Development of the Ethmoidal Structures of the Endocranium in the Anuran *Pipa pipa*

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ABSTRACT   Investigation of eight developmental stages by means of serial sections and subsequent graphic or wax model reconstructions, as well as by means of cleared-and-stained and dissected material, revealed that the ethmoidal endocranium in *Pipa pipa* consists in early states of a single horizontal ethmoid plate lacking labial cartilages. Later in the course of development, structures comparable with those in other anurans appear, though modified and of reduced size. These adult structures arise from the new cartilaginous tissue located above the former larval ethmoid plate, whereas the latter entirely disappear. This phenomenon can be observed also in *P. carvalhoi* and in *Xenopus laevis;* hence, it supposedly occurs in all pipids. On the other hand, in anuran larvae, which develop cornua trabecularum in the ethmoidal region, these persist in adults as part of the nasal septum. Positional and developmental differences suggest that, although the ethmoid plate and the cornua trabecularum arise from the same region of the cranial neural crest, they are not fully corresponding structures. Comparison with adults of other pipid genera confirmed the conclusion of some earlier investigators that *P. pipa* is the most specialized among pipids.

The basic scheme of the ethmoidal region of the endocranium, i.e., that part of the endocranium that extends from its anterior end posteriorly to the level of the postnasal wall, seems to be identical in the adult anurans of various taxonomic groups regardless of their way of life (see, e.g., Jurgens, '71). Among tadpoles, however, there are striking group differences, such as the presence or absence of the cornua trabecularum and of labial cartilages. These differences, which concern crucial features of the tadpole's ethmoidal endocranium, may be interpreted as being results of divergence, because the skeletal elements arise from similar anlagen of cranial neural crest (Sadaghiani and Thiebaud, '87). However, comparison of anurans with those labyrinthodonts for which corresponding data are available revealed that whereas similarities may be found between the labyrinthodonts and larval pipids, comparison with other anuras (both larval and adult) meets with problems. Furthermore, the cranial development in anurans characterized by trabecular horns compared with some premetamorphic stages of various pipids suggested that the cornua trabecularum and the ethmoid plate are not corresponding structures (Roček, '89). Thus it

seems that 1) divergence in larval structures could have been already at the labyrinthodont level and 2) the similarity in the ethmoidal region of adults may be the result of morphological convergence among anuran lineages as a consequence of historical constraints during their evolution.

Assessment of the significance of skull differences in anuran larvae is obscured by the fact that contemporary anuran systematics is mainly based on adults, and only a few studies have taken larvae into consideration (Orton, '53, '57; Starrett, '73; Sokol, '75). A comparison of larvae faces two difficulties, namely, larval specialization and developmental heterochrony. For example, the structure of the larval filter feeding apparatus varies with different feeding habits, yet such various specializations might evolve within a single taxon. The choice of characters for taxonomic evaluation must consider the larval type of specialization. Developmental heterochrony may influence timing of appearance and/or disappearance of larval structures. It is important to know whether exactly corresponding stages are being compared. This is not always easy, as normal tables are mostly based on external features, and these can vary substantially in closely

related forms (e.g., *Xenopus laevis* and *Pipa pipa*).

The reason why we have chosen the ethmoidal region of the endocranium is that with respect to its evolution it apparently belongs among the most conservative components of the anuran skull. This is evidenced by a comparison not only of fossil and extant representatives of the Anura but also of labyrinthodonts (and even crossopterygians; Jarvik, '42) with anurans as a whole. If we accept the view that some features present in ancestral forms may be reflected in the development of their descendants, and that taxonomy should reflect phylogeny (inferred in part from embryological evidence), any structural deviation from the common developmental mode may be of taxonomic importance. *P. pipa* was chosen because pipids, besides having some highly specialized features of reproduction in some species, also bear characters not observed in other anuran groups (i.e., the ethmoid plate and associated structures). The aim of the present paper is to describe in detail these structures and to clarify their evolutionary relationships.

MATERIALS AND METHODS

Larval and metamorphosing specimens of *P. pipa* were removed from adult females preserved in various collections. Live, young metamorphosed individuals were obtained from laboratory breeding. Fully grown specimens were collected in the vicinity of Manaus, Brasil.

The specimens were fixed in 4% formalin or (material from old collections) in alcohol. They were embedded in paraffin and sectioned serially in a frontal plane at 12.5 μm. Sections stained with Meyer's hematoxylin, Alcian blue, or erythrosin were used for graphic reconstructions. Similarly stained sections 25 μm thick were used for construction of wax models. Use of wax plates 1 mm thick enabled production of models with a magnification of ×40.

The sections of *P. pipa* and of *P. carvalhoi,*together with wax models based on them (and also models of *X. laevis*) are deposited in the Department of Palaeontology, Charles University, Prague (DP FNSP). Osteological and dissected materials of *Pipa* are also deposited there. Sections of *X. laevis* are deposited in the Institute of Evolutionary Animal Morphology, Moscow. Cleared-and-stained material of *P. pipa*was studied in the Department of Herpetology, Museum of Natural History, University of Kansas (KU).

One to five specimens were used for investigation of each stage. Because of the specialized larval development in *P. pipa* it was rather difficult to determine developmental stages comparable to the Nieuwkoop and Faber ('67) stages for *X. laevis.*However, some cranial characters, such as the position of the anterior tip of the notochord, the position of the commissura quadratocranialis anterior, the length of the Meckel's element, and so forth, served as indicators of relative age. As corresponding information is often lacking in the description of *X. laevis* stages, only approximative comparisons could be made.

RESULTS

Description of stages

Stage 40 (DP FNSP-PP OA)

The youngest larva investigated (Fig. 1A) was at a stage lacking lateral appendages, with partly resorbed yolk sac, and somites still recognizable on the body surface. It is probably older than the specimen described by Parker (1876, Pl. 60, Fig. 1). A considerable part of the ethmoidal region still consists of prechondral mesenchyme, and only its median part is differentiated into cartilage. The cartilage forms a thin ethmoid plate (sensu Nieuwkoop and Faber, '67, p. 87; not sensu Gaupp, 1893), which is slightly vaulted dorsally. Its principal part is termed the *planum internasale*. In the anterior part of the planum there is a shallow depression along the midline, bordered by indistinct anteroposteriorly oriented elevations on both sides. The latter increase moderately in height posteriad, and the median depression disappears; thus the dorsal surface of this elevated part of the planum internasale is flat. From this elevated part the septum nasi develops (cf. next stage). Near the postnasal wall, its upper margins extend laterad, thus dorsally covering the orifice of the short canalis olfactorius; by contrast, in Parker's specimen (1876, pp. 648–650, Pl. 60, Fig. 3) there are no traces of development of the olfactory canals or the septum nasi. The postnasal wall in our specimen is only moderately thicker than that of the anterior part of the ethmoid plate; but despite this, the cranial cavity is well-delimited anteriorly.

The anterior edge of the ethmoid plate extends laterally, thus supporting ventrally the anterior part of the nasal sac. This anterior part is sometimes called the *cartilago labialis superior* (e.g., Kotthaus, '33, p. 515, Fig. 1) or the *suprarostral* (Sokol, '77, p. 360,

Fig. 7), although its homology was not proved (see Discussion). The extended lateral parts are termed the *ethmoid flanges* by Sedra and Michael ('57, p. 14). The sac is depressed in accordance with the general shape of the skull. Both the choana and the naris externa are located approximately at the same level, the cavitas sacci nasalis being little more than a simple narrow canal connecting the two apertures. The thin ventrolateral extensions of the planum internasale (except for the ethmoid flanges) still consist of prechondral mesenchyme that has not differentiated into distinguishable morphological structures (cf., however, Parker, 1876, p. 650, Pl. 60, Fig. 3; note especially those portions that are incorrectly designated as parts of the cornua trabecularum, viz., the "recurrent cornua").

Stage ?40 (DP FNSP-PP OB)

The next investigated specimen (Fig. 1B) does not differ externally from that described above. However, the degree of chondrification is higher, and also the structural complexity of the nasal sac, as well of some other parts, suggests a more advanced stage.

The planum internasale remains the main structure of the ethmoidal region. Its former shape is preserved, but the primordial septum nasi is more pronounced and almost reaches the anterior margin of the ethmoid plate. The space above the plate is occupied by distinctly condensed mesenchyme histologically already resembling precartilage. Followed posteriorly, the septum increases in height and comes to consist of cartilage. Its dorsal surface is flat, and it is bordered laterally by rather sharp edges that, as in the previous stage, extend laterally to form a thin lamella, which forms a roof dorsally covering the nervus olfactorius. Farther posteriorly the nerve is enclosed in a short canalis olfactorius.

The anterior part of the ethmoid plate is extended into short horns directed postero-laterally; they continue as a strip of mesenchymal tissue called the *ligamentum cornu quadratum mediale* by Sedra and Michael ('57, p. 14, Fig. 5). Farther posteriorly the strip consists of cartilage again, forming thus the processus antorbitalis (see Table 1 for a list of synonyms). This mesenchymal and cartilaginous arch borders laterally the space where the olfactory organ is located, with the choana facing ventrally into the mouth cavity. The medial part of this organ occupies the space above the lateral margin of the planum internasale. The nervus olfactorius enters the nasal region through the olfactory canal and approaches the medial wall of the nasal organ. One can also distinguish the ophthalmicus nerve coming from the orbit and crossing the dorsal surface of the commissura quadratocranialis anterior and processus antorbitalis. Neither the processus muscularis palatoquadrati nor the palatoquadrate itself are sufficiently chondrified to allow precise determination of their morphology at this stage.

Stage 52 (DP FNSP-A2)

The stage shown in Figure 1C is characterized externally by having a spheroid body, with the tail leaning against the body flank. Hind limbs have developed into paddles with visible toes, fore limbs into a form of elongated bud, and some indication of fingers. The yolk sac is not yet fully resorbed.

