Ontogeny of Cranial Ossification in the Eastern Newt, *Notophthalmus viridescens* (Caudata: Salamandridae), and Its Relationship to Metamorphosis and Neoteny

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ABSTRACT

The ontogenetic sequence of cranial osteogenesis through adulthood is described in samples of newts from completely metamorphosing and partially neotenic populations. Cranial ossification proceeds in the same sequence in both samples. Seven stages of cranial development are described on the basis of conspicuous events that occur during ontogeny. These include four larval stages, metamorphs, efts, and adults. Neotenic adults have skulls that are metamorphosed completely and indistinguishable from the skulls of non-neotenic adults. Neoteny in these newts does not involve the skull and is limited to the postmetamorphic retention of some gill structures and, thus, is termed “limited neoteny.” The evolution of limited neoteny in newts as a correlated response to the inhibition of land-drive behavior is discussed.

Adult cranial osteology has played an important role in the classification of salamanders (notably, Cope, 1889; Dunn, ’26; Noble, ’31; Regal, ’66; Tihen, ’58; Wake, ’66; Wake and Ozeti, ’69). Many previous studies have detailed aspects of cranial structure and ontogeny, and related them to ecological specializations and metamorphosis (Fox, ’54; Monath, ’65; Papendieck, ’54; Parker and Dunn, ’64; Regal, ’66; Srinivasachar, ’62; Worthington and Wake, ’71; and references therein). Because neoteny (Pierce and Smith, ’79) occurs in all families of urodeles (Porter, ’72), meaningful comparisons of adult cranial structures are sometimes difficult to achieve. Likewise, because of differences in larval ontogeny, comparisons of larval cranial structures are also difficult to use (Larsen, ’63). Comparisons of complete ontogenetic sequences can provide a better basis from which to group salamander taxa and to interpret the ontogenetic details of neoteny and metamorphosis that are needed to support theoretic models relating ontogeny to phylogeny (Alberch et al., ’79; Alberch, ’85; Fink, ’82). Nevertheless, whole sequences of skull development have been described for only seven species of salamanders (*Salamandra salamandra*, Stadtmuller, ’24; *Eurycea bislineata*, Wilder, ’25; *Triturus vulgaris*, Erdmann, ’33; *Ambystoma mexicanum*, Keller, ’46; *Ambystoma texanum*, Bonebrake and Brandon, ’71; *Rhyacotriton olympicus*, Worthington and Wake, ’71; and *Aneides lugubris*, Wake et al., ’83).

A description is presented here of the ontogenetic sequence of cranial ossification, through adulthood, in two populations of the eastern newt, *Notophthalmus viridescens*, one of which is neotenic.

The salamander genus *Notophthalmus* is one of two genera of the family Salamandridae in the Nearctic Region. The eastern newt, *N. viridescens*, is the most widely distributed of the three species in the genus. It occurs throughout the eastern half of North America in a variety of habitats in which it displays alternative life history strategies (Gage, 1891; Pope, ’24, ’28; Noble, ’26, ’29; Bishop, ’41; Healy, ’70, ’73, ’74; Conant, ’75). The normal life cycle of *N. viridescens* involves aquatic eggs, aquatic larvae, a terrestrial juvenile (eft) stage of variable duration and a largely aquatic adulthood. In some areas the eft stage frequently is bypassed through neoteny (Mecham, ’67). Comparison of the ontogenetic sequences of craniogenesis in normal and neotenic populations will provide details on the relationship between neoteny and metamorphosis and on the functional and adaptive significance of neoteny in newts.

MATERIALS AND METHODS

A total of 206 specimens of *Notophthalmus viridescens*, representing two subspecies, was
examined. A series of 137 *N. v. louisianensis* at various developmental stages was collected during August 1983 to July 1984 from McGuire's Pond, 9.7 km south of Carbondale, Jackson Co., Illinois. Branchiate adults occur in this population (Brandon and Bremer, '66; Albert, '67) and comprised 68% of the adults at the time of collection. Another 10 larvae (September 1973), presumed to be neotenic juveniles on the basis of size and degree of branchiation, and an additional five branchiate adults (collected from November 1966 to July 1967) were examined from the same locality. For comparison, a series of *N. v. viridescens* containing 39 larvae (July 1966), 10 emergent efts (August 1975), and four larger efts (June, 1983) was examined from a population in which neoteny does not occur (Chadwick, '44, '50) at Lake Ravenel and vicinity, Highlands Biological Station, Macon Co., North Carolina. Numbers of specimens representing each stage of development are indicated in Table 1. The ontogeny of the hyobranchial apparatus will be described in a separate paper.

