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Title: DEVELOPMENTAL CRANIAL OSTEOLOGY OF THREE SPECIES OF *RANA* (ANURA)

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Robert M. Storm

Developmental series of *Rana pretiosa* (110 specimens), *R. cascadae* (100 specimens) and *R. aurora* (115 specimens) were bone stained and cleared in glycerin. The growth and developmental patterns of the skull and selected bones were followed from the first appearance of bone through adult stages. The sequential appearance of the bones was determined, and the number of teeth on the premaxillae, maxillae and prevomers were counted separately.

The developmental pattern of the skull and individual bones was similar in the three species although size and growth pattern differences were evident. The sequential appearance of cranial bones was similar in all species, except that the frontoparietal, parasphenoid, and exoccipital appeared three stages earlier in the larger *R. pretiosa* and *R. aurora*. Although considerable variation was noted, the number of teeth showed consistent differences throughout development.

# Developmental Cranial Osteology of Three Species of *Rana* (Anura)

by

Ronald Gail Altig

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# DEVELOPMENTAL CRANIAL OSTEOLOGY OF THREE SPECIES OF *RANA* (ANURA)

## INTRODUCTION

Skeletal characteristics continue to be important parameters in vertebrate taxonomy, and characteristics of both cranial and post-cranial elements are applicable throughout anuran classification (Nicholls, 1916; Carvalho, 1954; Goin, 1961; Chantell, 1968; Lynch, 1968). Unfortunately only adult characteristics are most often used, a fact criticized by some workers (Blair, 1962; Orton, 1953, 1957; Noble, 1927). External development as an aid to larval identification (Limbaugh and Volpe, 1957), expression of embryological effects of developmental type (Packer, 1966), physiological tolerances (Johnson, 1965), etc. have been important contributions. Developmental anatomy has been a popular research field in Europe, but some studies of the osseous skeleton have been made in the United States; see Stokely and List (1954) on *Pseudacris nigrita triseriata*, Lynn (1942) on *Eleutherodactylus nubicola*; Trueb (1966) on *Hyla septentrionalis*, and Duellman and Trueb (1966) on *Smilisca baudini*. These studies, involving various numbers of specimens from two families with different developmental types, present differences in developmental osteology. However, as stated by Trueb (*ibid.*), a rather meager amount of data on comparative developmental osteology of anurans is available.

Species of Rana in the United States have not been examined in detail as have some other groups, eg. Bufo (Blair, 1963) and Scaphiopus (Bragg, 1965). Species of concern in this study, Rana pretiosa, R. cascadae, and R. aurora, are included in Orton's (1952) wood frog group and apparently represent a closely related group. At present, all three hold specific status although R. cascadae has been shifted from a species (Slater, 1939), to a subspecies of aurora (Stebbins, 1951), and back to a species with suggested affinities to pretiosa (Dunlap, 1955; Dumas, 1966). Johnson (ibid. ) examined external development and physiological tolerances of R. p. luteiventris, and hybridization experiments have involved pretiosa and cascadae (Haertel, 1967) and aurora and cascadae (Porter, 1959). Except for positive proof of sympatric populations of cascadae and aurora, pairs of these three species are sympatric at points in their ranges.

Comparative osteological material of United States species is limited. Cope (1889) figured several skeletons and used osteological characteristics in the diagnoses, Zweifel (1955) mentioned some osteological features of the R. boylei group in comparison with R. aurora, and Chantell (1968) erected intrageneric groupings based on osteology. The only developmental cranial osteology of any detail concerns the European species, R. temporaria and esculenta. Ecker

(1889), Parker (1871), Gaupp (1906), Erdmann (1933), and the review by de Beer (1937) provide most of the information on these species.

The objectives of this study are to describe and compare the adult cranial osteology of the above three species of Rana occurring in the Pacific Northwest; in addition, the developmental and growth patterns of the skull and its constituent parts were examined. The profound size, shape, and proportional changes that the skull undergoes during metamorphosis are described. It is hoped that future manipulation of these data or data collected in the light of this information can be used taxonomically in this group.

# MATERIALS AND METHODS

One hundred and ten Rana pretiosa from Gold and Davis Lakes, Deschutes County, Oregon, 100 R. cascadae from the vicinity of Three Creek Lake, Deschutes County, Oregon, and laboratory crosses of adults from that locality, and 115 R. aurora from the vicinity of Corvallis, Benton County, Oregon (Table 1), were bone stained and cleared in glycerin; only the skull was prepared of most adult specimens. Through metamorphosis, specimens were staged according to Gosner (1960) and postmetamorphic stages were continued in numerical order as centimeter size classes; Gosner's stage 46 (10-20 mm snout-vent length) equals the end of metamorphosis, so stage 47 includes 21-30 mm individuals, stage 48 includes 31-40 mm individuals, etc. This system does not provide a uniform time scale as stages 30-46 may take three months while stages 47-53 may include four to five years. Body length could not be used as a basic parameter as the snout-vent length of a tadpole and a metamorphosed frog are not comparable measurements.