The planum internasale is now reduced to only its median portion adjacent to the septum nasi. Traces of disintegration can be seen on its lateral edge. Only within the posterior part of the nasal capsule does the planum internasale extend up to the medial surface of the processus antorbitalis. The septum nasi is narrow and rounded dorsally. The tectum is well developed in the posterior part of the septum, covering the anterior orifice of the canalis olfactorius.

The nasal capsule is separated from the braincase cavity by the postnasal wall, the dorsal surface of which anterior to the braincase is called the *planum praecerebrale*. Laterally, this partition is extended by an anteriorly directed process whose dorsal surface is flat, in accordance with the general shape of the head. It may be termed the *processus maxillaris anterior,* although its homology with the similar process in ranids, pelobatids, and other groups is doubtful (see Discussion). Laterally it coalesces with the processus antorbitalis, both together forming the <-shaped posterior part of the lateral wall of the nasal capsule (see Fig. 2B; see also Higgins, '20, Fig. 74, where this compound process in cross section is incorrectly designated the *cornu trabeculae*). Both processes enclose between them the nervus ophthalmicus, more precisely the ramus lateralis narium proprius. A thin and narrow horizontal lamina running from the medial surface of the proc. antorbitalis and reaching the nasal septum in the posterior part of the nasal capsule takes part in the formation of the floor of the capsule.

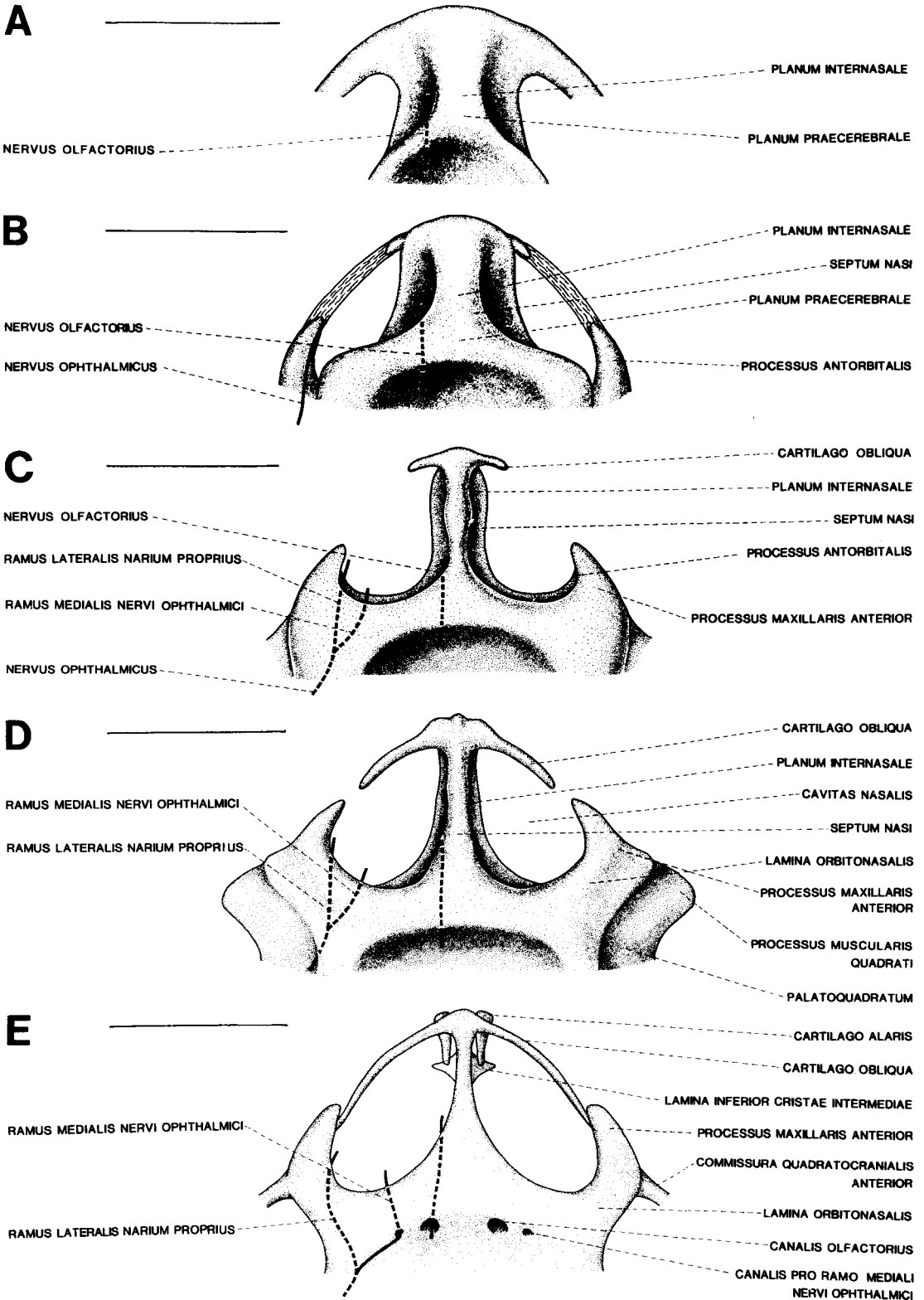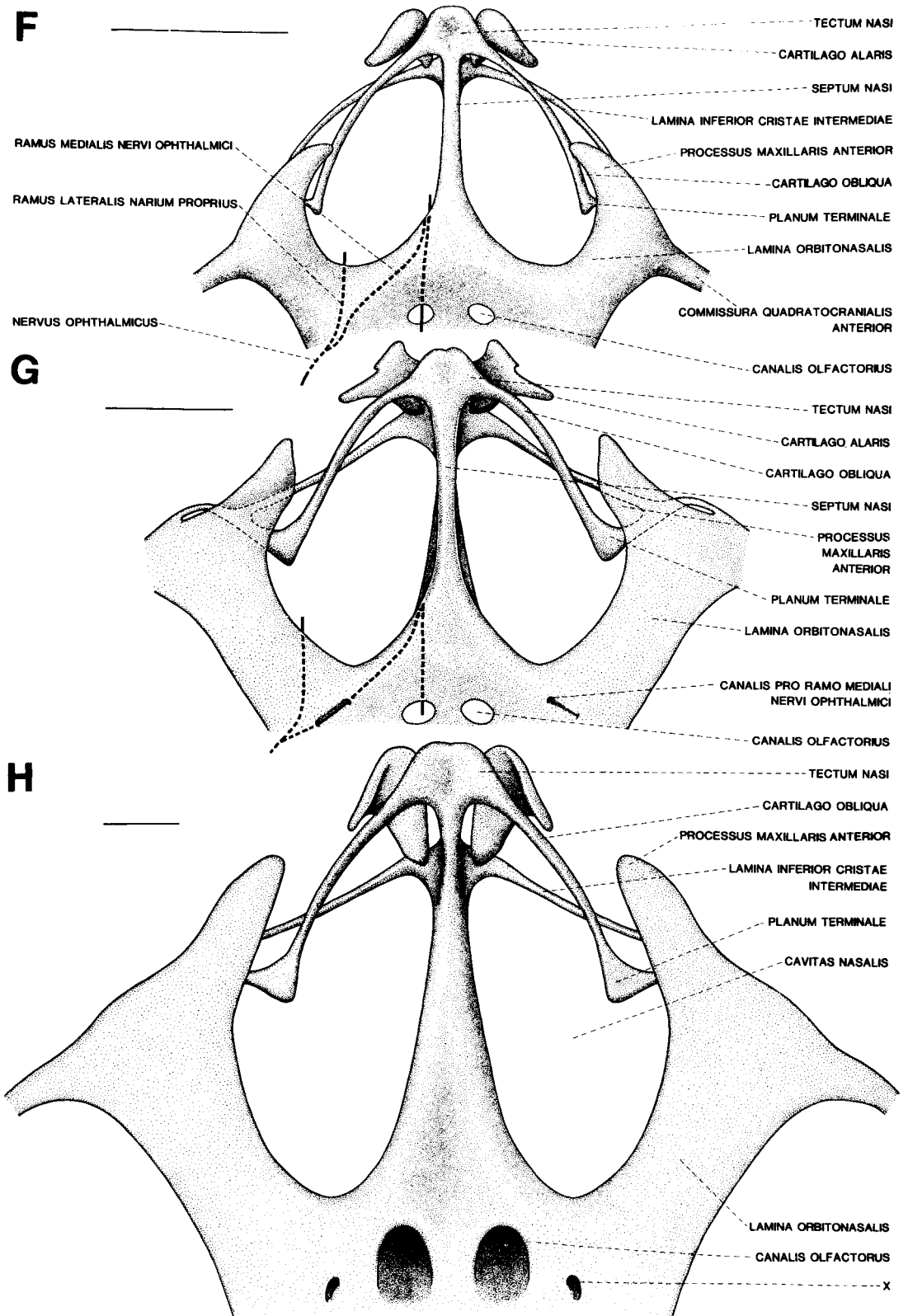The anterior end of the septum nasi extends considerably laterally, thus forming a

