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Anuran Postnasal Wall Homology: An Experimental Extirpation Study

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ABSTRACT The nasal placode was extirpated unilaterally in Gosner stage 18–20 embryos of *Rana sylvatica*, *R. palustris* and *R. pipiens*, in order to test alternative proposed schemes of homology for the ethmoidal attachment of the palatoquadrate in anurans and urodeles. Absence of the nasal sac has no pronounced effect on the formation of larval chondrocranial structures. In contrast, in metamorphosed animals the lamina orbitonasalis and inferior prenasal process are the only nasal capsule structures present on the operated side. The medial nasal branch of the deep ophthalmic nerve passes forward over the dorsal surface of the lamina orbitonasalis, rather than through an orbitonasal foramen. Comparison with previous experimental work on urodeles supports the traditional homology of the anuran lamina orbitonasalis with the antorbital process of urodeles and other vertebrates. J. Morphol. *238*:343–353, 1998.

KEY WORDS: homology; Lissamphibia; chondrocranium; olfactory placode

Homology is the fundamental concept of comparative morphology. There has nevertheless been much argument over the best way to define the term (Hall, '94). In a broad sense, the term refers to the relations of correspondence established by mapping the parts of one organism onto the parts of another. This is the sense in which it is used here. Establishment of a scheme of correspondence, or "(potential) homology" (Sattler, '94), is the necessary prelude to any search for phylogenetic homology (synapomorphy). Moreover, controversies over specific homologies usually involve argument over the details of this mapping. The present study attempts to resolve a 100-year-old controversy in the homologies of cranial elements between frogs and salamanders. These homologies are important because they form the basis for synapomorphies uniting frogs and salamanders with the third living amphibian group, the caecilians (Reiss, '96).

Criteria for the recognition of homology have been examined by numerous authors. All tend to be some form of the three principal criteria proposed by Remane ('52; quoted in Riedl ['78, p. 34]). These may be paraphrased as follows: (1) *positional:* similar position in comparable systems of features (e.g., similar position of a bone with respect to neighboring bones); (2) *structural: a*greement in numerous special features (e.g., similar histological structure of the testes despite differing positions among vertebrates); and (3) *transitional:* connection of dissimilar forms by a series of developmental and/or structural intermediates that fulfill the requirements of (1) and/or (2) (e.g., both embryos and fossils provide intermediates between mammalian auditory ossicles and piscine jaw bones).

The present study relies upon an additional criterion of homology, namely, similarity of inductive relationships. This is essentially an extension of the positional criterion, with the addition of a mechanistic relationship between the presence of one structure and an adjacent structure.

The specific case involves the homologies of the parts of the anuran palatoquadrate (cartilaginous upper jaw) and adjacent parts of the nasal capsule with those of salamanders and other vertebrates (reviewed by Jurgens, '70; Pyles, '88; Roček, '93; Reiss,

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'93, '97; Haas, '96). The attempt to establish homologies in this region is complicated by the complete restructuring of the upper jaw that occurs at metamorphosis in anurans (frogs) and the lesser remodelling that occurs in urodeles (salamanders). For orientation, a brief review of the anatomy is in order. To make the discussion less confusing, distinct terminology is purposely used for elements of dubious homology in the two groups. In particular, part of the postnasal wall is called the "lamina orbitonasalis" in frogs and the "antorbital process" in salamanders, although the terms are generally used interchangeably.

In anuran larvae, the anterior quadratocranial commissure connects the palatoquadrate directly with the trabecula, immediately behind the choana (Fig. 1A). A small projection present on the anterior edge of the commissure, the quadratoethmoidal process, attaches to a ligament that runs forward lateral to the choana. During metamorphosis, the part of the quadratocranial commissure medial to the quadratoethmoidal process is resorbed and the connection with the trabecula is lost (Fig. 1B). At the same time, a new lateral projection from the trabecula forms above the point of attachment of the quadratocranial commissure. This projection is the lamina orbitonasalis. (In some species, the base of the lamina orbitonasalis incorporates part of the quadratocranial commissure; Reinbach, '50). The distal end of the lamina orbitonasalis (the planum triangulare) develops a caudally directed process, the posterior maxillary process. This connects to the quadratoethmoidal process and remnant lateral part of the quadratocranial commissure (the adult pterygoid process) to form the adult subocular arch (Fig. 1B, C). Although the details vary, this general pattern holds for all anurans (reviewed by Swanepoel, '70; Reiss, '93; Roček, '93).