Descriptive data (eg. stage of appearance, developmental pattern, relationship to other bones) were recorded on individual specimen data sheets. Meristic data, obtained with an ocular micrometer in a variable-power dissecting microscope, were recorded on column paper. The following measurements were taken on each specimen (Figure 1):

Skull length--measured as the sagittal skull length from the anterior tip of the premaxillae posteriorly to a line connecting the posterior faces of the exoccipitals. Skull length measurements are subjective before S-38, 40 when the premaxillae appear as it had to be measured to where the premaxillae would appear; this was done to have a comparative measurement for the bones that were present before S-38.

Skull width--measured as the widest point of the skull from dorsal view at the level of the lower jaw articulation regardless of the position of the articulation.

Snout length--measured as the distance from the anterior tip of the frontoparietals forward to the anterior tip of the premaxillae.

Snout width--measured as the widest point of the snout from a dorsal view at the level of the anterior tips of the frontoparietals.

Exoccipital-squamosal distance--measured as the distance from the ventral tip of the squamosal posteriorly to the posterior face of the exoccipitals.

Maxillary gap--measured as the transverse distance between the anterior tips of the maxillae.

Frontoparietal length--measured as the longest longitudinal length.

Parasphenoid length--measured as the longest sagittal length.

Parasphenoid width--measured as the widest point of the alary processes.

The angle of slant of the vertical section of the squamosal was estimated, and prevomerine, premaxillary, and maxillary teeth were counted.

The ranges and means of meristic data are included in the appendix; only the means are presented on the graphs.

As used here, premetamorphic includes stages 30-41; metamorphic includes stages 42-46, and postmetamorphic includes stages 47-53; R. cascadae gets no larger than S-51.

Sources of error are especially important in a study of this nature since the measurements are small and expected differences slight. It has been shown (Akin, 1966; Bragg, 1967; Savage, 1962; Adolph, 1931) that environmental and social factors have definite effects on the growth rate and metamorphic size of tadpoles and frogs, in addition to what genetic factors might be operating. Laboratory crosses are especially susceptible to some of the above. Error in measurement due to small size and distortion caused by flesh, glycerin, and misalignment under the microscope can be reduced only by multiple measurements and frequent checks. Sample size must be as high as possible. Even so, natural and experimental error are no doubt high in the following data.

Due partly to choice and partly to accidental loss of data, detection of sexual dimorphism was not attempted; in some cases this may be important as the females seem to be larger than the males.

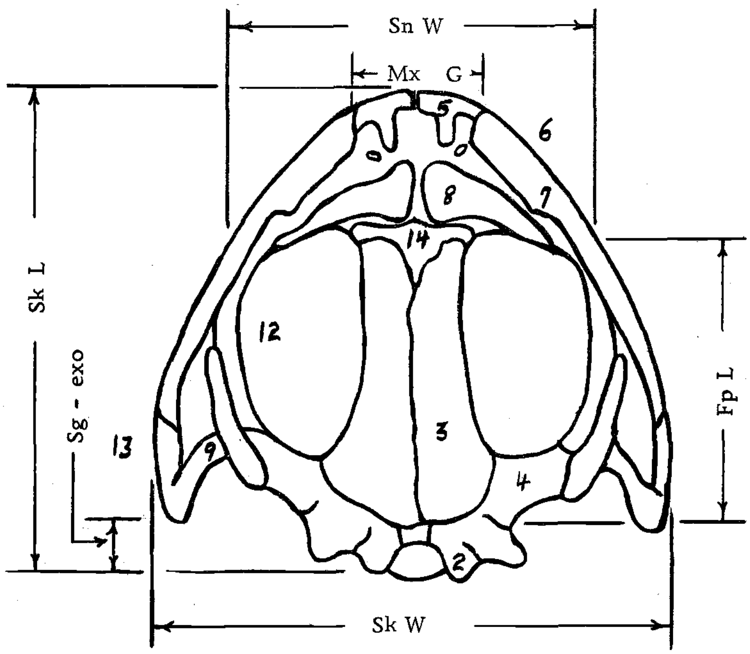
All discussion and illustrations that follow are based primarily on *Rana pretiosa* with differences due to the other species noted when pertinent. The bones are discussed in the order they appear in *R. pretiosa*.

Table 1. Number of specimens of *Rana pretiosa*, *R. cascadae*, and *R. aurora* examined in each developmental stage (see Materials and Methods).