A

NERVUS OLFACTORIUS

PLANUM INTERNASALE

PLANUM PRAECEREBRALE

B

NERVUS OLFACTORIUS

NERVUS OPHTHALMICUS

PLANUM INTERNASALE

SEPTUM NASI

PLANUM PRAECEREBRALE

PROCESSUS ANTORBITALIS

C

NERVUS OLFACTORIUS

RAMUS LATERALIS NARIUM PROPRIUS

RAMUS MEDIALIS NERVI OPHTHALMICI

NERVUS OPHTHALMICUS

CARTILAGO OBLIQUA

PLANUM INTERNASALE

SEPTUM NASI

PROCESSUS ANTORBITALIS

PROCESSUS MAXILLARIS ANTERIOR

D

RAMUS MEDIALIS NERVI OPHTHALMICI

RAMUS LATERALIS NARIUM PROPRIUS

CARTILAGO OBLIQUA

PLANUM INTERNASALE

CAVITAS NASALIS

SEPTUM NASI

LAMINA ORBITONASALIS

PROCESSUS MAXILLARIS ANTERIOR

PROCESSUS MUSCULARIS QUADRATI

PALATOQUADRATUM

E

RAMUS MEDIALIS NERVI OPHTHALMICI

RAMUS LATERALIS NARIUM PROPRIUS

CARTILAGO ALARIS

CARTILAGO OBLIQUA

LAMINA INFERIOR CRISTAE INTERMEDIAE

PROCESSUS MAXILLARIS ANTERIOR

COMMISSURA QUADRATOCRANIALIS ANTERIOR

LAMINA ORBITONASALIS

CANALIS OLFACTORIUS

CANALIS PRO RAMO MEDIALI NERVI OPHTHALMICI

Figure 1

F

TECTUM NASI

CARTILAGO ALARIS

SEPTUM NASI

LAMINA INFERIOR CRISTAE INTERMEDIAE

PROCESSUS MAXILLARIS ANTERIOR

CARTILAGO OBLIQUA

PLANUM TERMINALE

LAMINA ORBITONASALIS

RAMUS MEDIALIS NERVI OPHTHALMICI

RAMUS LATERALIS NARIUM PROPRIUS

COMMISSURA QUADRATOCRANIALIS ANTERIOR

NERVUS OPHTHALMICUS

CANALIS OLFACTORIUS

G

TECTUM NASI

CARTILAGO ALARIS

CARTILAGO OBLIQUA

SEPTUM NASI

PROCESSUS MAXILLARIS ANTERIOR

PLANUM TERMINALE

LAMINA ORBITONASALIS

CANALIS PRO RAMO MEDIALI NERVI OPHTHALMICI

CANALIS OLFACTORIUS

H

TECTUM NASI

CARTILAGO OBLIQUA

PROCESSUS MAXILLARIS ANTERIOR

LAMINA INFERIOR CRISTAE INTERMEDIAE

PLANUM TERMINALE

CAVITAS NASALIS

LAMINA ORBITONASALIS

CANALIS OLFACTORIUS

X

Figure 1

TABLE 1. Some anatomical terms used in the present paper and their synonyms

Present paper	Synonyms
Anterior section of the septum nasi	Planum verticale (Higgins, '20, p. 51, Fig. 74)
Cartilago alaris	Alinasal cartilage (Higgins, '20, p. 50)
Cartilago obliqua	Cornu trabeculae (Parker, 1876, p. 654, Pl. 60, Figs. 5, 6; Pl. 61, Figs. 2, 5)
Diverticulum medium sacci nasalis	Cavum medium (Paterson, '51)
Lamina inferior cristae intermediae	"Upper labial b" (Parker, 1876, p. 659, Pl. 61, Fig. 5)
Planum internasale	Internasal plate (Parker, 1876, p. 650)
	Planum basale (Higgins, '20, p. 49)
	"Gaumendach," "Gaumendachplatte" (Kotthaus, '33, p. 515, Fig. 1)
Planum praecerebrale	"Vordere Trabekelplatte" (Gaupp, 1893)
Primordial cartilago alaris	"Upper labial a" (Parker, 1876, p. 659, Pl. 60, Fig. 8; Pl. 61, Figs. 4, 5)
	"Upper labial c" (Parker, 1876, p. 659, Pl. 61, Fig. 5)
Processus antorbitalis	Prenarial lamina (Parker, 1876, p. 650)
	Quadrato-ethmoidal process (De Beer, '37, Pl. 74, Fig. 5)
	Processus cornu quadratus medialis (Sedra and Michael, '57, p. 14, Figs. 3, 5)
Processus maxillaris anterior	Prepalatine (Parker, 1876, p. 654, Pl. 60. Figs. 5, 6; Pl. 61, Figs. 2–5; Pl. 62, Figs. 2, 8)
	Lamina cribrosa (Winslow, 1898, p. 171)
	Planum tectale (Higgins, '20, p. 49, Fig. 74)
	Anterior process of the planum antorbitale (Paterson, '55, p. 227, Figs. 1, 3A, 5)
Proximal part of the lamina inferior cristae intermediae	Subnasal lamina (Parker, 1876, p. 659, Pl. 60, Figs. 5, 6; Pl. 61, Fig. 5)
Tectum nasi	Alinasal folds (Parker, 1876, p. 661) "Rudimentary alae nasi" (Parker, 1876, p. 654, Pl. 60, Figs. 5, 6, 8)

transverse lamina (primordium of the cartilago alaris), which anteriorly is connected to the underlying planum internasale by soft tissue only. The dorsal surface of the lamina runs out in a low ridge, indicating the course of the nasal septum. The lateral ends of this lamina continue as slender horns that represent the primordium of the cartilago obliqua. Lateral to the olfactory organ, in the prolonged tips of the cartilago obliqua, are islets of mesenchymal tissue that might represent the more posterior parts of this cartilage in the process of chondrification.

The postnasal wall is pierced by two other passages in addition to the canalis olfactorius. Close to the very posterior end of the olfactory organ can be seen the orifice of the can. rami medialis n. ophthalmici. The orifice of the can. pro ramo lateralis narium proprio is located on the medial line of coalescence between the proc. maxillaris anterior and proc. antorbitalis. Both canals merge approximately at the level of the posterior end of the can. olfactorii. Further posteriorly is only a single canal, which is a passage for the n.

Fig. 1. **A:** Ethmoidal region of *P. pipa,* estimated Nieuwkoop-Faber stage 40. Lateral parts still consist of prochondral tissue. **B:** Same in larger specimen that, however, externally does not differ from stage 40. Note the strip of mesenchymal tissue connecting the anterior part of the ethmoid plate with the processus antorbitalis. **C:** Same region in stage 52. Note that new, lateral branch of the nervus ophthalmicus is covered dorsally by the processus maxillaris anterior arising almost simultaneously with the septum nasi. **D:** Same region, stage 54. **E:** Same region, stages 56–58. **F:** Same region, stage 64. **G:** Same region in fully metamorphosed froglet (stage 66). Note the asymmetric arrangement of the distal parts of the cartilago obliqua and lamina inferior cristae intermediae. **H:** Same region in postmetamorphosed froglet, age 7 months, SVL 52 mm. X, orifice for the ramus frontalis perforans. All illustrations in dorsal aspect. Bars = 1 mm.

Fig. 2. Gradual substitution of the processus antorbitalis by processus maxillaris anterior during the course of development in *P. pipa.* A: Stage 40. Cross section through the ethmoidal region at the level of the posterior end of the olfactory organ (cut slightly obliquely so that the section goes through the postchoanal region on the right side). The nervus ophthalmicus runs above the processus antorbitalis. B: Same region in stage 52. Newly arisen processus maxillaris anterior fuses laterally with the vestige of the processus antorbitalis. The nervus ophthalmicus (its lateral branch) is situated between them. C: Same region (right part of the skull only) in a postmetamorphosed specimen. Lateral branch of the nervus ophthalmicus runs at the level below the processus maxillaris anterior and below the anteromedial part of the lamina orbitonasalis. C. MECK., cartilago Meckeli; F. ENDOCH., fenestra endochoanalis: N. OLF., nervus olfactorius; N. OPHTH., nervus ophthalmicus; NAS., os nasale; P. ANTORB., processus antorbitalis; P. MAX. ANT., processus maxillaris anterior continued as lamina orbitonasalis (L. ORB.); PL. INT., planum internasale; PL. PRAECER., planum praecerebrale; R. LAT. N. PROP., ramus lateralis narium proprius; R. MED. N. OPHTH., ramus medialis nervi ophthalmici; S. NAS., septum nasi; SAC. NAS., saccus nasalis. Bars = 1 mm.
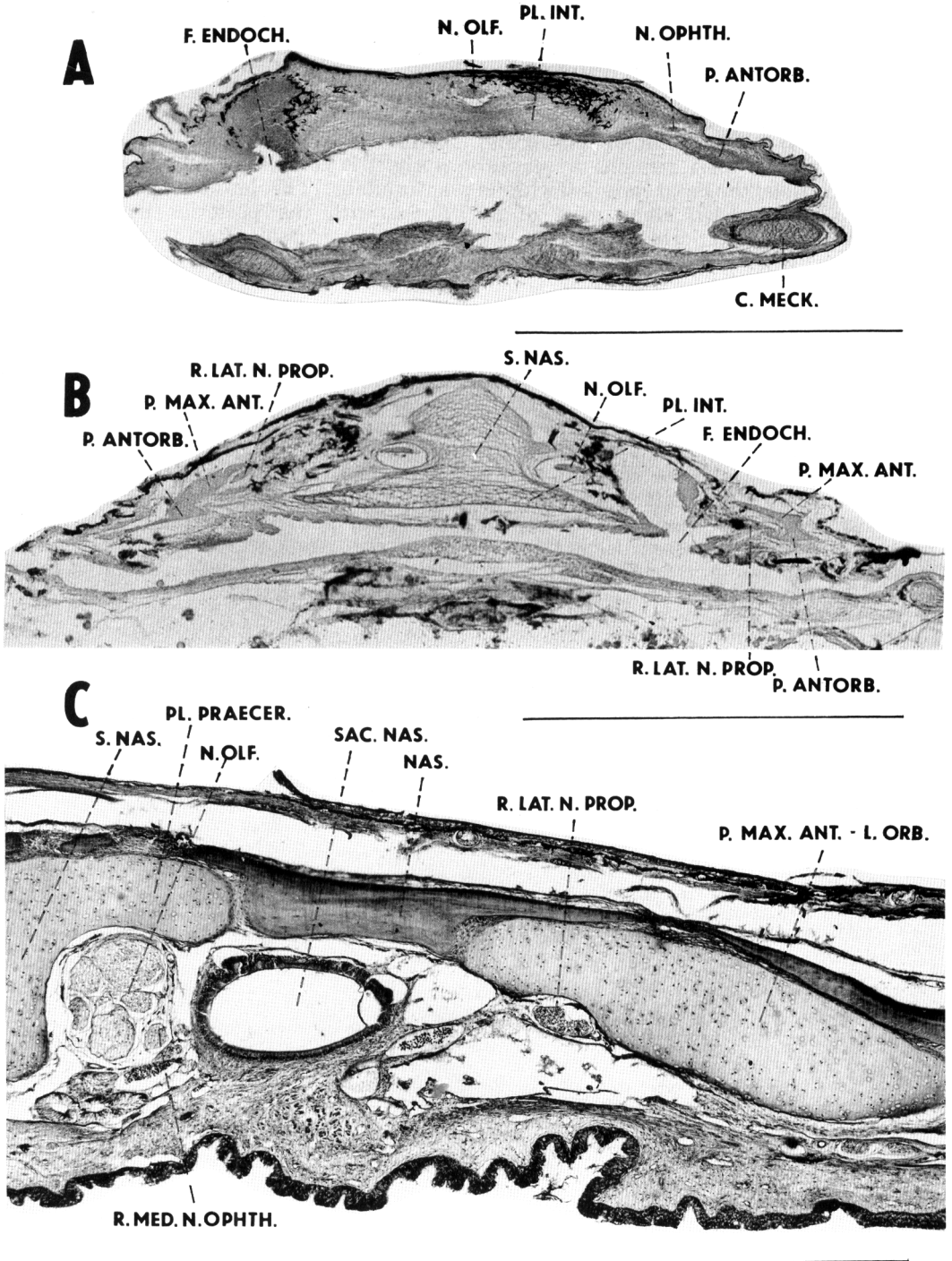
Figure 2