The ontogeny in salamanders appears rather different. In young larvae of basal (cryptobranchoid) salamanders, the anterior end of the palatoquadrate—the ptery-

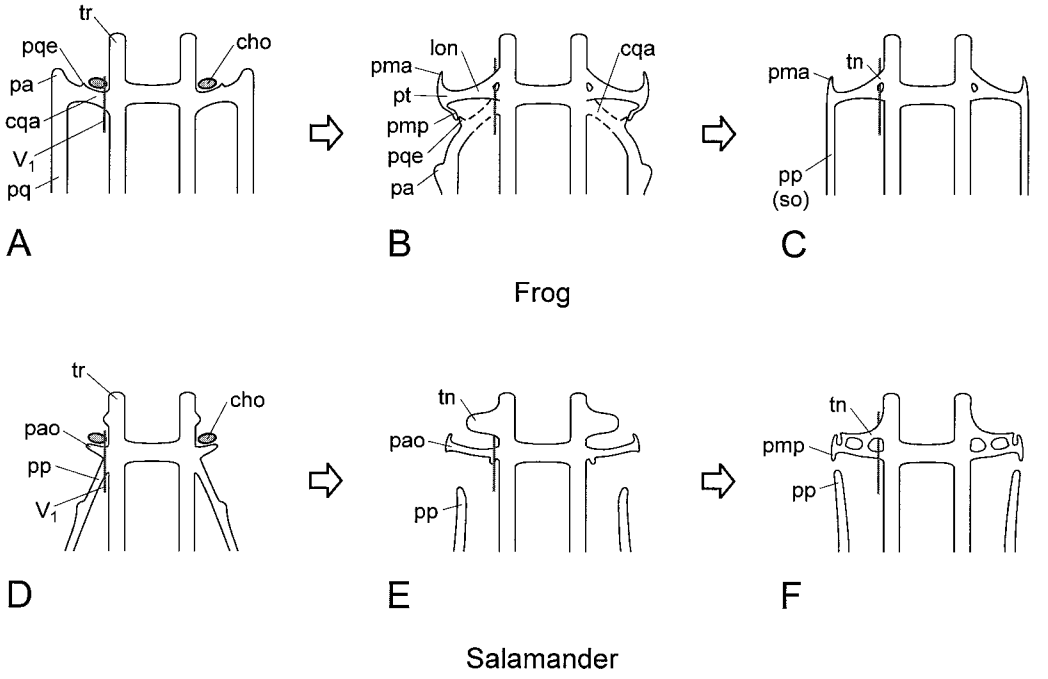

Fig. 1. Ontogeny of the ethmoidal region of the chondrocranium in anurans (A-C) and urodeles (D-F). Diagrammatic dorsal views. **A:** Frog larva. **B:** Midmetamorphic animal. Note degenerating anterior quadratocranial commissure. **C:** Juvenile froglet. **D:** Young salamander larva. **E:** Older larva. **F:** Juvenile salamander. cho, choana; cqa, anterior quadratocranial commissure; lon, lamina orbitonasalis; pa, articular process (of palatoquadrate); pao, antorbital process; pma, anterior maxillary process; pmp, posterior maxillary process; pp, pterygoid process (of palatoquadrate); pq, palatoquadrate; pqe, quadratoethmoidal process; pt, planum triangulare; so, subocular arch; tn, nasal tectum; tr, trabecula; V_1, deep ophthalmic branch of trigeminal nerve.

goid process—connects directly with the trabecula, immediately behind the choana (Fig. 1D; Lebedkina, '64; Regel, '64b, '68). A lateral projection from the trabecula, the antorbital process, develops in the same region. Depending on the species, the pterygoid process may shift its attachment to the antorbital process, or it may remain attached to the trabecula. In later larval stages, the anterior part of the pterygoid process is resorbed (Fig. 1E). At the same time, the lateral end of the antorbital process develops a caudally directed posterior maxillary process. In juvenile stages, the pterygoid process grows forward, approaching the posterior maxillary process. The pterygoid process and posterior maxillary process usually do not meet. Thus, unlike the situation in frogs, the subocular arch remains incomplete (Fig. 1F).

At least two general schemes of homology for elements in the region have been proposed (Fig. 2). Most authors regard the anuran lamina orbitonasalis as the homologue of the urodele antorbital process (e.g., de Beer, '37; see Fig. 2A). The pterygoid processes of adult anurans and urodeles would then be homologous, and the anterior quadratocranial commissure of anuran larvae homologous with the anteromedial part of the larval pterygoid process of urodeles (which chondrifies only in cryptobranchoid salamanders; see Edgeworth ['23, '25]). However, Regel ('64a), elaborating on suggestions by earlier authors (Gaupp, 1893; Higgins, '20), argued that the anterior quadratocranial commissure of frog larvae is homologous to the urodele antorbital process (see Fig. 2B). In this view, the lamina orbitonasalis of frogs is homologous not with the antorbital process of salamanders, but with the nasal tectum.