All specimens were killed in 10% ethanol or chloroform and fixed in 10% formalin. Sex and snout-vent lengths were recorded before the specimens were cleared and double-stained by the bone-cartilage staining procedure of Hanken and Wassersug ('81). Skulls were examined under a binocular dissecting microscope at a magnification of $\times 10$ to $\times 25$ and drawn with the aid of a camera lucida. Voucher specimens are deposited in the Museum of Natural History, University of Kansas (KU 203905-203988).

**RESULTS**

Seven developmental stages are defined on the basis of conspicuous developmental events during cranial ontogeny (Table 1). All cranial bones are paired except the parasphenoid and premaxilla, and are bilaterally symmetrical until the Eft Stage. Slight asymmetry in the paired bones and irregular suture lines develops after metamorphosis. Cranial ossification proceeds in the same sequence in newts from both geographic areas.

**Teeth**

The first ossification occurs in tooth-bearing elements early in Stage I when yolk is depleted and the ability to capture food becomes important. Teeth form first on the coronoid. Premaxillary, vomerine, palatine, and dentary teeth mineralize just before the respective bones ossify, early in Stage I (Fig. 1A, B), when balancers are still present. Teeth do not appear on the maxillary bone until late in the Eft Stage, and then only on the anterior portion and never on the jugal extension. Through metamorphosis all teeth are simple, pedicellate, and sharply pointed. Late in the Eft Stage, bifid teeth begin to appear medially on the premaxilla. By adult-

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**TABLE 1. Stages in cranial ontogeny in Notophthalmus viridescens and samples of specimens examined**

<table>
<thead>
<tr>
<th>Stage</th>
<th>Diagnostic feature of stage</th>
<th>Mean (SVL)</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Ossification of coronoids, dentaries, premaxillae, squamosals, vomers, palatines, and prearticulars</td>
<td>7.0</td>
<td>5.5-9.0</td>
</tr>
<tr>
<td>II</td>
<td>Ossification of frontals, exoccipitals, parietals, pterygoids, prootics, quadrates, orbitosphenoids, parasphenoids, and opisthotics</td>
<td>12.9</td>
<td>9.0-16.0</td>
</tr>
<tr>
<td>III</td>
<td>Ossification of opercula, prefrontals, maxillae, otic capsule, and processes of frontosquamosal arch</td>
<td>16.5</td>
<td>13.0-20.0</td>
</tr>
<tr>
<td>IV</td>
<td>Ossification of the nasals, and completion of the frontosquamosal arch</td>
<td>22.7</td>
<td>15.0-30.0</td>
</tr>
<tr>
<td>Metamorphs</td>
<td>Palatine–pterygoid disintegration; loss of palatines and coronoids; new jugal process on maxillae; rearrangement of vomerine teeth</td>
<td>22.3</td>
<td>18.0-29.0</td>
</tr>
<tr>
<td>Efts</td>
<td>Appearance of bifid teeth, maxillary teeth, and articular ossicles</td>
<td>24.2</td>
<td>17.0-37.5</td>
</tr>
<tr>
<td>Adults</td>
<td>Lengthening and solidification of skull; appearance of coronoid process on mandible; completion of palate</td>
<td>46.6</td>
<td>39.5-60.0</td>
</tr>
</tbody>
</table>

1 Snout–vent length.  
2 Specimens from Illinois (IL) and North Carolina (NC).  
* Four efts (June 1993 sample) not included in calculation.
hood most teeth are bifid, slightly more expanded, and sharp, and resemble typical hynobiid teeth (Tihen, '58).

**Coronoid**

The first bones to stain strongly are the coronoids. They appear medial to the dentary and are heavily edentate (Fig. 1A). The coronoid remains centered on the dentary, extending slightly dorso posteriorly in Stage II (Fig. 2C). Throughout Stages III and IV the coronoid becomes more elongate and progressively more narrow, until it disintegrates during metamorphosis (Figs. 3C, 4C).