ophthalmicus entering the orbitonasal carti-
lage from the orbit.

Stage 54 (DP FNSP-PP Veselý A I)

Stage 54 (Fig. 1D) can be distinguished
externally from the preceding one only by the
higher degree of the resorption of the yolk sac
and by further development of fingers and
toes. The septum nasi remains a vertical
partition between the nasal capsules, with its
upper margin rounded along most of its
length except for anteriorly where there is a
thin mesenchymal condensation forming the
tectum nasi. The planum internasale is nar-
row anteriorly, with its upper surface on both
sides of the septum facing dorsolaterally; as
the septum is triangular in cross section
(wider ventrally), the upper surface of the
planum is confluent with the lateral surface
of the septum. Posteriorly, the septum
becomes thicker and the planum (forming the
floor of the nasal capsule adjacent to the
septum) is wider too, its lateral margins thus
diverging posteriorly. Viewed ventrally, the
planum is deeply depressed below the sep-
tum; this depression is more pronounced
anteriorly. The posterior part of the planum

is, histologically, well delimited from the sep-
tum and displays signs of disintegration (Fig.
3). The septum terminates anteriorly in a
rounded tip. The tectum gives off posterolat-
erally a thin rod-like cart. obliqua.

The proc. maxillaris anterior is, at its ante-
rior limit, a flat, thin cartilage with its upper
surface facing dorsolaterally. Farther poste-
riorly it is completed by a horizontal proc.
antorbitalis. The latter is posteriorly con-
fluent with the posterior portion of the
planum internasale, thus forming a floor to
the posterior part of the nasal capsule. The
proc. maxillaris anterior is also considerably
broadened posteriorly and finally reaches
that part of the septum that dorsally covers
the orifice of the can. olfactorius. Both proc.
antorbitalis and proc. maxillaris anterior
enclose the ramus lateralis narium proprius.
The can. pro ramo medialis n. ophthalmici
enters the nasal cavity on the posteriormost
end of the latter. Both canals are branches of
that for the n. ophthalmicus that enters the
postnasal cartilage from the orbit. The post-
nasal wall extends laterally in a thin horizon-
tal plate that corresponds to the proc. muscu-
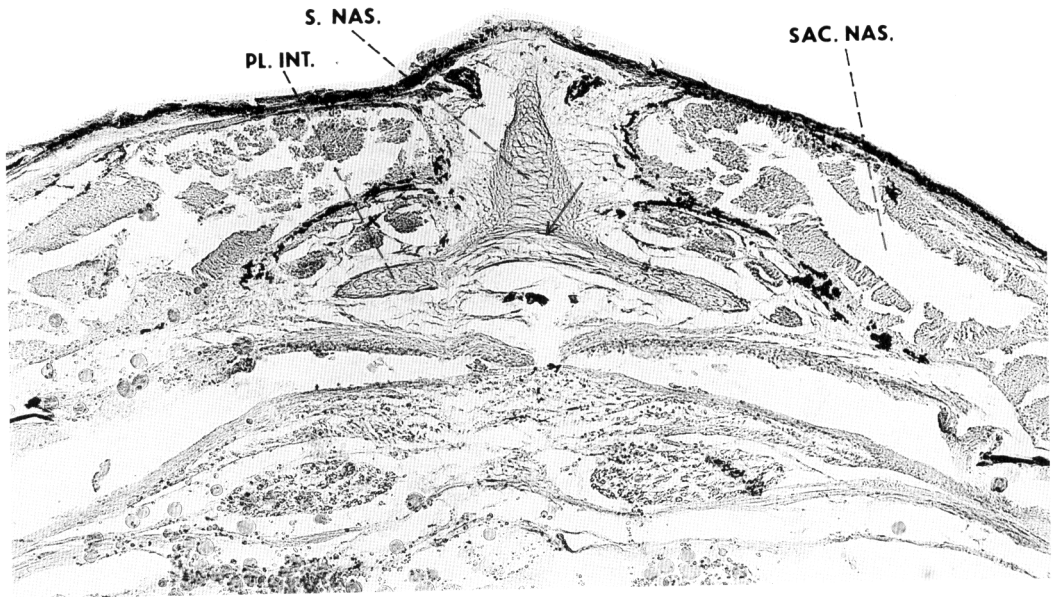laris palatoquadrati.

Fig. 3. *P. pipa,* stage approximately 52. Cross section through the septum nasi and planum
internasale to show the line of division (arrow) between the structures. For abbreviations, see Figure
2. Bar = 1 mm.

Stages 56–58 (DP FNSP-PP Veselý B II)

Stages 56–58 (Fig. 1E) differ from the foregoing one in having the yolk sac resorbed completely, by greater development of the legs, and by its absolute larger size. The snout–vent length (SVL) is 15 mm (as the body is now straight, it is possible to make this measurement accurately). This stage corresponds approximately to that illustrated by Parker (1876, Pl. 60, Figs. 5, 6).

The planum internasale is resorbed completely so that the lower margin of the septum is rounded and free except for a short section about one-third of the way posteriorly where thin horizontal laminae, triangular in shape, extend laterally from the lower edge of the septum. Each of them represents the proximal part of the developing lamina inferior cristae intermediae and is not a vestige of the planum internasale. The nasal capsule lacks a floor for almost its whole extent.

The septum nasi is rounded anteriorly. The small tectum gives off posterolaterally on either side the slender cart. obliqua. This cartilaginous rod reaches below the anterior tip of the proc. maxillaris anterior. Approximately at midheight, the anterior end of the septum is connected laterally with a thin vertical cartilage, which is the primordial cart. alaris. Its ventral part is bent posteriorly and continues as a cartilaginous rod up to the dorsal surface of the proximal part of the lamina inferior cristae intermediae. The posterior part of this rod was designated the *upper labial c* by Parker (1876, p. 659, Pl. 61, Fig. 5).

The postnasal wall has a more extensive planum praecerebrale (which plays a more significant role in roofing the posterior part of the capsules) than in the previous stage; the ventral part of the wall has shifted posteriad. Consequently, the anterior part of the braincase is not well delimited against the planum praecerebrale, and it is considerably more shallow than in earlier stages. The course of can. olfactorius is no longer horizontal, but is more vertical. The n. ophthalmicus pierces the low and indistinct lateral wall of the braincase from the orbit, and just before it enters this cavity it bifurcates. One branch, the ramus lateralis narium proprius, runs anteriad and enters the nasal capsule on the medial surface of the fused proc. maxillaris anterior and proc. antorbitalis; the other branch, the ramus medialis n. ophthalmici, enters the braincase cavity, follows its wall for a short distance, and pierces the postnasal wall anteroventrally, similarly to the n. olfactorius.

The compound processus maxillaris anterior/antorbitalis does not differ morphologically from the corresponding structure in the foregoing stage; however, the commissura quadratocranialis anterior, which was previously a wide, ventrolaterally directed connection with the palatoquadratum, becomes a slender cartilaginous rod, directed posterolaterally. The proc. muscularis quadrati has disappeared.

Stage 62 (KU 204076)

The description of this stage is based on a stained specimen. Both pairs of legs are well developed; the tail is partly reduced. Body length is 14.2 mm.

The basic scheme of the ethmoidal region essentially corresponds to that in the preceding stages except for the cart. obliqua, whose tip on each side almost reaches the level of the postnasal wall when viewed dorsally. The primordium of the cart. alaris is not in contact with the proximal part of the lamina inferior cristae intermediae (but cf. stages 56–58 and 64). The lamina is longer and more slender.

The postnasal wall has become an almost horizontal plate, with the can. olfactorius and can. pro ramo medialis n. ophthalmici short and nearly vertical. There is an indistinct outgrowth on the anterolateral edge of the proc. maxillaris anterior approximately at the transition between this process and the commissura quadratocranialis anterior. This might be a vestige of the bridge with the fused obliqua and lamina inferior cartilages (see next stage, Fig. 1F).

The floor of the braincase, as well as its lateral parts adjacent to the ethmoidal region, are composed of membranous tissue.

Stage 64 (DP FNSP-P 4)

Stage 64 (Fig. 1F) is characterized externally by a reduction of the length of the tail to about one-third of the body length. SVL is 17 mm.

The septum nasi for its posterior two-thirds is a simple vertical partition. The orifice of the can. olfactorius is roofed dorsally by the enlarged planum praecerebrale extending over the posteromedial corner of the capsule. The anterior one-third of the septum is T shaped, having a thin and narrow tectum. The cart. obliqua almost reaches the basal part of the proc. maxillaris anterior.