Regel's argument is based on the following points: (1) the antorbital process of urodeles develops in association with the anterior end of the palatoquadrate and is thus a palatoquadrate derivative, (2) the palatine bone develops beneath the antorbital process of urodeles and beneath the medial remnant of the anterior quadratocranial commissure in frogs (Reinbach, '50), (3) the antorbital process of urodeles forms early in development as a mesenchymal condensation immediately behind the choana, as does the quadratocranial commissure of frogs, (4) the part of the salamander nasal tectum forming the dorsal part of the postnasal wall develops much later than the antorbital process, just as the lamina orbitonasalis of frogs forms much later than the quadratocranial commissure, (5) the part of the urodele postnasal wall that forms by growth of the nasal tectum and by chondrification of the mesenchyme situated between the tectum and the antorbital process occupies the same position as the anuran lamina orbitonasalis, and (6) the antorbital process of urodeles still forms if the nasal placode is removed early in development, even though the remainder of the nasal capsule, including the "part of the postnasal wall" just mentioned, does not. This shows that the salamander antorbital process is not part of the true nasal capsule (as the anuran lamina orbitonasalis presumably is).

This last point suggests an experimental approach to the problem. As noted by Regel, it has long been known that if the nasal

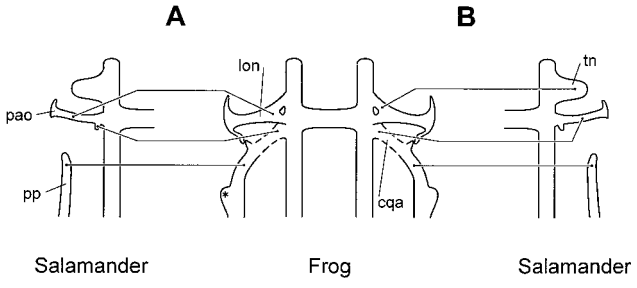

Fig. 2. Two possible hypotheses for homology of elements in the ethmoidal region of the chondrocranium between frogs and salamanders, as shown by comparison of a midmetamorphic frog (center) with late larval salamanders (sides). **A:** Traditional hypothesis. Anuran lamina orbitonasalis (lon) homologous with urodele antorbital process (pao). **B:** Hypothesis of Regel ('64a). Anuran anterior quadratocranial commissure (cqa) homologous with urodele antorbital process. Anuran lamina orbitonasalis homologous with urodele nasal tectum (tn). Note that the homology of the caudal part of the salamander pterygoid process (pp) is not disputed.

placode of salamander embryos is removed so that the nasal sac does not form, the entire cartilaginous nasal capsule also fails to form, with the exception of the antorbital process (Burr, '16; Schmalhausen, '39; Regel, '64a; Corsin, '67, '72; Toerien and Roussouw, '77). Similar results have been reported in turtles and birds, where part of the postnasal wall also still forms in the absence of a nasal placode (Toerien and Roussouw, '77). However, comparable experiments on anurans have not been performed.

On Regel's ('64a) hypothesis, the anuran lamina orbitonasalis should fail to form in the absence of a nasal sac, like the urodele nasal tectum but unlike the urodele antorbital process. This prediction was tested in this study by unilaterally extirpating the nasal placode from anuran embryos and raising the operated animals through metamorphosis. The results show that by this criterion Regel's scheme is incorrect. The anuran lamina orbitonasalis in fact does correspond to the urodele antorbital process.

MATERIALS AND METHODS

Egg masses of *Rana sylvatica*, *R. palustris*, and *R. pipiens* were collected from the field (New Hampshire, Massachussetts, and New York) in early spring. Preliminary experiments had shown the earliest stage at which the nasal placode could be removed without regeneration to be stage 18 (Gosner, '60). Surgeries (N = 96) were carried out on stage 18, 19, or 20 embryos. Embryos were operated on in petri dishes of 1:3,000 MS222 (tricaine methane sulfonate, Sigma, St. Louis, MO) in 10% Holtfreter's solution. A pit was made in Permaplast clay in the bottom of the dish and the embryo was placed tail-first in the pit. The right or left nasal placode was removed with glass needles and a hairloop. A sketch was made of the operated area, and the embryo was removed to fresh 10% Holtfreter's solution for recovery. The unoperated side of the embryo served as a control.

Embryos were raised at 14° C in individual containers of dechlorinated tap water. Feeding stages were given boiled lettuce or spinach. Animals were fixed in 10% neutral-buffered formalin or aqueous Bouin's solution. Four were fixed immediately following surgery, the remainder at various larval and early juvenile stages. Of these, 35 animals—representing a range of stages and apparent effect of the surgery—were selected for analysis. Eleven tadpoles were cleared-and-stained for cartilage as wholemounts (Dingerkus and Uhler, '77). The condition of the nasal sac was assessed by examining the specimens with transmitted light before clearing-and-staining. The remaining tadpoles and the juveniles were embedded in Paraplast, sectioned transversely, and stained with Gill's hematoxylin and eosin. Ten tadpoles, four midmetamorphic animals, and ten juveniles were sectioned.