**Dentary**

At their appearance in Stage I the dentaries are long conspicuous bones with their anterior, terminal knobs approaching the mental gap (Fig. 1A). No distinction could be made between dentary and mentomeckelian elements as has been done in some ambystomatids (Srinivasachar, ’62); thus, it is likely that the mentomeckelian portion is absent in *Notophthalmus* as it is in *Salamandra* (Par ker, 1877). In Stages II through III, the skull increases in length and the mental gap narrows until the dentaries articulate loosely with each other, and in Stage IV form a posterior mental projection. The posterior end of the dentary in Stage IV is compressed laterally and bears a blunt terminus. Mediolaterally, the dentary articulates with the needle-like prearticular for about half of the length of the dentary. In the Eft Stage the dentary is long and thick in lateral aspect (Fig. 5C). In adults, its outer face continues to thicken, especially posteriorly, forming a “coronoid process” of varying height, and more teeth appear (Fig. 6C).

**Vomer**

The vomer is the major larval tooth-bearing bone. In Stage I, the vomer lies just anteromedial to the eye in the same plane with the palatines (Fig. 1B). In Stages II through III the vomer is elongated and lies posterior to the premaxilla and ventrolateral to the anterior end of the parasphenoid (Figs. 2B, C, 3B, C). In Stage II, the vomer is irregularly rectangular with rounded anterior ends (Fig. 2B) that become more pointed in Stage III (Fig. 3B). Teeth cover the entire ventral surface of the vomer and the posterior edge of the bone loosely abuts the palatine. In Stage IV, the posterior edge has an interdigitating articulation with the palatine (Fig. 4B). Elongation continues with an anterior edentate portion lengthening toward the premaxilla and widening laterally toward the maxilla. Widening continues through metamorphosis so that each vomer fuses with the

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**Abbreviations**

CI, columella; CP, coronoid process; CR, coronoid; D, dentary, E, exoccipital; FR, frontal; FSa, frontosquamosal arch; M, maxilla; N, nasal; O, opisthotic ossification; Or, orbitosphenoid; P, parietal; Pa, prearticular; Pal, palatine; Pf, prefrontal; Pm, premaxilla; Pm–d, premaxilla–dorsal ramus; Pm–de, premaxilla–dentigerous ramus; Po, prootic; Pt, pterygoid; Q, quadrate; Sq, squamosal; V, vomer.
Fig. 2. Stage 11 larval skull of *Notophthalmus viridescens*. Dorsal (A), ventral (B), and lateral (C) aspects.

Fig. 3. Stage 111 larval skull of *Notophthalmus viridescens*. Dorsal (A), ventral (B), and lateral (C) aspects.
Fig. 4. Stage IV larval skull of *Notophthalmus viridescens*. Dorsal (A), ventral (B), and lateral (C) aspects.

Fig. 5. Eft Stage skull of *Notophthalmus viridescens*. Dorsal (A), ventral (B), and lateral (C) aspects.
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ipsilateral premaxilla and maxilla and forms the entire medial and anterior rim of the choanal notch in the Eft Stage (Fig. 5B). Posteriorly, the edentate portion narrows and grows posteriorly under the parasphenoid. The association of the posterior, tooth-bearing extension of the vomer with the parasphenoid is so close that the teeth appear to be on the parasphenoid bone (Fig. 5B). In the late Eft and Adult Stages, the vomers fuse anteriorly, leaving a small median nasal passage, and form the roof of the mouth and the choanal notch (Fig. 6B). Owing to progressive posterior constriction of the vomers, two long rows of vomerine teeth extend well back onto the parasphenoid.

**Palatopterygoid**

The dual nature of the palatopterygoid, representing the fusion of the palatine (anteriorly) and the pterygoid (posteriorly) is evident. The palatine appears in Stage I as an irregular-shaped bone posterolateral to the vomer (Fig. 1B). The dentigerous palatine persists until metamorphosis as the only tooth-bearing element of the palatopterygoid. In Stage II, the pterygoid portion appears; it is somewhat constricted behind the palatine, but expanded at the posterior end (Fig. 2B). By Stage III, the palatopterygoid still is constricted medially, but bears a wide connection to the quadrate and prootic, whereas the palatine remains unchanged (Fig. 3B, C). The palatine grows medially to interdigitate with the vomer in Stage IV, and fuses with the otic capsule and quadrate (Fig. 4B, C). During metamorphosis, the narrow strip of bone connecting the palatine and pterygoid disintegrates and the entire palatine is lost. The pterygoid, reduced in length during metamorphosis, becomes fused more solidly to the prootic and quadrate in the Eft Stage (Fig. 5B, C). In the Adult Stage, the anterior spine of the pterygoid extends posteriorly and is attached to the maxilla by a ligament to form the posterolateral edge of the orbit (Fig. 6B, C).