The distal section of the oblique cartilage is rather extended; this extension may be called the *planum terminale.* Close to its tip, this cartilage gives off laterally a subtle outgrowth, which approaches the lower surface of the proc. maxillaris anterior.

The lamina inferior cristae intermediae, which leads off horizontally from the ventral part of the septum, is depressed medially, while laterally (directed below the anterolateral margin of the proc. maxillaris anterior) it becomes slender. The cart. alaris maintains its original vertical position; however, it has lost its contact with the septum. It is convex anteroventrally and concave posterodorsally; its lower, rod-like, end leans on the dorsal surface of the proximal part of the lamina inferior.

The postnasal wall, as well as those structures that are adjacent to the commissura quadratocranialis anterior, remain basically the same as in the foregoing stage. The brain extends up above the planum praecerebrale, so that the course of the can. olfactorii is nearly vertical. The n. ophthalmicus enters the braincase wall from the orbit and runs for a short distance anteromedially. Just before it reaches the surface of the braincase (which is extremely shallow at this level) it splits into the medial and lateral rami; both run anteriorly in a single canal along the border between the basal plate of the braincase and the lamina orbitonasalis. The ramus lateralis enters the nasal cavity on the ventral surface of the orbitonasal wall close to its anterior margin, above the posterior section of the choana. The ramus medialis appears in the nasal cavity approximately at the same level as the former, but runs anteromedially in a groove on the lower surface of the planum praecerebrale, where it joins the olfactorius nerve just before the latter enters the nasal cavity.

Stage 66 (DP FNSP-PP Veselý D IV, SVL 19 mm; KU 204125, SVL 30.5 mm)

Stage 66 (Fig. 1G) is externally a fully developed froglet without a tail. A specimen of apparently the same stage was described by Higgins ('20, pp. 49–51).

The basic scheme of the ethmoidal region is identical with that of the foregoing stage, except for the following characters. 1) The primordium of the alar cartilage is more complex in shape. It has three processes: one directed anterodorsally, another laterally, and the third bent posteriorly. 2) The cart.

obliqua is curved laterally close to the planum terminale and is connected with the distal end of the lamina inferior cristae intermediae by a thin bridge. Both cartilago and lamina are either intimately joined to the lower surface of the lateral part of the proc. maxillaris anterior or continue as a slender rod to join the anterolateral margin of the commissura quadratocranialis anterior. The specimen KU 204125 displayed both conditions. The former condition was found also by Higgins ('20, p. 50). It seems probable that Parker's figure of this stage (1876, Pl. 61, Fig. 5) was based on a specimen in which both the alar cartilage and especially the lamina inferior (called by him the *upper labial b*) were displaced.

The passages of the branches of the ophthalmicus nerve and the n. olfactorius are the same as in the previous stage, but the ramus medialis n. ophthalmici is exposed for a short distance in a groove on the anterolateral surface of the braincase cavity. The nerve was covered as in stage 64 (Fig. 1F), whereas in a still earlier stage it was exposed (Fig. 1E). It seems that this feature is a matter of individual variation rather than age-dependent character. A similar condition for passages of the nerves was described by Higgins ('20, p. 50).

Stage 66 (DP FNSP-PP postmetamorphosed)

The final stage (Fig. 1H) investigated by means of a wax model, was a froglet of SVL 52 mm, aged of 7 months, with the septum nasi not yet fully ossified. The ethmoidal region extends far posterior to the anterior end of the commissura quadratocranialis anterior. Only the most anterior section of the septum nasi is completed by the tectum; besides this, the nasal orifices of the can. olfactorii are roofed by the extended planum praecerebrale and the postnasal wall. The planum is flat with a shallow midline depression that houses the anterior process of the frontoparietal (a similar depression on the lower margin of the posterior section of the septum nasi houses the anterior portion of the parasphenoid).

The proc. maxillaris anterior is flat and thin and reaches the level of the anterior end of the lamina inferior cristae intermediae. The lamina orbitonasalis is also depressed, although not so thin. At the transition between the lamina orbitonasalis and the proc. maxillaris anterior there is a distinct elevation on the ventral surface. At the same

level, the commissura quadratocranialis anterior turns laterally, almost at a right angle, with its proximal portion flattened dorsoventrally and its distal portion in the form of a slender rod.

The two major rod-like cartilages maintain their previous position. The cart. obliqua runs from the tectum nasi posterolaterally along the surface of the olfactory organ, approximately following the border between the diverticulum superior and medium, and reaches posteriorly the level of the midsection of the septum nasi. Within this posterior termination it has an extension (the planum terminale). The lamina inferior cristae intermediae runs posterolaterally from the lower margin of the septum; proximally it is a small, flat, triangular plate (Parker [1876, p. 661] maintains that this structure, which he called the *subnasal lamina* at an earlier stage, has disappeared by this stage). Most of the lamina inferior, however, is a thin rod running posterolaterally into the space below the proc. maxillaris anterior, crossing the lower surface of the diverticulum medium, and separating, by its distal section, this diverticulum from the organ of Jacobson. Both cartilages are connected with one another by a slender, crescent-shaped bridge. The lamina inferior runs posterolaterally to the vicinity of the lateral edge of the proc. maxillaris anterior and gives rise to the bridge with the cart. obliqua (or, better said, with the planum terminale) just mentioned before terminating. Parker (1876, p. 661, Pl. 62, Figs. 7, 8) mentions only one cartilage, which he incorrectly called the *cornu trabeculae.*

The cart. alaris is, when viewed dorsally, a more or less horizontally flat structure. Its lateral margin is elevated, thus protecting ventrolaterally that part of the olfactory organ called the *vestibulum* (Paterson, '51, pp. 384, 390, Fig. 1). This lateral margin extends posterolaterally as a distinctly pointed outgrowth. Posteromedially, the alar cartilage reaches the triangular plate, forming the proximal part of the lamina inferior, and approaches it dorsally. However, in spite of this intimate contact both structures do not fuse synchondrotically. Another process is given off from the medial margin of the alar cartilage, bending above the dorsal surface of the cartilage. Completely isolated and located ventrally from the alar cartilage is an elongated, anteroposteriorly oriented short rod. As this is in contact with the pars palatina praemaxillae, it might be the proc. praena-

salis communis (see Discussion; cf. also Trueb and Cannatella, '82, p. 29).

The postnasal wall is flat, so the can. olfactorii continue as marked grooves posteriorly, covered intimately by the frontoparietal. The ramus medialis n. ophthalmici enters the nasal cavity in the close vicinity of the orifice of the can. olfactorius, but well separated from it. The ramus lateralis narium proprius enters the cavity on the lower surface of the postnasal wall, approximately at the posteromedial end of the lamina orbitonasalis. Both canals arise as a bifurcation of the can. nervi ophthalmici that enters the braincase cartilage from the orbit. Shortly before it splits into its two terminal branches it gives off another one that runs onto the dorsal surface of the braincase cartilage and then posteriorly in its own groove (Fig. 4). This branch may be identical to the ramus frontalis perforans of *Rana* (Gaupp, 1899, p. 137, Fig. 36). This latter branch is not mentioned by Arnold (1898).

What we just described in the juvenile frog is not exactly like what Parker (1876, Pl. 62, Figs. 7, 8) illustrated for the adult. As we did not section any fully grown specimens, because of their large size, it is hard to say whether the condition figured by Parker indicates still further development or simply incorporates inaccuracies like those found in his figures and descriptions of earlier stages. However, because the general structure of the ethmoidal endocranium in our last two investigated stages, differing in both size and age, is nearly identical, we rather think the adult structural scheme was attained.

Summary of development
Planum ethmoidale

The first clearly defined structure within the ethmoidal region is the ethmoid plate, consisting mainly of the planum internasale. Its anterior edge represents larval upper jaws (used in free-swimming *Pipa* larvae but not in *P. pipa*). Although these do not here serve their original purpose, as in other pipids, they still maintain the shape of laterally extending chondrified outgrowths. Lateral parts of the region in these early stages are not yet differentiated into any distinguishable structure, except possibly for a strip of rather condensed mesenchymal tissue that borders the ethmoidal region anterolaterally. This arch was not chondrified in our specimens of *P. pipa* (cf. Parker, 1876, Pl. 60, Fig. 3), except as a small rod anteriorly and as the proc.
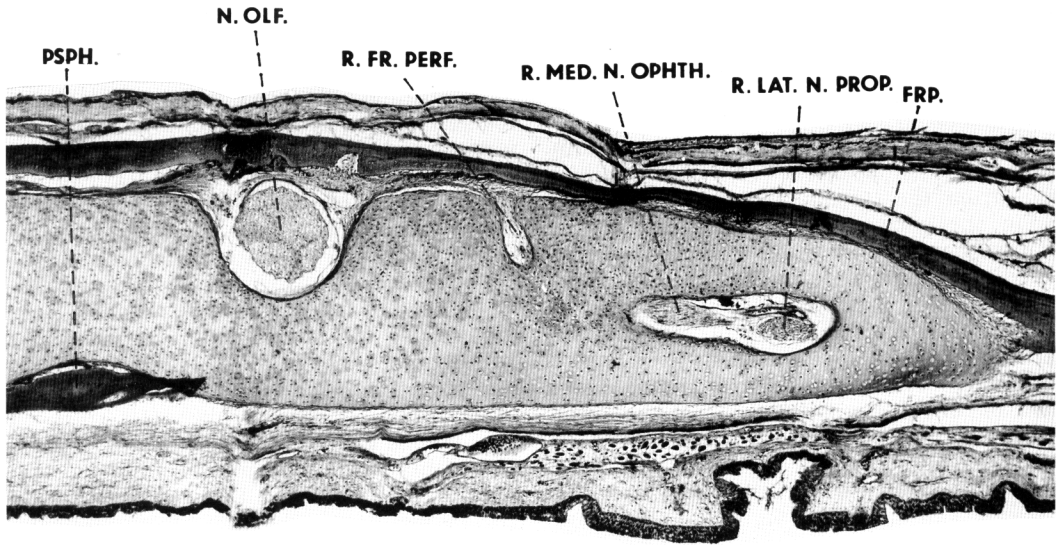
Fig. 4. *P. pipa*, SVL 52 mm, age 7 months. Cross section through the anterior part of the braincase, posterior to the planum praecerebrale (right side only), through the point of branching of the nervus ophthalmicus. FRP., os frontoparietale; PSPH., os parasphenoideum; R. FR. PERF., ramus frontalis perforans. For other abbreviations, see Figure 2. Bar = 1 mm.

antorbitalis. However, both of these chondrified components disintegrate and disappear, the anterior one in comparatively early stages and the proc. antorbitalis in stages 62–66.