A 3D recontruction of the nasal cartilages of one juvenile was prepared. Sections were drawn with the aid of a camera lucida, then digitized using a flat-bed scanner. Outlines of chondrocranial structures were created using the tracing function of Adobe Illustrator and rasterized sections aligned using Adobe Photoshop, both running on a Power Macintosh 7100 microcomputer. The sections were compiled to form a 3D data set, and the 3D data input into IBM Visualization Data Explorer running on a Silicon Graphics Indigo High Impact Workstation. After filtering to smooth contours, a reconstruction was created using the isosurface function of Data Explorer.

RESULTS

Of the 96 operated animals, 75 survived long enough to assess the effect of the surgery on the nasal sac. Partial or complete regeneration of the nasal placode was common, as has been observed by many others working on anurans (Bell, '07; Zwilling, '40; Toerien and Roussouw, '77; Byrd and Burd, '93). The frequency of regeneration declined with developmental stage at the time of surgery. Only 19% of the animals operated at stage 18 (N = 36) showed no regeneration of the placode, whereas 44% of those operated at stage 19 (N = 34) and 60% of those operated at stage 20 (N = 5) lacked regeneration.

Larvae

In the larvae examined (N = 21; stages 26–29), all of the larval ethmoidal cartilages are present on the operated side. This includes the trabecula and trabecular horn, and the anterior quadratocranial commissure. However, in cleared-and-stained tadpoles in which the nasal sac is absent or reduced the trabecular horn is often shifted somewhat laterally compared with the unoperated side and is often narrower at its distal end. A slight reduction in trabecular diameter is also apparent in sectioned material (Fig. 3). In specimens without a nasal sac

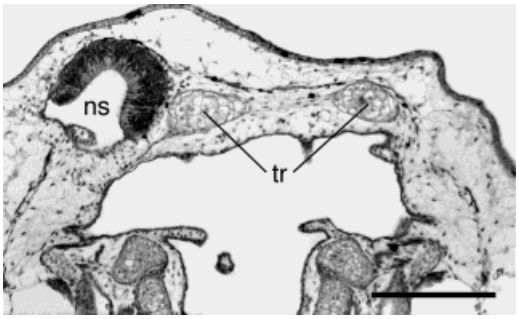

Fig. 3. Transverse section through stage 27 tadpole of *Rana palustris*. The right nasal placode was removed at stage 19. Note absence of nasal sac (ns) on the operated side. The trabecula (tr) is present on both sides, but is smaller on the operated side. Scale = 250 μm.

(and choana), the quadratocranial commissure of the operated side is frequently shifted somewhat farther forward along the trabecula than that on the unoperated side.

Midmetamorphic animals

Of four animals fixed during metamorphosis, two (both stage 41) show no regeneration of the nasal sac on the operated side. On the unoperated side of these animals, all of the normal nasal cartilages are forming (Fig. 4). The orbitonasal foramen, transmitting the medial nasal branch of the ophthalmic, is surrounded laterally by the young cartilage of the postnasal wall (Fig. 4C), which is continuous dorsally with the nasal tectum (Fig. 4B). The ventrolateral part of the postnasal wall is the lamina orbitonasalis (see Discussion). The lateral end of the lamina orbitonasalis curves anteriorly around the nasal sac to end in a point—the anterior maxillary process. The posterior maxillary process has not yet formed, but is represented by mesenchyme connecting the quadratoethmoidal process to the lamina orbitonasalis (Fig. 4B). The anterior quadratocranial commissure, which consists of older cartilage, connects to the trabecula below the orbitonasal foramen and thus forms the ventromedial part of the postnasal wall (Fig. 4C).

In contrast, on the operated side of these animals, almost all nasal cartilages are absent. The postnasal wall consists only of the quadratocranial commissure and lamina orbitonasalis, so that the deep opthalmic nerve passes freely forward (Fig. 4C). The lamina orbitonasalis is a flat plate of young cartilage extending anteriorly and laterally