**Premaxilla**

The premaxilla of Stage I is a single bone with wide, arcuate dentigerous processes that extend laterally along the snout and with two perpendicular dorsal rami (Fig. 1B). In Stage II through III the dorsal rami overlap the frontals (Figs. 2A, 3A). In Stage IV, the dentigerous rami extend laterally to touch

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Fig. 6. Adult Stage skull of *Notophthalmus viridescens*. Dorsal (A), ventral (B), and lateral (C) aspects.
the maxillae and form a rostral notch (Fig. 4A). Dorsally, a palatal shelf extends posteriorly toward the vomers (Fig. 4A). The premaxilla changes little through metamorphosis, but by the Eft Stage, its fusion with the nasal is complete, leaving a medial nasal passage in the notch between the dorsal rami (Fig. 5A). In the Eft and Adult stages the premaxilla develops a large transverse shelf that reaches to the palate in front (Figs. 5B, 6B).

Prearticular
The thin, pointed prearticular bone appears in Stage I medial to the distal half of the dentary (Fig. 1A), with the anterior point wedged between the coronoid and the dentary. In Stages II through IV, the prearticular becomes trough-like as the lateral surface curves dorsally. The posterior end of the prearticular and its articulating surface enlarge and the anterior end expands to project just beyond the coronoid (Figs. 2C, 3C, 4C). By the Adult Stage, the high point of the prearticular, in lateral aspect, culminates in the "coronoid process" that is matched on the outside by the dentary (Fig. 6C). Owing to increased growth throughout the later eft period, the adult has a markedly larger and thicker squamosal which dominates the skull laterally and marks the widest part of the skull (Fig. 6A). Here, a large scabrous keel demarcates the dorsolateral surface of the skull, and another large keel runs down the lateral side of the squamosal to provide strength to the jaw articulation and more surface area for muscle attachment (Fig. 6C). Parker's (1877) illustration of the larval squamosal in no way resembles the one described here.

Articular
The articulars seem to ossify after about a year in the Eft Stage and are present in large efts and all adults. Of four approximately one-year-old efts examined, two still lacked articulars. In another, the articular was cartilaginous and in the fourth it was ossified. The articular ossifies as a small wedge posteriorly between the dentary and the prearticular, with its articulating surface facing posterodorsally to the quadrate.

Squamosal
The squamosal appears in Stage I as a thin sliver of bone behind the eye (Fig. 1B). In Stage II, a thin otic process forms and curves dorsomedially to a position at which it contacts the otic capsule in Stage III (Fig. 2A, B). A frontal process projects forward as the beginning of the frontosquamosal arch (Fig. 2C) that is unique to the salamandrids (Wake and Ozeti, '69). The dorsal process is keeled and extends obliquely downward to articulate with the forming quadrate bone. In Stages III and IV, the hammer-shaped squamosal increases in size and widens dorsolaterally (Figs. 3C, 4C). By Stage IV, the frontal process expands to meet the frontal bone to complete the frontosquamosal arch, and the ventral process fuses solidly with the quadrate (Figs. 3C, 4C). In the Eft Stage, the frontal process of the squamosal fuses with the frontal bone to enclose the temporal fossa and form the bony dorsum of the orbit (Fig. 5A, C). Owing to increased growth throughout the later eft period, the adult has a markedly larger and thicker squamosal which dominates the skull laterally and marks the widest part of the skull (Fig. 6A). Here, a large scabrous keel demarcates the dorsolateral surface of the skull, and another large keel runs down the lateral side of the squamosal to provide strength to the jaw articulation and more surface area for muscle attachment (Fig. 6C). Parker's (1877) illustration of the larval squamosal in no way resembles the one described here.

Parasphenoid
The parasphenoid ossifies in Stage II and extends from between the vomers to the foramen magnum in a parallel plane just dorsal to the palatal bones (Fig. 2B, C). It has an elongate pear shape with an anterior notch and exhibits no major configurational change through its ontogeny. It fuses with the surrounding bones and the otic capsule in the Eft Stage. Parker (1877) described and illustrated a much longer anterior notch with the rear portion of the parasphenoid pinched off to form a posterior lobe and described this as a rare condition for this bone. None of my specimens approximates his description (see Figs. 2B, 3B, 4B).

