otic capsule there is a small cartilaginous process, the larval crista parotica (Pusey, 1938; de Sá, 1988), for the attachment of the otic ligament.

In *Pelobates cultripes*, the element covering the frontoparietal fontanelle develops from five centers of ossification. Although a similar pattern of dermal roof formation has been reported for *Pelobates fuscus* and the extinct †*Eopelobates* (Rocek, 1988), it has not been reported for any other extant taxon. Other authors (e.g., Cannatella, 1985; Henrici, 1994) have referred to this roofing element as the frontoparietal; however, based on topological position and timing of ossification, the medial and posterolateral elements are not homologous with the frontoparietal of other anurans.

The presence of a palatine bone (= neopalatine of Duellman and Trueb, 1986) in pelobatoids has been a point of speculation and contention for many authors (e.g., Zweifel, 1956; Kluge, 1966; Rocek, 1980). It has been suggested that the palatine has been lost or has been fused to either the vomer or the maxilla (as discussed by Rocek, 1980). Hall and Larsen (1998) suggested that the palatine

was present in *Spea intermontana* based on the existence of two centers of vomerine ossification. They suggest that the posterolateral ossification center, which subsequently fuses to the medial ossification center, is most likely the palatine bone. Their argument is based primarily on topological similarity. However, as was mentioned by Hall and Larsen (1998), two centers of ossification have been reported in *Pseudacris triseriata* which also possesses a palatine bone (Stokely and List, 1954). Although topological similarity may help us recognize potentially homologous structures, it is not a valid criterion for determining homology (del Pinna, 1991). A test of congruence (Patterson, 1982), or the presence of both potentially homologous structures in the same organism, can be used to negate homology. Therefore, it is inappropriate at this point to suggest that a palatine is present in pelobatoids.

The sequence of ossification of cranial elements in *Pelobates cultripes* resembles that of most other anurans (Tables 3, 4); however, a few differences warrant further discussion. In comparing my results with those of Rodríguez Talavera (1990) on *P. cultripes*, I found few differences (Table 3), most relating to the timing of ossification of the upper and lower jaw. These variations most likely are the result of either interindividual/population differences or the limited number of static stages in our respective ontogenetic series. Contrary to Rodríguez Talavera (1990), in my sample, I found that the vomerine teeth begin forming at the same time (but from a separate ossification center) as the body of the vomer. I am not aware of the mention of early vomerine tooth development in any other pelobatoid, nor did I find evidence of this in *Spea bombifrons* or *S. multiplicata*.

Compared to other taxa, the timing of ossification of the prootic seems to be similar among pelobatoids (or at least pelobatids, sensu Ford and Cannatella, 1993). The prootic begins to ossify either immediately following the onset of ossification of the parasphenoid, frontoparietal, and exoccipital (always the first three elements to ossify) or concomitant with the formation of the exoccipital (after the onset of ossification of the parasphenoid and frontoparietal). In the basal taxa considered (*Bombina*, *Discoglossus*), the prootic ossifies much later in development (postmetamorphosis).

In *Pelobates* and *Pelodytes*, the mentomeckelian is one of the last bones to ossify (postmetamorphosis). In other pelobatid taxa, the mentomeckelian ossifies before metamorphosis. This may either be the result of precocial development of the mentomeckelian in *Spea* or delayed ossification in other taxa. Because of the presence of both patterns in non-pelobatoid taxa, it is difficult to determine the evolution of this pattern within the pelobatoids.

By comparing the relative timing of ossification of skeletal regions (cranial, axial, forelimb, hind limb) among taxa

Table 3. Comparison of cranial ossification sequences among pelobatoid taxa. Bars to the left indicate elements appearing simultaneously. Data for *Spea multiplicata* were coded directly from specimens (Specimens Examined). Other data were collected from literature as follows: *S. bombifrons*, Wiens (1989); *S. intermontana*, Hall and Larsen (1998); *Pelobates cultripes* and *Pelodytes punctatus*, Rodríguez Talavera (1990).

<i>Pelobates cultripes</i>	<i>Pelobates cultripes</i> ^a	<i>Pelodytes punctatus</i>	<i>Spea intermontana</i>	<i>Spea multiplicata</i>	<i>Spea bombifrons</i>
parasphenoid	parasphenoid	parasphenoid	parasphenoid	parasphenoid	parasphenoid
frontoparietal	frontoparietal	frontoparietal	frontoparietal	frontoparietal	frontoparietal
exoccipital	exoccipital	exoccipital	exoccipital	exoccipital	exoccipital
prootic	prootic	prootic	prootic	prootic	prootic
"medial extrascapular"	"medial extrascapular"	premaxilla	premaxilla	premaxilla	premaxilla
"lateral extrascapular"	"lateral extrascapular"	septomaxilla	nasal	nasal	nasal
premaxilla	premaxilla	nasal	septomaxilla	septomaxilla	maxilla
nasal	septomaxilla	maxilla	maxilla	maxilla	septomaxilla
maxilla	nasal	squamosal	angulosplenic	dentary	squamosal
septomaxilla	maxilla	angulosplenic	dentary	squamosal	angulosplenic
vomer	squamosal	dentary	vomer	angulosplenic	vomer
sphenethmoid	angulosplenic	vomer	pterygoid	vomer	dentary
squamosal	vomer	pterygoid	pterygoid	pterygoid	pterygoid
pterygoid	dentary	sphenethmoid	hyoid	sphenethmoid	sphenethmoid
quadratojugal	teeth	-Metamorphosis-	quadrate	hyoid	hyoid
dentary	pterygoid	sphenethmoid	neopalatine	mentomeckelian	mentomeckelian
angulosplenic	sphenethmoid	quadratojugal	sphenethmoid	quadrate	quadrate
teeth	quadratojugal	hyoid	mentomeckelian	-Metamorphosis-	stapes
hyoid	hyoid	mentomeckelian	-Metamorphosis-	stapes	operculum
-Metamorphosis-	-Metamorphosis-	stapes	dermal	operculum	-Metamorphosis-
mentomeckelian	mentomeckelian	operculum	sphenethmoid		
			stapes		

^aFrom Rodríguez Talavera (1990).