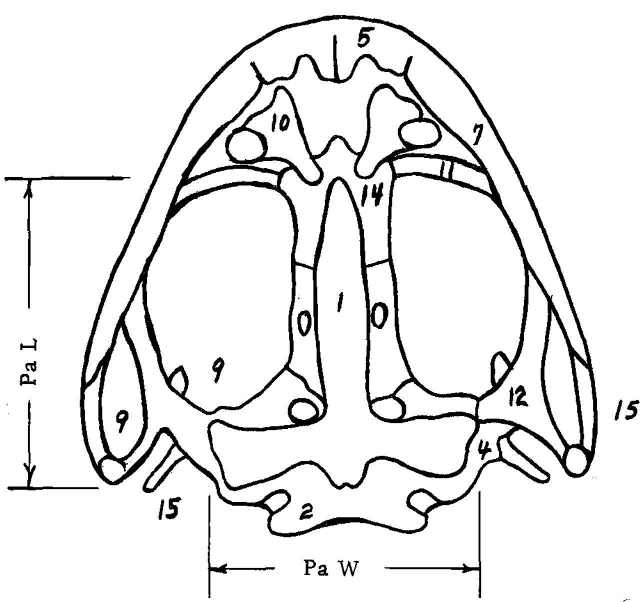
| Stage | Species | | |
|---|---|---|---|
| | pretiosa | cascadae | aurora |
| 30 | 3 | 0 | 0 |
| 31 | 4 | 0 | 0 |
| 32 | 2 | 0 | 2 |
| 33 | 6 | 0 | 3 |
| 34 | 5 | 6 | 6 |
| 35 | 5 | 6 | 3 |
| 36 | 5 | 6 | 6 |
| 37 | 4 | 5 | 6 |
| 38 | 5 | 6 | 6 |
| 39 | 6 | 3 | 6 |
| 40 | 0 | 4 | 4 |
| 41 | 5 | 4 | 6 |
| 42 | 5 | 4 | 6 |
| 43 | 4 | 5 | 6 |
| 44 | 4 | 5 | 5 |
| 45 | 3 | 4 | 1 |
| 46 | 5 | 9 | 6 |
| 47 | 4 | 1 | 12 |
| 48 | 4 | 3 | 7 |
| 49 | 1 | 4 | 1 |
| 50 | 11 | 15 | 3 |
| 51 | 5 | 10 | 6 |
| 52 | 9 | -- | 7 |
| 53 | 5 | -- | 7 |

Figure 1. Dorsal (A) and ventral (B) views of a frog skull showing measurements taken and identification of bones; the lower jaw was omitted. Legend: 1, parasphenoid; 2, exoccipital; 3, frontoparietal; 4, prootic; 5, premaxilla; 6, septomaxilla; 7, maxilla; 8, nasal; 9, squamosal; 10, prevomer; 11, palatine; 12, pterygoid; 13, quadratojugal; 14, sphenethmoid; 15, columella; Sk L, skull length; Sk W, skull width; Sq-ex, squamosal-exoccipital distance; Sn L, snout length; Sn W, snout width; Fp L, frontoparietal length; Mx G, maxillary gap; Pa L, parasphenoid length; Pa W, parasphenoid width.

A


Sn W
Mx G
5
6
8
7
14
Sk L
12
Sg - exo
Fp L
3
13
9
4
2
Sk W

B


5
10
7
11
14
1
Pa L
9
12
15
4
2
Pa W

# RESULTS

## Skull Development

### Sequential Appearance of Bones

The sequential appearance of cranial bones (Table 2) may be correlated with various factors; the most notable difference between R. pretiosa, cascadae, and aurora is the earlier appearance of the parasphenoid, exoccipitals, and frontoparietals in the two larger species. Although these elements do not appear until three stages later in cascadae, development in the larger species is slow so that by S-38-39, all three show a similar configuration. Stage 33 pretiosa and aurora are about the same size as S-36 cascadae.

Other differences are minor; over half the bones appear during metamorphosis with the sphenethmoid being the only element appearing after metamorphosis.

### Skull Length vs. Body Length

Head length of juvenile vertebrates is usually proportionately larger than the adults as shown by R. pretiosa (Graph 1-A) and less clearly by cascadae. R. aurora appears to maintain an evenly proportional head throughout development. It usually metamorphoses larger than the other two, and it is visibly noticeable that the

Table 2. Sequential appearance by stage of cranial bones of *Rana pretiosa*, *R. cascadae*, and *R. aurora*.

| Bone | Species | | |
|---|---|---|---|
| | pretiosa | cascadae | aurora |
| Parasphenoid | 32 | 36 | 33 |
| Exoccipital | 33 | 36 | 33 |
| Frontoparietal | 33 | 36 | 34 |
| Prootic | 38 | 38 | 39 |
| Premaxilla | 38 | 38 | 40 |
| Septomaxilla | 39 | 40 | 41 |
| Dentary | 42 | 42 | 42 |
| Maxilla | 42 | 40 | 41 |
| Nasal | 42 | 41 | 42 |
| Squamosal | 42 | 42 | 42 |
| Angular | 43 | 42 | 42 |
| Prevomer | 43 | 45 | 44 |
| Palatine | 44 | 43 | 45 |
| Mentomeckelian | 45 | 46 | 44 |
| Pterygoid | 45 | 43 | 44 |
| Quadratojugal | 45 | 43 | 44 |
| Columella | 45 | 46 | 46 |
| Hyoid | 46 | 46 | 46 |
| Sphenethmoid | 47 | 48 | 48 |

juveniles do have such proportionately large heads. Adult *pretiosa* have noticeably small heads and adult *cascadae* resemble S-51 *pretiosa*.