Orbitosphenoid
The side walls of the braincase begin to ossify in Stage II when the orbitosphenoid forms, medial to the eye, around the optic foramen. The orbitosphenoid sometimes touches the ventrolateral edge of the parietal (Fig. 2C). In Stage III, the orbitosphenoid is free and irregularly shaped (Fig. 3C). By the end of Stage IV, the entire bone is ossified and fused to the prootic, parietal, frontal, prefrontal, and parasphenoid (Fig. 4C). This is in contrast to the condition in Ambystoma texanum in which expansion and fusion of the orbitosphenoid occurs after metamorphosis (Bonebrake and Brandon, '71). No further change occurs in the orbitosphenoid through
metamorphosis, but its shape in Stage IV larvae, efts, and adults is highly variable (cf. Figs. 4C, 5C, 6C).

**Frontal**

Widely separated frontal bones appeared in Stage II; each bone underlies the dorsal ramus of the premaxilla and bears a posterior point that slightly overlaps the parietal (Fig. 2A, C). A small squamosal process projects posterolaterally toward the squamosal. In Stage III, each frontal widens and the squamosal process becomes its dominant feature (Fig. 3A, C). In Stage IV, the squamosal process of the frontal establishes a wide articulation with the frontal process of the squamosal, and solid contact is made with the orbitosphenoid, nasal, and prefrontal bones (Fig. 4A). From the frontosquamosal arch a brow ridge runs across the frontal and continues onto the prefrontal to form the dorsal aspect of the orbit (Fig. 4C). Another weak ridge forms along the middle of each frontal bone and continues onto each parietal. In the Eft and Adult Stages, this ridge becomes pronounced and runs from the dorsal ramus of the premaxilla to curve convexly over the frontal, parietal, and opisthotic (Fig. 6C).

**Quadrate**

The quadrate appears in Stage II anterior to the ventral process of the squamosal (Fig. 2C). In Stage III, the quadrate enlarges and articulates with the pterygoids medially (Fig. 3B, C). In Stage IV, the quadrate is pyramidal in shape, and touches the squamosal on its lateral face, the pterygoid on its medial face, and the prearticular on its ventral face with its free face projecting ventromedially (Fig. 4C). In the Eft Stage, the quadrate is slightly reduced in size, but fused more completely with the pterygoid and squamosal (Fig. 5B). By the Adult Stage, the articulating facets are greatly expanded laterally, and bear a groove that receives the articular bone of the mandible (Fig. 6B, C).

**Nasal**

The appearance of the nasal marks the beginning of Stage IV. The pair of bones first form as thin sheets of bone that gradually expand in the space between the prefrontal, maxilla, premaxilla, and frontal to overlap the dorsal ramus of the premaxilla (Fig. 4A, C). In the Eft Stage, the nasals are not always completely ossified, but by the Adult Stage, ossification is complete, leaving the naris where the nasal, maxillary, and the premaxilla bones converged (Fig. 6A, C). There is no septomaxilla, contrary to Parker's (1877) report.

**Parietal**

The parietal bone begins to ossify in Stage II, underlying the frontal, and has a midlateral curve bending ventrally (Fig. 2A, C). By Stage III, posterolateral expansion reaches the otic capsule (Fig. 3A). In Stages III and IV, medial growth of each parietal closes the frontoparietal fenestra (Figs. 3A, 4A). By Stage IV, the parietal has grown laterally and ventrally to articulate with the frontal, orbitosphenoid, and parasphenoid and thereby complete the braincase (Fig. 4C). In the Eft Stage, the parietals fuse medially (Fig. 5A) and cranial crests develop (Fig. 5C). Other than the enlargement of the crests (Fig. 6C), little further change occurs.

**Maxilla**

The maxilla appears late in Stage III as a small, toothless ossification posterolateral to the premaxilla and anteroventral to the prefrontal (Fig. 3A, B, C). Through Stage IV the maxilla grows anteriorly to articulate with the premaxilla. A flattened facial process enlarges dorsally into the cheek to meet the nasal and prefrontal (Fig. 4A, B, C). Later in Stage IV, a small jugal process appears (Fig. 4A, C) and becomes greatly elongated in the Eft Stage (Fig. 5A, B, C). Then, in older efts, a few small teeth, in line with the premaxillary teeth, begin to appear anteriorly on the maxilla. In adults, the teeth are well developed, but extend posteriorly only to the level of the choanae (Fig. 6B). Teeth do not occur on the long jugal extension of the maxilla.