(Table 5) several patterns emerge. In the taxa compared, the cranium is generally the first portion of the skeleton to ossify; it may or may not occur simultaneously with the onset of ossification of other skeletal regions. In the taxa considered, the only exception to this is in *Rhinophrynus dorsalis*, in which the axial skeleton begins to ossify one Gosner stage earlier than the cranium. In the series of *Pelobates cultripes* that I examined, I found that the cranium and axial skeleton begin ossification by the same stage. This differs from Rodríguez Talavera's (1990) findings that the cranium begins to ossify two stages earlier than the axial skeleton in *P. cultripes*. This may be the result of individual or interpopulational variation, differences in rearing environment, or an artifact of specimen preparation.

Variation in ossification sequence within a species has been shown by several authors (e.g., Hall and Larsen, 1998; Moore, 1989) and should be considered when making interspecific comparisons.

In the three species of *Spea* examined (Table 5), the cranium ossifies one Gosner stage earlier, or concomitantly with, the remaining skeletal regions, all of which ossify at the same time. In the other pelobatoids examined, the cranium ossifies much earlier than the appendicular skeleton—at least three or four Gosner stages earlier. It is possible that this pattern represents a heterochronic change in *Spea* relative to other pelobatoid taxa. However, because the timing of ossification events in *Scaphiopus* are not known, it is premature to speculate on the significance of this phenomenon.

Table 4. Comparison of cranial ossification sequences among non-pelobatoid taxa. Bars to the left indicate elements appearing simultaneously. Data were collected from literature as follows: *Bombina orientalis*, Maglia and Pügener (1998); *Discoglossus sardus*, Pügener and Maglia (1997); *Rhinophrynus dorsalis*, Trueb (1985); *Xenopus laevis*, Trueb and Hanken (1992); *Chacophrys pierotti*, Wild, (1999); *Hyla lanciformis*, de Sá (1988).

<i>Bombina orientalis</i>	<i>Discoglossus sardus</i>	<i>Rhinophrynus dorsalis</i>	<i>Xenopus laevis</i>	<i>Chacophrys pierotti</i>	<i>Hyla lanciformis</i>
parasphenoid frontoparietal exoccipital septomaxilla premaxilla nasal vomere maxilla — -Metamorphosis- angulosphenial squamosal dentary quadratojugal pterygoid sphenethmoid prootic interfrontal mentomeckelian	parasphenoid frontoparietal exoccipital premaxilla septomaxilla nasal maxilla vomere angulosphenial dentary squamosal quadratojugal teeth -Metamorphosis- sphenethmoid pterygoid prootic mentomeckelian	parasphenoid exoccipital frontoparietal maxilla prootic nasal premaxilla sphenethmoid angulosphenial dentary quadratojugal septomaxilla squamosal vomere pterygoid -Metamorphosis-	frontoparietal parasphenoid exoccipital prootic angulosphenial maxilla premaxilla nasal septomaxilla dentary pterygoid squamosal vomere sphenethmoid — -Metamorphosis-	frontoparietal parasphenoid exoccipital premaxilla maxilla septomaxilla angulosphenial squamosal prootic nasal vomere dentary pterygoid sphenethmoid quadratojugal -Metamorphosis-	frontoparietal parasphenoid exoccipital prootic premaxilla septomaxilla maxilla nasal angulosphenial squamosal dentary sphenethmoid mentomeckelian -Metamorphosis- quadratojugal vomere pterygoid palatine stapes

Table 5. Relative timing of ossification of skeletal regions of pelobatoid and non-pelobatoid frogs. See legends of Tables 3 and 4 for sources of data. Numbers refer to Gosner (1960) stages, except for *Spea intermontana*, which were staged according to the table of Hall et al. (1997). Gosner stages are provided only to facilitate comparisons of relative ossification of skeletal regions. Comparisons of Gosner stages at which events occur are not appropriate among taxa (Maglia and Pügener, 1998).

Region	<i>Pelobates cultripes</i>	<i>Pelobates cultripes</i> *	<i>Spea multiplicata</i>	<i>Spea bombifrons</i>	<i>Spea intermontana</i>	<i>Pelodytes punctatus</i>
cranial	31	34	37	36	36	34
axial	31	36	38	36	37	35
forelimb	35	38	38	36	37	37
hind limb	35	38	38	36	37	37

* From Rodríguez Talavera (1990).

Region	<i>Bombina orientalis</i>	<i>Discoglossus sardus</i>	<i>Rhinophrynus dorsalis</i>	<i>Xenopus laevis</i>	<i>Chacophrys pierotti</i>	<i>Hyla lanciformis</i>
cranial	37	34	33	34	38	32
axial	37	36	32	35	38	33
forelimb	37	36	37	39	38	37
hind limb	36	36	37	39	38	38

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