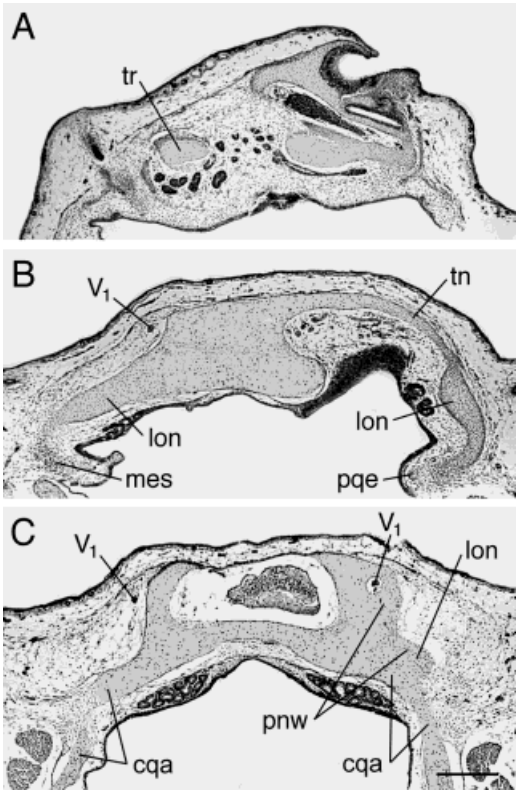

Fig. 4. Transverse sections, from anterior to posterior, through stage 41 *Rana pipiens*. Left nasal placode removed at stage 20. **A:** Normal nasal sacs and cartilages are present on the unoperated side, only the trabecula (tr) is present on the operated side. **B:** On unoperated side, the nasal tectum (tn) covers the nasal sac, connecting with the lamina orbitonasalis (lon). Dense mesenchyme connects the lamina orbitonasalis with the quadratoethmoidal process of the palatoquadrate (pqe). On the operated side, the lamina orbitonasalis extends out from the trabecula. Dense mesenchyme (mes) connects the lamina orbitonasalis with the quadratoethmoidal process, which is caudal to this plane of section. **C:** Connection of anterior quadratocranial commissure (cqa) with the trabecula. Note young cartilage of the postnasal wall (pnw) on the unoperated side, enclosing the medial nasal branch of the ophthalmic nerve (V_1) in a foramen. Scale = 250 μm.

from the tip of the quadratocranial commissure (Fig. 4B) and ending anteriorly in a point corresponding to the anterior maxillary process. As on the unoperated side, a mesenchymal band connects this plate of cartilage with the quadratoethmoidal process (Fig. 4B). The only other cartilage present on the operated side is the trabecula, which has not yet begun to be resorbed anteriorly (Fig. 4A).

Juveniles

Of 10 animals fixed after metamorphosis (stages 45–46), four show no regeneration of the nasal sac, three show partial regeneration, and three show complete regeneration. The condition of animals with no regeneration of the nasal sac (Figs. 5A, B, 6) closely resembles that found in stage 41 animals. All normal nasal cartilages are present on the unoperated side. On the operated side, however, only the lamina orbitonasalis (with its anterior and posterior maxillary processes) is consistently present. In three of the four cases, an additional cartilaginous process (Fig. 6, ppi) is present, extending ventrally from the anterior part of the lamina orbitonasalis. This appears to represent the inferior prenasal process. In two cases a small cartilage nodule occurs on the operated side near the anterior maxillary process, and one of these has an additional nodule medially (Fig. 6, cn). As in the midmetamorphic animals, the orbitonasal foramen is absent, and the medial nasal branch of the ophthalmic runs freely forward over the dorsal surface of the lamina orbitonasalis (Figs. 5B, 6).

In the three specimens with partial regeneration of the nasal sac, conditions are somewhat variable. The nasal sac is most commonly represented by a closed, simple vesicle. This vesicle is partly surrounded by cartilage (Fig. 5C), but most normal nasal structures are absent. Interestingly, even this small degree of regeneration of the nasal sac is uniformly associated with the presence of a complete postnasal wall, pierced by the orbitonasal foramen (Fig. 5D). However, two midmetamorphic (stage 43) animals with partial regeneration were also examined. In one of these, there is no postnasal wall, nor any sign of the deep ophthalmic branch of the trigeminal. The lamina orbitonasalis is separated from the trabecula by a small gap,