## Skull Length

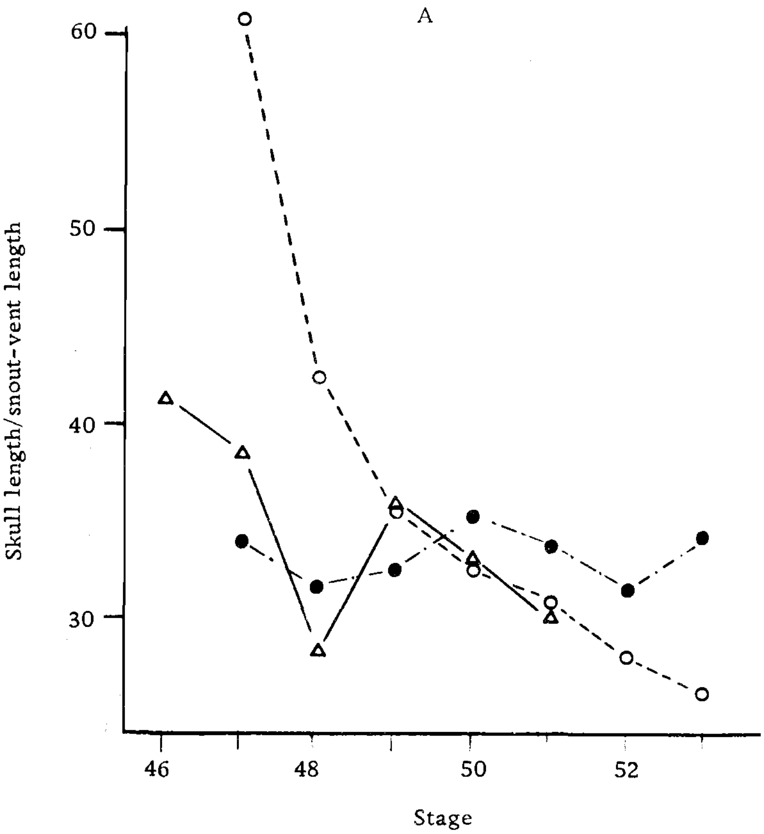
Figure 2 shows a developmental series of schematic *R. pretiosa* skulls with the midpoint of the sagittal line as common center; these outlines suggest how the skull grows in the various aspects.

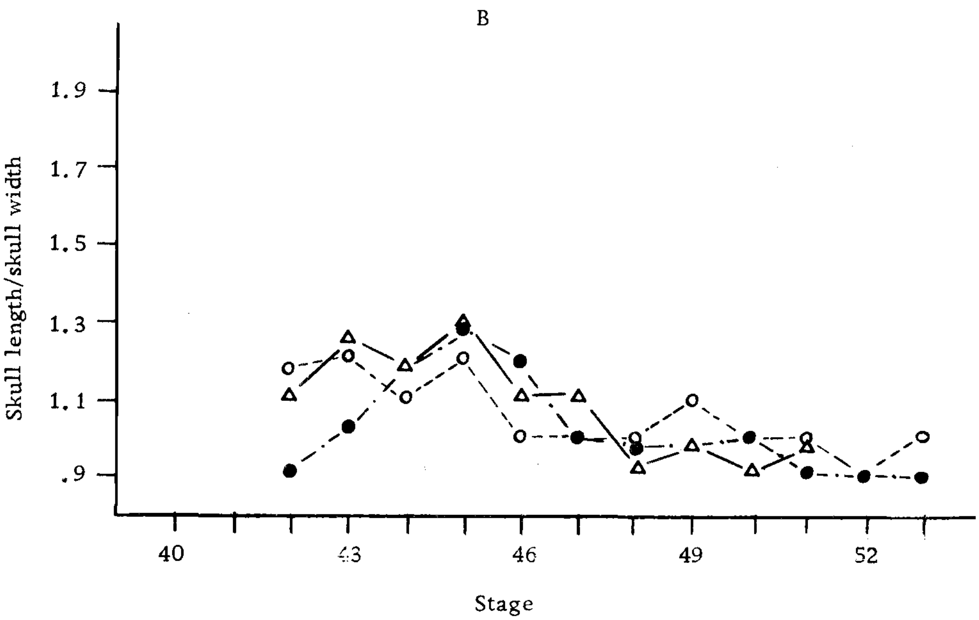
Graph 2-A shows the growth of skull length; through metamorphosis there is no increase in length. In fact, there is a slight reduction due to formation of the skull associated primarily with the premaxillae. After metamorphosis the skull increases in length with rate and maximum size varying with the species. The difference in skull size should be noted for *aurora* and *pretiosa* which are similar sized frogs. The latter frog has a small head. Adult specimens of the smaller *cascadae* resemble S-51 *pretiosa*.