Similarly to these lateral parts of the ethmoidal region, the planum internasale also undergoes reduction and finally disappears completely (approximately during stages 56–58). Hence, these early elements of the larval ethmoidal endocranium are lacking in the adult.

Septum nasi

The septum nasi arises on the midline, above the planum internasale, close to the postnasal wall, and continues to grow anteriorly. It can be well distinguished in early stages (e.g., stage 40), although it is confluent with the planum. Only later, with increasing disintegration of the latter, can one distinguish both structures histologically in sections (Fig. 3).

Tectum nasi

The tectum nasi arises only in the anteriormost section of the septum, although there are signs of other mesenchymal condensations temporarily forming the narrow roof of the nasal capsule. Whether the roof above the orifice of the can. olfactorius and above the posterior part of the nasal capsule may be termed the *tectum* is questionable, because it is produced by the postnasal wall and later by a medial expansion of the proc. maxillaris anterior and anteromedial part of the lamina orbitonasalis.

Solum nasi

The solum nasi in early larval stages consists of the planum internasale and the proc. antorbitalis. Both support the olfactory organ ventrally. With the subsequent reduction of these larval structures the solum vanishes, and the only structure that can serve as the floor of the capsule is the proximal part of the lamina inferior cristae intermediae.

Processus maxillaris anterior/antorbitalis

This process develops anteriorly from the lateral portion of the postnasal wall. Its compound origin is evidenced by the ramus lateralis narium proprius. This nerve runs first on the dorsal surface of the horizontally located proc. antorbitalis (Fig. 2A). Later the process is completed by the proc. maxillaris anterior,

which results in enclosure of the nerve in the space between them (Fig. 2B; see also Higgins, '20, p. 50). In advanced stages the proc. antorbitalis disappears and the nerve becomes free from the ventral side. This is why it runs, after entering the nasal capsule, for considerable distance along the ventral surface of the lamina orbitonasalis and below the level of the proc. maxillaris anterior (Fig. 2C).

Commissura quadratocranialis anterior

The areas of this commissure and of the anterior part of the palatoquadrate are subject to another significant change. Shortly after it chondrifies, the palatoquadrate is a horizontal plate located at the level of the braincase floor. This elongated plate runs parallel to the lateral braincase wall. Hence, the fenestra subocularis, when viewed dorsally, is a rather narrow slot. In its anterior portion, the palatoquadrate deviates laterally into the horizontal proc. muscularis palatoquadrati. The commissura is in these early stages the vertical connection of the postnasal wall with the anterior section of the palatoquadrate. Between stages 54 and 58 (Fig. 1D,E) the commissura becomes a rodlike structure directed posterolaterally, resulting in a very spacious fenestra subocularis. Concomitant with this positional change, the proc. muscularis palatoquadrati disappears.

Postnasal wall

The postnasal wall undergoes no abrupt or major alterations; however, changes in the courses of nerves that pierce this wall indicate that changes in proportion occur. First, the orbitonasal wall becomes longer, which is evidenced by the course of the ramus lateralis narium proprius (Fig. 1D,E). The orifice of the ramus medialis, which at early stages enters the nasal cavity in its most posterior part, is located more medially in older stages. This repositioning suggests that the point of branching of both rami has shifted laterally, possibly caused by lateral growth of the partition between the nasal cavity and the braincase (Fig. 1E,F). The process of elongation of the orbitonasal wall continues also in late stages so that the anteroposterior diameter of the nasal capsule increases. This is evidenced also by the posterior extent of the cart. obliqua. While in younger specimens the cart. obliqua attains almost the level of the postnasal wall, in a postmetamorphosed specimen (Fig. 1H) it reaches only one-half the length of the proc. maxillaris anterior.

The partition between the nasal capsule and the braincase cavity also changes from a vertical to a more horizontal position. This results in the planum praecerebrale slanting down into the cranial cavity without any distinct border and the anterior edge of the postnasal wall shifting to above the posterior part of the olfactory organ. Consequently the can. olfactorii and, to a lesser extent, the can. pro ramo medialis n. ophthalmici have more vertical courses. The cranial cavity gets shallower, and in adults its anterior part is limited to a low space between the flat braincase (which has no distinguishable walls at this level; see Fig. 4) and the frontoparietal. It is also noteworthy that the bottom of the braincase becomes membranous approximately at stage 62.

In connection with the postnasal wall, one process in the sequence of changes should be mentioned, although it was not evident in our specimens; most probably it happens in very early stages before the septum nasi starts to develop. In *X. laevis* (Kotthaus, '33, pp. 544, 564) and *P. carvalhoi* (Roček, personal observation), both n. olfactorii in early stages run on the surface of the postnasal wall to reach the nasal capsule. Later they are covered dorsally by new cartilage, which forms the planum praecerebrale. Both nerves thus become enclosed within the canals. The cartilage subsequently continues to grow anteriorly, forming the septum nasi. This is already the stage represented as the earliest one from our material.

Cartilago obliqua

The cartilago obliqua arises approximately at stage 52. It grows posteriorly, reaching first the tip of the proc. maxillaris anterior. Later, as a consequence of the elongation of the orbitonasal wall and of the displacement of this process laterally, the cartilage terminates medial to it. Still later, approximately at stages 56–58, the proximal part of the lamina inferior cristae intermediae arises and continues to grow posterolaterally as a slender, crescent-shaped cartilage. Subsequently, it becomes straight and connected by a cartilaginous bridge to the planum terminale. Noteworthy is its temporary synchrotic connection with the lateral part of the proc. maxillaris anterior. In metamorphosed animals distal parts of both cartilages closely

approach the lower surface of the proc. maxillaris, but remain separate from it.

Cartilago alaris

The alar cartilage first appears as a lateral, vertical extension of the septum nasi, which acts as an anterior wall of the nasal capsule. Later it becomes more horizontal, so that its originally ventral process reaches the proximal section of the lamina inferior cristae intermediae. At stage 62 the alar cartilage ceases to be connected with the septum (i.e., with the proc. praenasalis medius).

DISCUSSION

In anurans, the terminology applied to the cranial structures, including those found in development, is usually derived from the condition in *Rana,* which was among the earliest species described satisfactorily from an anatomical point of view (see De Beer ['37, p. 198] for review of older literature, including the outstanding contributions of Gaupp; more recent studies by Reinbach ['51], De Jongh ['68], and Plasota ['74] are also based on *Rana*).

In *Rana, Pelobates,* and the majority of other anurans, the principal structures of the ethmoidal region are the cornua trabecularum that extend anteriorly from the larval postnasal wall. With metamorphosis, the adult ethmoidal configuration arises by the appearance of new cartilage that connects the trabecular horns medially (Roček, '81, Fig. 20; cf. Born, 1876, pp. 606, 609, 622; De Jongh, '68, p. 34). This composite median cartilage gives rise to the septum nasi. Thus principal larval ethmoidal structures are retained in adult anurans.

The development of the ethmoidal region in pipids, on the other hand, seems to differ from that described in *Rana.* In pipid larvae, the trabecular horns are absent. Parker (1876, p. 650), apparently influenced by the common view on the origin of the septum nasi in other anurans (see, e.g., Stöhr, 1882, pp. 85, 86), considered the planum internasale of larval *P. pipa* incorrectly as a coalesced internasal portion of the trabeculae that distally becomes free again and continues as "recurrent cornua." In Parker's Figure 3 (Pl. 60), he designated these structures as *cornua trabecularum.* In later stages, he considered as cornu trabeculae the cart. obliqua (Parker, 1876, Pl. 60, Figs. 5, 6; Pl. 61, Figs. 2, 5; Pl. 62, Fig. 8). Obviously he regarded both larval and adult structures homologous (Parker, 1876, p. 654). Higgins ('20, pp. 49–51) repeated Park-

er's statement about coalesced trabeculae, and in accepting that interpretation he concluded that the septum nasi (his planum verticale) is a reduced internasal plate and that "the planum verticale has developed by a fusion, in the middle line of the skull, of the trabeculae" (p. 51). All of these misinterpretations were based on incorrect presuppositions that larval and adult ethmoidal structures in *Pipa* are homologous. Paterson ('51, Figs. 8, 9; '55, p. 226, Fig. 3B) designated as cornu trabeculae the lamina inferior cristae intermediae. This identification caused her some problems ('55, pp. 227–228), and she even mentioned the correct possibility that the lamina inferior should be considered. Other investigators were also influenced by Parker's and Higgins' statements. For instance, Kotthaus ('33, p. 515) maintained that the "Gaumendach" is a result of the cornua trabecularum, and Sokol ('75, p. 18) believed that in pipids, as in *Rhinophrynus,* there is a median bar of cartilage that supports the nasal septum and that the remains of intertrabecular fenestra are occluded by cartilage; but he did not give any evidence for this statement, and we have not found anything that would support this view.