**Exoccipital**

This bone appears in Stage II, with the occipital condyle squared off posteromedially to receive the cervical vertebra (Fig. 2B). Posteriorly, the exoccipitals are rounded to form the rear of the skull (Fig. 2C) and a process curves ventrally toward the parasphenoid (Fig. 2A). A pointed, curved sheet of bone extends laterally over the dorsal otic surface (Fig. 2B) and although indistinguishable from the rest of the exoccipital, apparently represents the opisthotic (see Otic Capsule). The sheet of bone continues to expand and rapidly forms most of the otic capsule by Stage III (Fig. 3A, B, C). A small crescentic
condyle remains, extending posteroventrally, forming half of the round neural notch.

Prefrontal

The prefrontal ossifies in Stage III as a triangle of bone between the frontal and the small maxilla (Fig. 3A, C). In Stage IV, the prefrontal spreads laterally and ventrally toward the maxilla, anteriorly toward the nasal, medially toward the frontal, and posteroventrally to fill in the side wall of the braincase along with the orbitosphenoid (Fig. 4A, B, C). Aside from the development of an orbital rim, no further change occurs in the prefrontal.

Otic capsule

In Stage II, opisthotic and prootic ossifications appear medially to the otic capsule (Fig. 2A, B, C). Formation of the double-walled otic capsule progresses rapidly between Stages II and III. The opisthotic ossification spreads dorsally and ventrally around the otic capsule from the rear and eventually cuts under the squamosal and parietal. Simultaneously, the prootic expands posteriorly and dorsally over the anterior part of the capsule and fuses to the pterygoid. Before the capsule ossifies fully, the oval operculum forms within the much larger fenestra ovalis (Fig. 3A, B). Contrary to Wake and Ozeti ('69) the columella is strongly ossified. In Stages III and IV, the foramen for the trigeminal nerve is visible anteromedially in the prootic (Figs. 3B, 4B). In metamorphosis the pterygoid rotates slightly laterally so that it has a broader articulation with the prootic dorsoventrally.

SUMMARY OF STAGES

Stage I

The coronoids, premaxilla, vomers, and palatines all appear bearing teeth (Fig. 1). The dentaries, prearticulars and squamosals appear as well.

Stage II

Ossifications of the parasphenoid, frontals, exoccipitals, parietals, and pterygoids mark the beginning of Stage II (Fig. 2). The squamosals thicken as the prootics, opisthotics, quadrates, and orbitosphenoids begin to ossify.

Stage III

Appearance of the opercula marks the beginning of this stage (Fig. 3). Cheek bones (prefrontals and maxillae) appear and the converging processes of the frontosquamosal arches become evident.

Stage IV

The nasals appear and the frontosquamosal arches are completed (Fig. 4). The otic capsules are complete, but the nasal capsules still are partially cartilaginous.

Metamorphosis to the Eft stage

The onset of metamorphosis is signalled by the break of the palatine—pterygoid junction, which is followed by the disintegration of the palatines and anterior portion of the pterygoids as the pterygoids realign in a more ventrolateral direction (Fig. 5). As metamorphosis continues, the coronoids are lost, the lateral parts of the vomers expand anteriorly to surround the choanal notches partially, while the posterior, edentate portions of the vomers elongate posteriorly and extend well under the parasphenoid. The jugal processes of the maxillae become greatly elongated, and there is a complete ossification and thickening of the frontosquamosal arches. The articular bones also appear in later eft stages, first cartilaginous and then ossified. Bifid teeth eventually begin to appear and teeth form anteriorly on the maxillae in line with the teeth on the premaxilla.

Adult stage

In the adults, ossification and elongation completes the formation of the massive osteocranium, but there is little difference between larger efts and adults (Fig. 6). The palate is complete, and a long, arcuate line of teeth runs onto the maxilla from the premaxilla. One distinctive character of the adult stage is the high point or "coronoid process" posterior to the teeth on the mandible. The skulls of branchiate adults are indistinguishable from those of normally transformed adults.

One complete neotene was found in the Illinois population in 1976 by Ronald A. Brandon. Externally, this gravid female (SVL = 48 mm) is like the other branchiate adults except that it has bushy gills, open gill slits and gular fold, and a pointed snout. Examination of the cleared and stained skull of this individual shows that it is completely neotenic, retaining all characters of a Stage IV larva (cf. Figs. 4, 7). None of the events of metamorphosis has occurred and the only adult characteristic of the skull is the pres-
ence of an ossified articular. The hyoid apparatus is completely larval in morphology as well, although most of the elements have ossified. This specimen is the only complete neotene known from more than 1400 specimens examined from this population.