## Skull Width

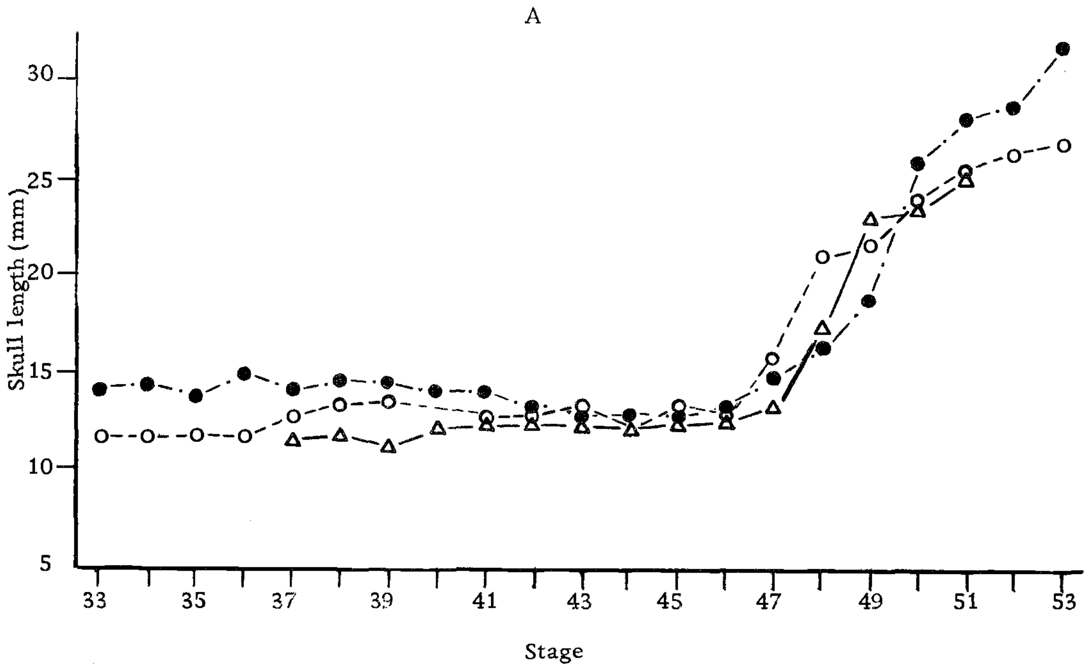
Skull width (Graph 2-B) could not be measured until S-42 when the squamosal appeared; from this point through metamorphosis there is a slight reduction in skull width due to a slight medial component in the posterior migration of the lower jaw articulation. Immediately after metamorphosis the skull again increases in width.

Graph 1. The ratios of skull length/snout-vent length (A) and skull length/skull width (B) vs. stage of development. Legend: solid circles and broken line, *R. aurora*; open circles and dotted line, *R. pretiosa*; open triangles and solid line, *R. cascadae*. Only the mean for each stage is presented on the graphs.


A
60
50
40
30
Skull length/snout-vent length
46
48
50
52
Stage


B
1.9
1.7
1.5
1.3
1.1
.9
Skull length/skull width
40
43
46
49
52
Stage

Graph 2. Skull length (A) and skull width (B) vs. stage of development in *R. pretiosa*, *R. cascadae*, and *R. aurora*. See Graph 1 for legend.