Contrary to previous investigators, we can state that the ethmoidal endocranial region in early larvae of *Pipa* consists exclusively of a simple, horizontal *ethmoid plate.* This term should not be confused with that used by Gaupp (1893) or with the like-named structure designating the fused part of the cornua trabecularum in *Pelodytes* (Sokol, '81, p. 166), which persists in adults as part of the solum nasi. The anterior edge of the ethmoid plate serves as the larval upper jaw (there are no separate upper labial cartilages as in *Rana*). In the course of larval development, all ethmoidal structures disappear (see also Sedra and Michael, '57, p. 24), and adult structures originate from new material located dorsal to the planum (Kotthaus ['33, p. 544] speaks about "ein sekundäres Gaumendach"; see also his Fig. 24).

Because of the positional and developmental differences between the cornua trabecularum and the planum internasale (or the ethmoid plate) and because of the fact that (for just-mentioned reasons) they cannot be derived one from another, it is probable that they are not fully corresponding (Roček, '89), although both derive from the same region of cranial neural crest (Sadaghiani and Thiebaud, '87). From this point of view, attempts to apply ranid terminology to pipids

seem inappropriate (see also Paterson, '51, p. 383; '55, p. 224; Kotthaus, '33, p. 565). For instance, use of the term *suprarostral* (or the term *cart. labialis superior*) is fully justified in *Rana,* but not in pipids (cf. Sokol, '77, p. 360; see also Kotthaus, '33, p. 523; Edgeworth, '30, p. 185, Fig. 1). Serious terminological problems also arise when adult ethmoidal structures are compared.

An example is the process that arises anteriorly from the lateral section of the postnasal wall. In the present paper it is called the *proc. maxillaris anterior.* As described above, it replaces another rather similar process that was present underneath it in earlier developmental stages. We call this first process the *proc. antorbitalis.* Parker (1876, p. 655) incorrectly considered both processes (the definitive one that he called the *prepalatine* and the one developing earlier that he called the *prenarial lamina*) identical structures. Winslow (1898, p. 171) termed the definitive adult process the *lamina cribrosa.* Higgins ('20, p. 50), despite the fact that he regarded the compound antorbitalis/maxillaris anterior process as the trabecula or cornu trabeculae (see Higgins, '20, Fig. 74), correctly identified the topographic relations of the ramus lateralis narium proprius to the proc. maxillaris anterior (termed by him the *tectale*) above it and to the proc. antorbitalis (called by him the *antorbitale*). He noticed that the latter is greatly reduced. The proc. maxillaris anterior of the present paper is termed by Paterson ('51, Figs. 14, 15; '55, p. 227, Figs. 1, 3A, 5) the *anterior process of the planum antorbitale* or the *planum antorbitale.* It follows from its topographic relations to the ramus lateralis narium proprius and to the olfactory organ that it is more appropriate to term the process in question the *proc. maxillaris anterior,* although its origin (as will be discussed below) is different from that in other anuran genera such as *Pelobates.* Paterson ('51, Figs. 14, 15; '55, p. 225, Fig. 3A,B) applied the term *proc. maxillaris anterior* (in *P. carvalhoi*) to a subtle outgrowth from the anterolateral margin of the commissura quadratocranialis anterior. While in *P. carvalhoi* this synchondrotic fusion with the posterior ends of the rod-like cartilages (termed the *cart. obliqua* and the *lamina inferior cristae intermediae*) persists in adults (Paterson, '55, Fig. 3B), in *P. pipa* it occurs only for a short period during larval development (Fig. 1G).

There are two rod-like cartilages in the adult ethmoidal region. The upper one runs posterolaterally from the anterodorsal part of the nasal capsule to the medial edge of the proc. maxillaris anterior, and the lower one springs from the lower margin of the septum nasi in its anterior section. The posterior ends of both are connected with one another underneath the proc. maxillaris anterior and, as just mentioned, briefly also with the lateral edge of the overlying structures. In all pipids the upper one is called the *cart. obliqua* because of its oblique course similar to that in *Rana.* More equivocal is the homologue of the lower cartilage, which is called the cornu trabeculae by Higgins ('20, pp. 50–51), who misinterpreted Parker's figures. At the same time Higgins ('20, Fig. 74) designated as *cornu trabeculae* the fused proc. antorbitalis and proc. maxillaris anterior. Paterson ('55, p. 226, Fig. 3B) followed Higgins' identification. However, in all anurans possessing cornua trabecularum, these "horns" spring from the postnasal wall close to one another, medially to the can. olfactorius (see also Born, 1876, p. 600). The cartilage in question thus cannot be the cornu trabeculae. Instead, judging by the fact that the cartilage on each side is connected with the cart. obliqua by the planum terminale, it may be identified as the lamina inferior cristae intermediae (cf. also Jurgens, '71, p. 17). What makes this conclusion questionable is that the process runs posterolaterally beneath the diverticulum medium sacci nasalis, and close to its distal end it separates this diverticulum from the organ of Jacobson. The lamina inferior cristae intermediae, by definition, should delimit the recessus inferior of the nasal capsule; i.e., it should separate the diverticulum medium and inferius (although the diverticulum inferius is sometimes divided into the medial organ of Jacobson and the so-called recessus lateralis of the cavum inferius; see Ramaswami, '39, p. 47; Paterson, '51, p. 406). This is the case with neither *P. pipa* nor *P. carvalhoi* (Paterson, '51, Figs. 8, 9; '55, Fig. 3B). Instead, in *Pipa* the diverticulum inferius is located far behind the posterior extension of the lamina inferior. However, the unusual topography in *Pipa* may be secondary, caused by the extreme flattening of the skull in both species. Thus, although the homologies are not absolutely established, the term *lamina inferior cristae intermediae* seems to be most appropriate for the cartilage in question (cf. Jurgens, '71, p. 53).

The horizontal cartilage situated lateral to the anterior end of the septum nasi can be identified, with little doubt, as the cart. ala-

ris. Its most anterior portion ventrally supports the naris externa, and farther posteriorly its rather elevated anterolateral margin protects that part of the nasal sac that is called by Paterson ('51, no. 384, 390, Fig. 1; '55, Fig. 3A,B) the *vestibulum*. Hence these relations to the nasal organ justify calling this structure the *alar cartilage* in *P. pipa*. Parker (1876, p. 659, Pl. 61, Fig. 5) called it the *upper labial a* (see also Paterson, '45, p. 334).

Establishing the homologies for the processes of the alar cartilage is more complicated. One of these processes is a subtle rod that springs from the medial margin of the alar cartilage and runs parallel with the dorsal surface of this cartilage posteriorly. Paterson ('55, p. 229, Fig. 3B) identified a similarly located outgrowth of the cart. alaris in *P. carvalhoi* as *proc. praenasalis superior*. In that species, however, it is directed not only backward but also downward (below the alar cartilage) to make contact with the premaxilla, while in *P. pipa* it is above the cartilage. In *P. pipa* it plays a role in separating parts of the olfactory organ; it supports ventrally the anterior part of the structure Paterson called the *infundibulum*. In *P. pipa* there is also another cartilage free and closely adjacent to the medial part of the ventral surface of the cart. alaris. As it is in contact with the premaxilla, it may be homologous with the proc. praenasalis superior or communis (see below), which has lost its contact with other endocranial elements.

The cart. alaris reaches posteriorly to the extended proximal part of the lamina inferior cristae intermediae. It is not confluent with it in adults (cf. Winslow, 1898, p. 171) but may fuse with it synchondrotically in some earlier developmental stages (with the individuality of both elements being maintained). This transient contact was also reported for immature *P. pipa* by Paterson ('55, p. 229), but she noted ('55, p. 230) that in *P. carvalhoi* both cartilages are well separated. The intimate contact and even fusion of both cartilages in *P. pipa* thus may indicate how specialization of cranial structures proceeded in this species.

Provided the above identifications are correct, the following conclusions can be drawn about adult ethmoidal structure among pipids: In *Xenopus* (exemplified by *X. laevis*) the tectum is present along the whole length of the septum, whereas in *Hymenochirus* and both *Pipa* species it is limited only to the anteriormost section of the septum. In *Hymenochirus* (Paterson, '45, p. 331) the

tectum is better developed than in *Pipa*, for it exceeds laterally the level where the cart. obliqua splits from it; and throughout the greater part of the nasal region it forms a narrow dorsal plate on each side of the septum.

The solum nasi is lacking in all three genera, and the septum has its lower margin free. Sedra and Michael ('57, p. 59) considered the solum nasi in *Xenopus* confluent with the cart. praenasalis superior. Kotthaus ('33, p. 546) used the term *solum nasi* for his "Gaumendach," which is, however, a synonym of the ethmoid plate that disappears in later stages.

The cart. obliqua is a long, slender cartilage in *Xenopus* and in *Pipa*, reaching the planum terminale underneath the proc. maxillaris anterior. It is connected with the distal end of the lamina inferior cristae intermediae (Jurgens ['71, p. 16] maintained that in *P. carvalhoi* the cart. obliqua is free, though extended into the planum terminale). However, in *Xenopus* the planum terminale forms part of the lateral wall of the nasal capsule, just behind the posterior end of the cart. alaris. Moreover, from the junction of the cart. obliqua and the lamina, a slender, cylindric process arises posteriorly, which runs toward the vertically situated fenestra endochoanalis. Thus, although in *Pipa* and *Xenopus* both cartilages are present, in *Xenopus* their structure is more complicated. In *Hymenochirus* (Paterson, '45, p. 331) the cart. obliqua ends freely, for neither the planum terminale nor the lamina inferior are present.

The cart. alaris in *Pipa* differs mainly by its size and position from that in *Xenopus*. In the latter it is vertical, slightly convex outward, and contributes to the anterolateral wall of the nasal capsule. From its ventromedial edge it gives off an outgrowth running backward and fusing with the cartilage under the fenestra endochoanalis. In *Xenopus*, this outgrowth is called by Jurgens ('71, p. 14) the *cart. praenasalis communis* (see also Trueb and Cannatella, '82, p. 29; Sedra and Michael, '57, p. 59). Another connection of the alar cartilage with surrounding structures is a short bridge that links its medial margin with the extended proximal part of the lamina inferior. In both *Pipa* species the alar cartilage is free, but in both there can be vestiges of the proc. praenasalis communis. Also the bridge connecting the alar cartilage with the lamina inferior seems to be preserved in *P. pipa* as a slender outgrowth parallel to its dorsal surface. In *Hymenochirus*, Paterson

('45, p. 332) found a short, ventrally directed process that she called the *cart. praenasalis superior,* but undoubtedly it is a homologue of the proc. praenasalis communis (sensu Jurgens, '71, p. 14).