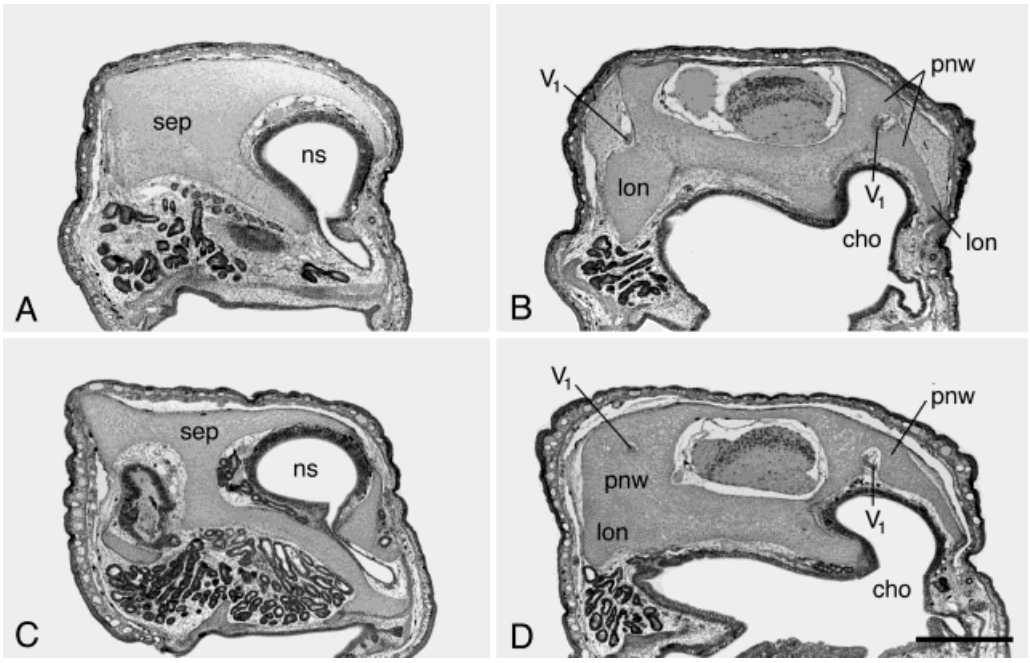

Fig. 5. Transverse sections through juveniles. **A:** Stage 45 *Rana sylvatica*, left nasal placode removed at stage 18. Note absence of nasal sac (ns) on operated side, also thick nasal septum (sep). **B:** Same specimen, further caudad. Note passage of medial nasal branch of deep ophthalmic nerve (V_1) through notch on operated side, above the lamina orbitonasalis (lon), but through foramen in postnasal wall (pnw) on unoperated side. Choana (cho) absent on operated side. Also note reduction of telencephalon. **C:** Stage 46 *R. sylvatica*, left nasal placode removed at stage 20. Note partial regeneration of nasal sac on operated side, and capsular cartilage above and below. **D:** Same specimen, further caudad. Note medial nasal branch of the ophthalmic piercing the postnasal wall on operated side, above the lamina orbitonasalis. The orbitonasal vein passes through a separate foramen. Scale = 500 µm.

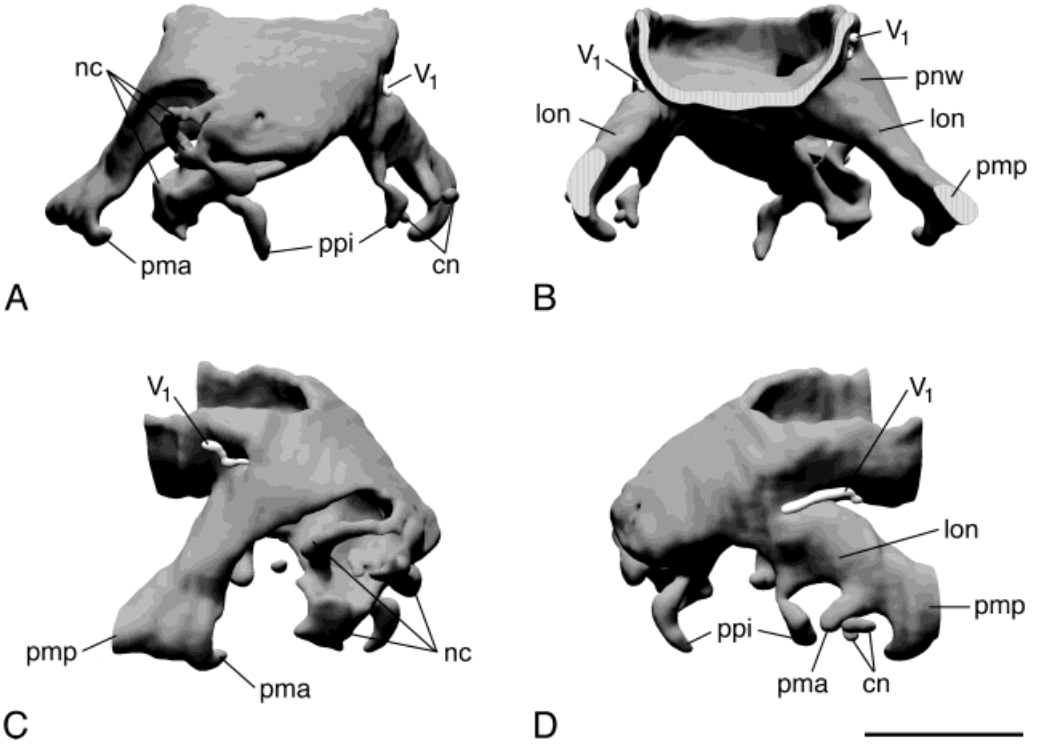

Fig. 6. Reconstruction of anterior chondrocranium of a juvenile (stage 45) *Rana sylvatica* (same specimen as Fig. 5A, B). The left nasal placode was removed at stage 18. **A:** Rostral view. **B:** Caudal view. **C:** Oblique right lateral view. **D:** Oblique left lateral view. Note absence of most nasal cartilages on the operated side, including the dorsal part of the postnasal wall. Scale = 1 mm. cn, cartilage nodules; lon, lamina orbitonasalis; nc, nasal cartilages; pma, anterior maxillary process; pmp, posterior maxillary process; pnw, postnasal wall; ppi, inferior prenasal process; V_1, medial nasal branch of deep ophthalmic nerve.

so that the pterygoid process effectively continues forward directly into the anterior maxillary process without ever attaching to the skull base.