A
Skull length (mm)
30
25
20
15
10
5
33
35
37
39
41
43
45
47
49
51
53
Stage

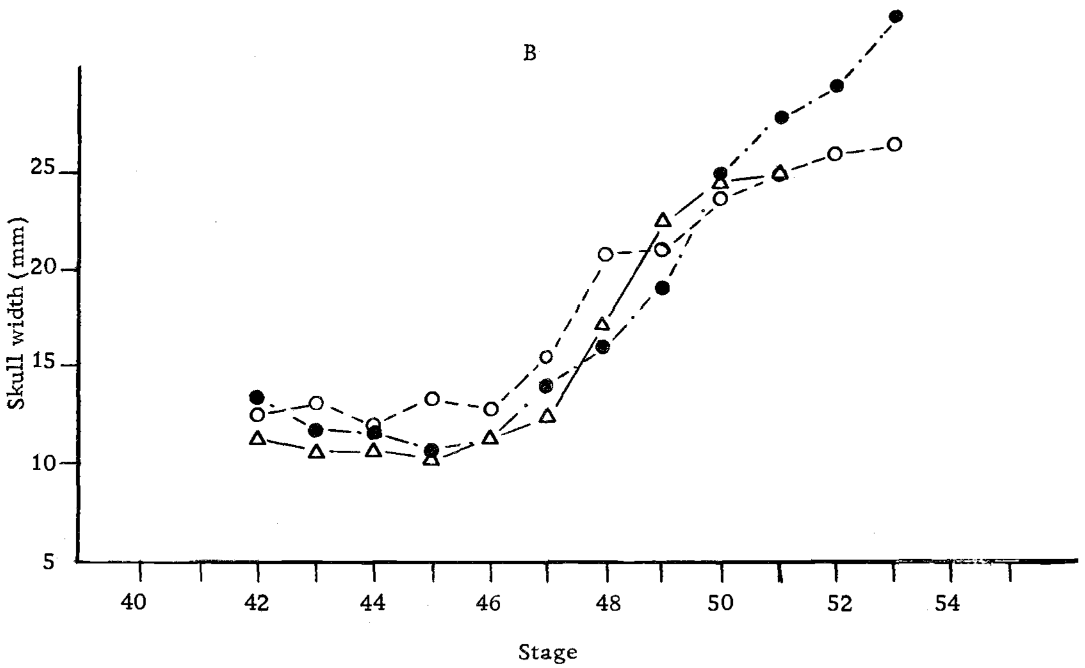
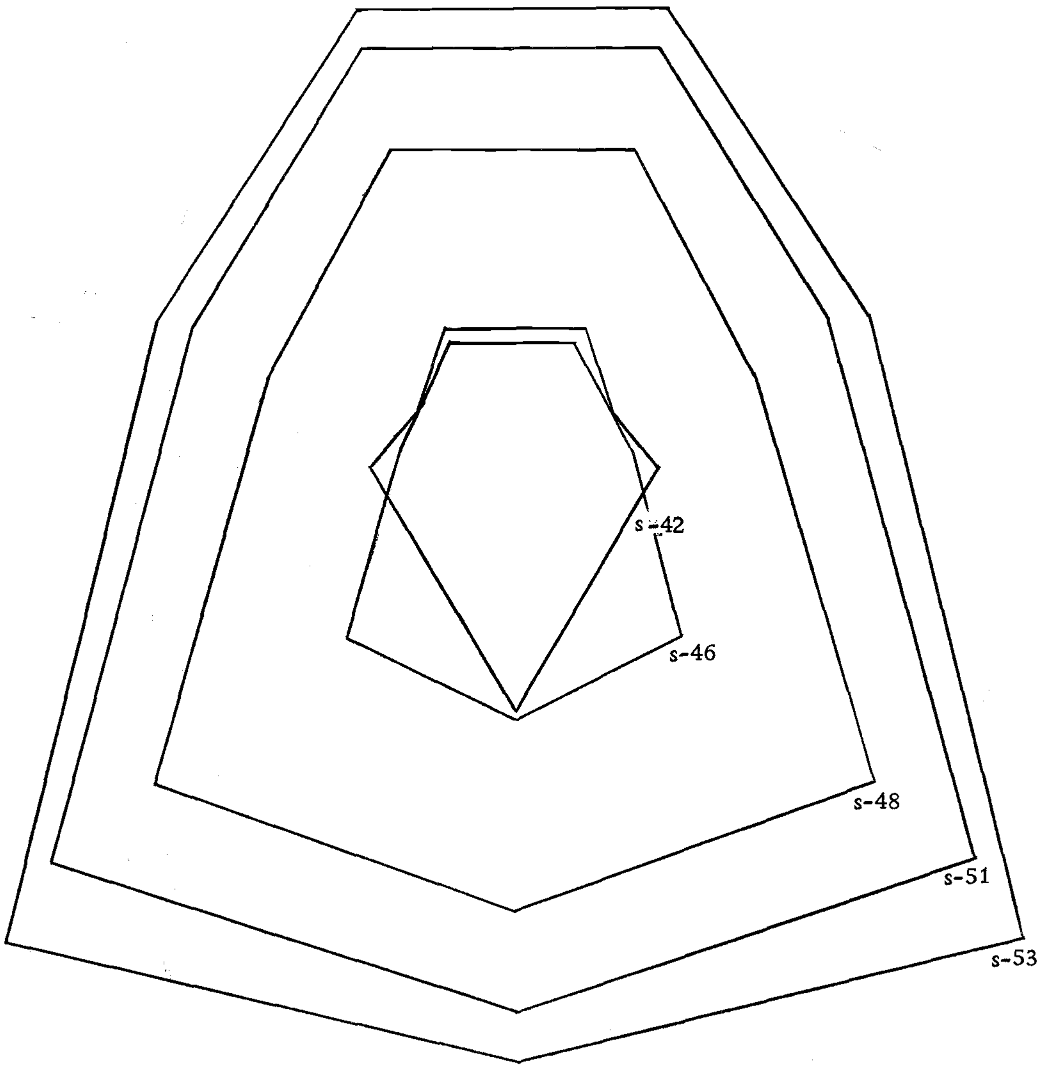

B
Skull width (mm)
25
20
15
10
5
40
42
44
46
48
50
52
54
Stage

Figure 2. Schematic skull outline derived from average measurements Rana pretiosa stages 42, 46, 48, 51, and 53. 6.4 X.


s-42
s-46
s-48
s-51
s-53

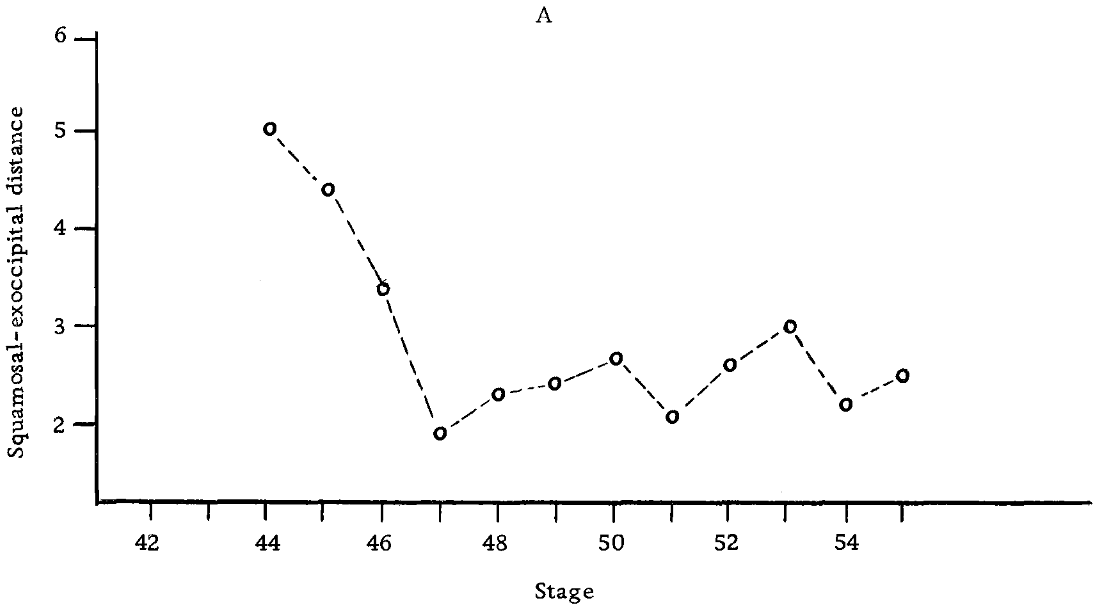
Graph 1-B shows the relation of skull length/skull width; the skull becomes longer than wide until S-45 because of the slight medial movement of the jaw articulation. Following this there is a steady decline to a plateau so that the adult frogs all have heads that are about as long as broad.