Besides these characters, one can also mention the presence of the ventral cartilaginous support of the fenestra endochoanalis. This distinguishes the ethmoidal region of *Xenopus* from those of *Hymenochirus* and *Pipa.*

Figure 5 summarizes differences of the ethmoidal region in adults of *Xenopus, Hymenochirus,* and *Pipa.* It may be stated that *Xenopus* seems to be least derived from the basic pipid scheme (see also Paterson, '51, p. 383; cf. Trueb and Cannatella, '86, p. 441). whereas *Hymenochirus* and *Pipa* have their nasal regions considerably simplified. In those two genera some structures are vestiges only. It is worth noting that only a few features in *Hymenochirus* and *Pipa* can be considered as consequences of flattening of the skull (e.g., horizontal position of the cart. alaris). Their other features developed independently of this flattening (e.g., disappearance of the lamina inferior in *Hymenochirus,* but its presence in *Pipa*). Generally the ethmoidal regions of *Pipa* and *Hymenochirus*

are morphologically closer to one another than to those of *Xenopus* (see also Paterson, '45, p. 334; Jurgens,'71, p. 20, Fig. 16). In both of the former species these regions appear to be derived from the scheme present in the latter.

Another point of discussion is the comparison of larval features in various pipids. All genera may be characterized by the presence of the ethmoid plate instead of the cornua trabeculae. Its gradual disappearance was observed in *X. laevis* (Roček, personal observation; Sedra and Michael, '57, p. 24), *P. pipa* (this paper), *P. carvalhoi* (Roček, personal observation), and *Hymenochirus* (following Sokol, '62, p. 277; Paterson, '45, pp. 329–337). Our results establish that the ethmoid plate serves only as a temporary support for developing adult ethmoidal structures and later disappears completely.

The same phenomenon of appearance and then disappearance can be followed in the lateral part of the ethmoidal region, where the proc. antorbitalis develops. There are, however, some difficulties if this structure should be identified in *Xenopus.* While in early stages of *Xenopus* there is only a single process that can be identified as the proc.

TECTUM NASI	CARTILAGO OBLIQUA	LAMINA INFERIOR CRISTAE INTERMEDIAE	CARTILAGO OBLIQUA LAMINA INFERIOR CRISTAE INTERMEDIAE
Xenopus ↓ (reduction) *Hymenochirus* ↓ (reduction) *Pipa*	*Xenopus* (with additional structures) ↓ *Pipa* (simple rod) ↓ *Hymenochirus* (free, without planum terminale)	*Xenopus* (well developed) ↓ *Pipa* (slender) ↓ *Hymenochirus* (lacking)	*Pipa pipa* (connected with one another) ↓ *Pipa carvalhoi* (separated)

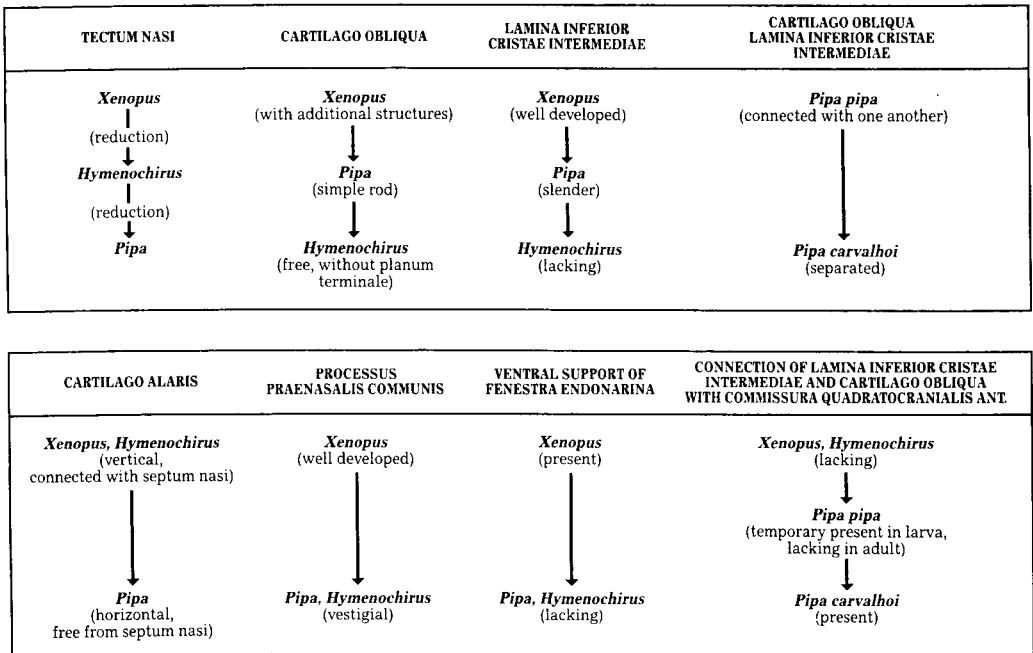| CARTILAGO ALARIS	PROCESSUS PRAENASALIS COMMUNIS	VENTRAL SUPPORT OF FENESTRA ENDONARINA	CONNECTION OF LAMINA INFERIOR CRISTAE INTERMEDIAE AND CARTILAGO OBLIQUA WITH COMMISSURA QUADRATOCRANIALIS ANT.
Xenopus, Hymenochirus (vertical, connected with septum nasi) ↓ *Pipa* (horizontal, free from septum nasi)	*Xenopus* (well developed) ↓ *Pipa, Hymenochirus* (vestigial)	*Xenopus* (present) ↓ *Pipa, Hymenochirus* (lacking)	*Xenopus, Hymenochirus* (lacking) ↓ *Pipa pipa* (temporary present in larva, lacking in adult) ↓ *Pipa carvalhoi* (present)

Fig. 5.   Possible evolutionary trends in the ethmoidal region of the endocranium in pipids, deduced from the condition in adults.

antorbitalis (proc. cornu quadratus medialis; sensu Sedra and Michael, '57, Fig. 3), in metamorphosing specimens there are two outgrowths similar to one another. One was just mentioned, and the second is called the *lamina orbitonasalis* (sensu Sedra and Michael, '57, Fig. 15). It has been claimed (Sedra and Michael, '57, p. 23) that the two outgrowths are connected with one another through a band of prochondral tissue marked posteriorly by the foramen (termed by Sedra and Michael as the *foramen* for "ramus communicans between n. ophthalmicus profundus V and n. palatinus VII"). Thus, it is not impossible that the outgrowth called the *lamina orbitonasalis* by Sedra and Michael is, in fact, the proc. maxillaris anterior. Later (in stage 61; see Sedra and Michael, '57, Fig. 19) both processes fuse together, which is evidenced by the position of the foramen just mentioned. The proc. antorbitalis is originally located ventrolaterally to the proc. maxillaris anterior. In metamorphosing larvae of *Xenopus* it forms the lateral part of the postnasal wall. Its gradual disappearance can be traced from the fact that the mentioned foramen becomes located more to the lateral margin of the postnasal wall (Sedra and Michael, '57, Fig. 27), which means that the lateral part of the postnasal wall is decreasing in size.

Thus it can be concluded that despite some positional differences the development of the proc. maxillaris anterior is essentially the same in *Pipa* and *Xenopus*. For *Hymenochirus* data are not available. The developmental pattern, however, differs from that in *Pelobates,* in which the proc. maxillaris anterior arises by fusion of an element that is free in the tadpole and has a close topographic relation with the cart. labialis superior, located laterally to the lamina orbitonasalis. In the metamorphosing tadpole of *Pelobates* this element is still distinct. There it forms a lateral extension of the postnasal wall, lateral to the can. pro ramo laterali narium proprio. This canal arises by enclosure of the nerve between the cartilaginous element just mentioned and the lamina orbitonasalis (Roček, '81, p. 51, Fig. 22). Thus, while in pipids the proc. maxillaris anterior arises as an integral part of the postnasal wall by condensation of mesenchyme in advanced larval stages, in *Pelobates* it arises from a pre-existing free cartilaginous structure that was part of the larval viscerocranium (most probably the epipraemandibular; see Roček, '81, Fig. 22).

Finally it should be noted that there is heterochrony in *P. pipa* cranial development compared with that of *P. carvalhoi* and *X. laevis* (see Parker, 1876, p. 648). In all pipids (most probably including *P. pipa*) the olfactory nerves first run on the surface of the postnasal wall to reach the olfactory organs. Only later are they covered dorsally by the arising planum praecerebrale, and thus become enclosed in two canals. This was reported by Kotthaus ('33, pp. 544, 564) for a *X. laevis* tadpole of 53 days (stage 64). However, in our *Xenopus* material the can. olfactorii were well developed already by stages 55–56. In *P. pipa*, these canals were already present even in our earliest stage (i.e., 40). This contrasts strikingly with *P. carvalhoi,* in which the first traces of the arising planum praecerebrale (in the prochondral state) were found as late as stage 56. Similar heterochronic variation may be found also in the case of the first appearance of the septum nasi and other structures. The early appearance of adult ethmoidal structures in *P. pipa* may be accounted for by its peculiar pattern of larval development and similarly may explain the late appearance of the dermal bones. Both shifts appear to be related to the shift away from a free-living larvae to "direct" development.

It may be concluded that despite the above-noted differences in the early development of the ethmoidal region of the endocranium, as well as in the adult structure, pipids as a group are quite uniform. On the other hand, some peculiarities in pipid larval development make comparisons with structures in other groups of anurans investigated previously rather doubtful.

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