**DISCUSSION**

Only one description of the skull of *Notophthalmus viridescens* has appeared (Parker, 1877), based on two larvae and one adult; however, it differs from the description presented here with respect to the parasphenoid and squamosal bones, and also reports the presence of septomaxillae (see Results). Life history in the *Notophthalmus viridescens viridescens* population sampled is typical of the species. Aquatic larvae become terrestrial efts for 1–8 years before returning to the water to become permanently aquatic adults (Chadwick, '44, '50). Along the Atlantic Coastal Plain and in about a dozen inland localities, where the terrestrial terrain provides a poor alternative to water, neoteny has been reported (Mecham, '67). *N. v. louisianensis* of this study are from one of the inland populations that exhibits both the usual (completely transformed) and neotenic strategies. Larvae either metamorphose into efts, remaining on land for 1–2 years before becoming aquatic adults, or they metamorphose directly into aquatic juveniles, and retain some gill apparatus (Brandon and Bremer, '66; Albert, '67; Gates, '78).

In this study, cranial metamorphosis was well defined in neotenic newts and occurred after the larval Stage IV. Changes in the skull at metamorphosis (loss of coronoids and palatines, new jugal processes of maxillaries) seem to be adaptations for a change to terrestrial feeding. The minor changes (growth) in the skull between efts and adults occurred gradually and over a long period of time. Changes known to occur in adults upon their return to water (changes in skin texture, pigmentation, restoration of the lateral line, keeled tail, aquatic retina, and increase in ammonotelism; see Grant, '61) seem to be related more to the consequences of a return to water and to sexual maturity (secondary sex characters) than the result of a “second metamorphosis” or the reversal of the first metamorphosis of Grant ('61).

All adults in this study, whether branchiate or not, had identically transformed skulls. This confirms Brandon and Bremer's

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**Fig. 7.** Skull of a completely neotenic (nonmetamorphosed) adult *Notophthalmus viridescens*. 
Branchiate adults have fully transformed skulls. Neoteny is limited to retention of some hyobranchial and external gill structures. This represents a different and limited type of neoteny, in which no delay in cranial metamorphosis is involved and variable retention of some gill structures (limited neoteny) is essentially postmetamorphic. The limited nature of neoteny in these newts also is shown by (1) the gradual loss of gill structure in aquatic neotenes with age (Gates, '78), (2) the rapid loss of gill structures in neotenes removed from water (Noble, '29; Morgan and Sondheim, '32; Healy, '70; Gates, '78), (3) the great annual fluctuation of the percentage of branchiate adults in McGuire’s pond (Gates, '78, personal observation), and (4) the great variability of retention of gill structures (Reilly, personal observation).

The adaptive significance of limited neoteny in newts may be related more to behavioral than morphological selection as has been proposed for Taricha granulosa (Marangio, '78). Because thyroxin controls both metamorphosis and “land drive” in newts (Grant et al., '65), selection for decreased thyroxin secretion to inhibit “land drive” may provide the hormonal basis for the limited postmetamorphic retention of larval morphology (gill structures) as a “correlated response” (Mayr, '63). The incomplete metamorphosis of the gill apparatus and the persistence of aquatic habitat preference in newts with completely metamorphosed skulls may result from the involvement of different tissues having different response thresholds to thyroxin. If this were true, then selection to raise or lower the level of circulating thyroxin could result in the variation in metamorphic response observed in various populations. For example, if circulating thyroxin exceeded the thresholds of all target tissues, complete metamorphosis would result. If it did not reach the threshold of any particular target tissue, complete neoteny would result. Thus the branchiate adults with transformed skulls in McGuire’s pond might result if circulating thyroxin exceeded the threshold needed for the cranium to metamorphose but did not reach the threshold needed for the gill structures and habitat preference to change. Whatever the mechanism, the significance of retaining larval behavior (aquatic habitat preference) and thereby surviving in populations with hostile terrestrial surroundings far outweighs the value of limited retention of gill structures that are not necessary for survival of aquatic adult newts.

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Literature Cited
Gates, D.W. (1978) Relation of Prolonged Retention of Larval Characters to Sex, Size, Age, and Season in