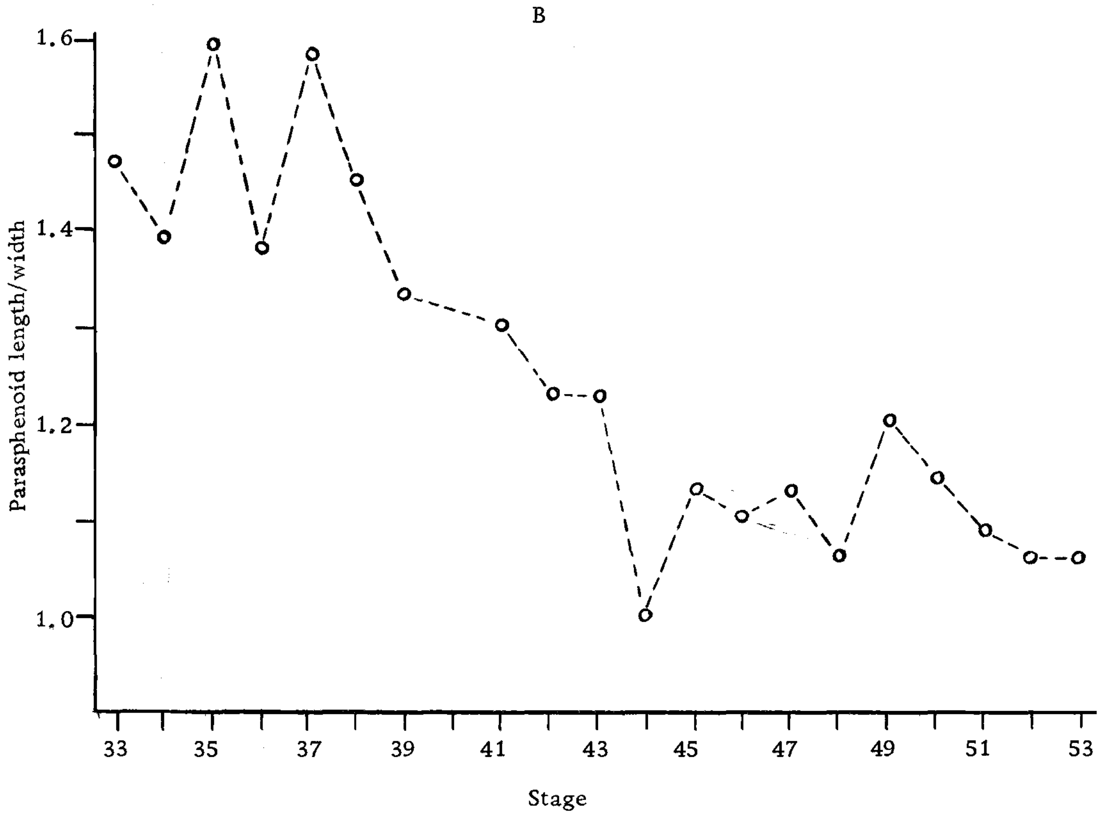
Squamosal-exoccipital Distance

As an accommodation to the small gape and specialized mouthparts of the larval frog, the mandibular articulation first lies far forward even with the anterior margin of the eye. The squamosal starts to ossify (S-42) while the articulation is in this position and immediately begins its posterior migration (Graph 3-A, pretiosa only) so as to reduce the squamosal-exoccipital distance to near its minimum by metamorphosis; variation of this distance is considerable. In the three species under examination, this migration ceases just in front of the posterior face of the exoccipitals, while in other species, eg. Rana catesbeiana, it continues so that the jaw articulation lies far posterior to the exoccipitals and provides a much larger gape.