In the three postmetamorphic specimens in which the nasal sac regenerated, all nasal cartilages are usually equally well developed on the operated and unoperated sides, although slight variations exist. For example, in one specimen a small hole is present in the caudal part of the nasal tectum on the unoperated side. In another, the orbitonasal vein and medial nasal branch of the ophthalmic enter the nasal capsule through separate foramina on the operated side.

DISCUSSION

The present study attempts to resolve a problem in homology of skeletal elements between frogs and salamanders by means of their developmental dependence on another, well-established homology, namely, that of the nasal placode. The underlying assumption in this approach is that homologous elements will respond to extirpation of the nasal placode in identical ways in the two groups.

Potential problems

There is much that could be criticized about the present approach to establishing homologies, and the specifics of the experiments involved. First, there is abundant evidence that inductive relationships can be evolutionary labile. An oft-cited example of this phenomenon is the ability of the lens to self-differentiate in one species of ranid frog, whereas in another it requires an inductive stimulus from the optic cup (de Beer, '71). Nevertheless, many inductive relationships are quite stable over evolutionary time. A striking example of this phenomenon is the ability of xenoplastic (between species) transplants to respond appropriately to the host

environment (Le Douarin and McLaren, '84). This has been especially important in chick-quail transplantation studies of cell fate, where it is relied upon with few apparent problems. Conservation of inductive relationships has also been shown to exist in neural crest transplants between frogs and salamanders (Wagner, '49). In the present case, the similarity in response seen to nasal placode removal across diverse vertebrate groups (Toerien and Roussouw, '72) argues for the reliability of the criterion.

A second potential criticism is that the surgery may be removing the cell populations normally fated to give rise to the elements of the nasal capsule, rather than just an inductive stimulus for their formation. The cartilaginous nasal capsule of vertebrates is generally thought to derive from the neural crest (e.g., Le Lièvre, '78; Noden, '87). At the stage of the surgery, neural crest cells form a mesenchymal population immediately deep to the nasal placode (Stone, '29). These mesenchymal precursor cells of the capsule might escape through the open wound, accounting for the reduction in nasal cartilages seen after surgery. In fact, in some but not all of the surgeries performed, mesenchymal cells were seen escaping from the wound before it healed. However, the consistency of results obtained—and the strict correlation seen between the presence of a regenerated nasal sac and the presence of nasal cartilage—argues against this factor being significant.

An additional complication is that some authors consider the cartilaginous nasal capsule to be derived from the nasal placode itself (e.g., Toerien and Roussouw, '77), rather than the neural crest. If this is true, reduction of the nasal capsule after placode removal (and failure to regenerate) is not surprising. However, the same concern also applies to the experiments on salamanders and other vertebrates. In either case, what is significant is the *difference* in effect on the postnasal wall and the remainder of the nasal capsule. This makes the interpretation of results obtained robust with respect to different possible interpretations of the underlying mechanism.

Interpretation of homologies

With respect to larval chondrocranial structures, the results obtained after placode removal are similar to those reported by Toerien and Roussouw ('77) for a single larva of *Discoglossus pictus* (the only data previously available). The anterior quadratocranial commissure still forms in the absence of a nasal sac, as is expected on either hypothesis of homology. The slight shift in position of the trabecula and palatoquadrate is explicable in terms of a general movement toward the space left unoccupied by the missing nasal sac. The slight reduction in robustness of the trabecular horn, however, could be due to the loss of a growth stimulus from the nasal sac. It is also possible that some of the mesenchymal cells lost from the wound before healing contributed to this reduction, but the symmetry of the chondrocranium in animals with a regenerated nasal sac argues against this interpretation.

With respect to juvenile chondrocranial structures, the results obtained are similar to those for salamanders and other vertebrates (Toerien and Roussouw, '77) in the total absence of most nasal cartilages on the operated side, with the notable exception of the ventral part of the postnasal wall. The continued presence of the inferior prenasal process, which is homologous with the trabecular horn of other vertebrates (Stephenson, '51), is also typical. The significance of the variably present cartilage nodules is unclear.

These results clearly provide no support for the homology proposed by Regel ('64a) between the urodele antorbital process and the anuran quadratocranial commissure (Fig. 2B). Instead, they support the traditional homology between the urodele antorbital process and the anuran lamina orbitonasalis (Fig. 2A). A further corollary is the homology of the anuran anterior quadratocranial commissure with the urodele pterygoid process, specifically the medial connection found in larvae (see Reiss, '97). However, the results suggest that the part of the anuran postnasal wall homologous to the urodele antorbital process is indeed smaller than has been thought traditionally.

Gaupp (1893, pp. 327–328), in a careful treatment of this issue, considered the lamina orbitonasalis (his "antorbital process") to be the part of the postnasal wall (his "pars plana nasi") ventral and lateral to the orbitonasal foramen. Although terminology has varied, this concept has generally been accepted. The present results suggest instead that only the most ventral part of the anuran postnasal wall should be homologized with the urodele antorbital process.

The region of the postnasal wall that lies immediately above this, but ventral to the orbitonasal foramen, does not form in the absence of the nasal sac (see Figs. 4C, 6B) and should be considered part of the nasal tectum. Although rejecting the homology of the quadratocranial commissure and the antorbital process, this interpretation agrees with Regel ('64a) in the comparison between the more dorsal part of the anuran postnasal wall and the region of the wall that fills in by chondrification in salamanders.

In this interpretation (which has been followed in the section above), the anuran lamina orbitonasalis is not a vertically oriented plate of cartilage, but instead a horizontal bar. The distal end of this bar is expanded to form the planum triangulare (with its anterior and posterior maxillary processes). Thus the anuran lamina orbitonasalis closely resembles the urodele antorbital process not only in developmental relationships, but also in form.

Comparative anatomy of the region supports this interpretation. In salamanders with a well developed postnasal wall (e.g., *Ambystoma*: Papendieck, '54; *Pseudotriton*: Joubert, '61; *Hynobius*: Regel, '64b; *Cryptobranchus*: Jurgens, '70) the medial orbitonasal foramen is quite large, and transmits not only the medial nasal branch of the deep ophthalmic nerve, but also the ventral nasal branch. The medial nasal branch passes through the dorsal part of the foramen, whereas the ventral nasal branch passes through the ventral part of the foramen, directly above the antorbital process. In anurans, there is no ventral nasal branch of the ophthalmic, and this is precisely the area that is filled in with cartilage.

Recently, Roček ('93) has argued that the dorsolateral part of the anuran postnasal wall incorporates a distinct visceral arch element, the epipremandibular. The present experiments do not bear directly upon this question, because *Rana* does not have the lateral nasal foramen present in adults of more basal anurans (Jurgens, '70), nor the additional larval suprarostral cartilage that apparently contributes to this portion of the postnasal wall in some taxa. However, in that the dorsolateral region of the postnasal wall does not form in the absence of the nasal sac in *Rana*, the present results provide no support for this interpretation.

Evolution of metamorphosis

The present study grew out of a larger project aimed at understanding the evolutionary origins of anuran metamorphosis (cf. Wassersug and Hoff, '82; Alberch, '87; Rose and Reiss, '93). Based on the homologies proposed here, it is clear that there is a striking similarity between some gradual ontogenetic changes in salamanders and metamorphic changes in anurans. For example, the antorbital process of urodeles and lamina orbitonasalis of frogs are proposed to be homologous. However, the former appears very early in ontogeny and develops gradually during the larval period, whereas the latter appears only at metamorphosis and rapidly achieves its adult configuration. Likewise, a connection between the pterygoid process (anterior quadratocranial commissure of anurans) and the trabecula occurs early on in both groups. In anurans this connection is replaced by a more lateral connection only at metamorphosis, whereas in urodeles the pterygoid process begins to shift laterally (and loses its medial connection) during mid-larval stages. Nevertheless, in both groups we can distinguish a shift from a more medial "larval pterygoid process" to a more lateral "adult pterygoid process" (Reiss, '97), with a consequent widening of the interpterygoid vacuity.

Elsewhere I have shown that some metamorphic changes in the palate of frogs and salamanders, particularly the widening of the interpterygoid vacuity, are shared by the third living amphibian group, the caecilians (Reiss, '96). These shared changes can be interpreted as synapomorphies supporting the hypothesis that the three groups form a monophyletic clade, the Lissamphibia (Milner, '88; Trueb and Cloutier, '91; Laurin and Reisz, '97). However, identification of shared changes depends on the scheme of homology—or mapping—adopted. Under Regel's ('64a) scheme (Fig. 2B), there is no widening of the interpterygoid vacuity at metamorphosis in frogs. Under the scheme supported here (Fig. 2A), there is. This study thus provides an example of the more general point that the synapomorphies we establish depend critically on the prior adoption of a particular scheme of homology. This problem is not limited to morphology. The identical situation exists in studies of DNA sequence evolution, where synapomorphies in base composition depend critically on the prior mapping (alignment) adopted.

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