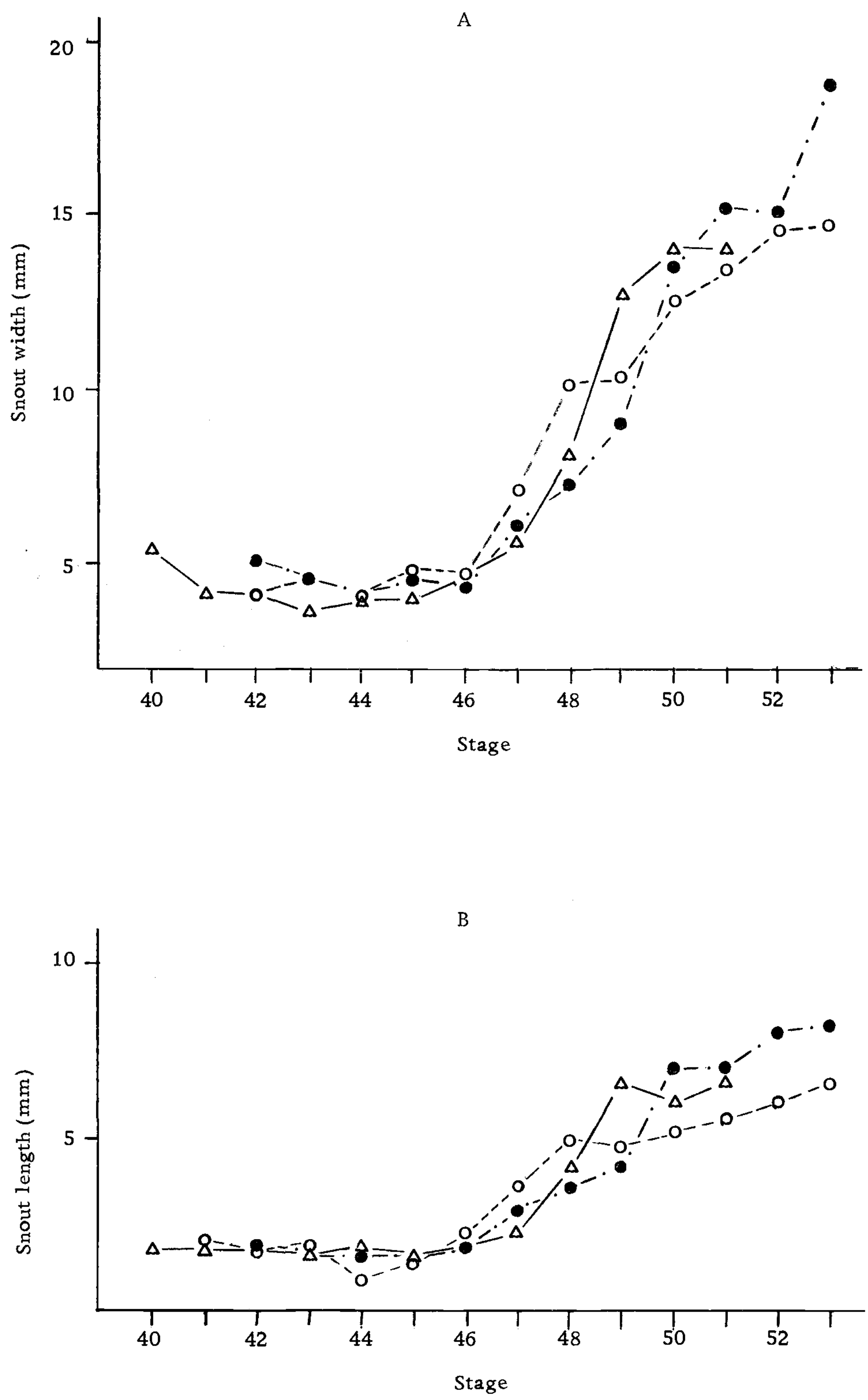
After metamorphosis, the squamosal-exoccipital distance is maintained at about 1-2 mm; a slight increase after metamorphosis may indicate an extension of the posterior section of the skull after location of the jaw articulation.

Graph 3. Squamosal-exoccipital distance (A) and the ratio of parasphenoid length/width (B) vs. stage of development in *R. pretiosa*.


A
Squamosal-exoccipital distance
6
5
4
3
2
42
44
46
48
50
52
54
Stage


B
Parasphenoid length/width
1.6
1.4
1.2
1.0
33
35
37
39
41
43
45
47
49
51
53
Stage

Graph 4. Snout width (A) and snout length (B) vs. stage of development in *R. pretiosa*, *R. cascadae*, and *R. aurora*. See Graph 1 for legend.



A
20
15
10
5
Snout width (mm)
40
42
44
46
48
50
52
Stage
B
10
5
Snout length (mm)
40
42
44
46
48
50
52
Stage

Snout Length

Snout length (Graph 4-B) remains constant through metamorphosis when it starts to lengthen; R. pretiosa and cascadae show a faster rate during S-46-49, while aurora increases faster later when the other two slow down. Adult aurora have the longest snout while pretiosa and cascadae resemble each other.

If plotted as a ratio of snout length/skull length, all three species show a reduction to S-44-45 followed by a rise to a plateau (S-46, aurora; S-47 pretiosa; S-49, cascadae). The snout contributes an average of about 31% of the skull length in all species.

Snout Width

Snout width (Graph 4-A) shows a similar growth pattern as snout length, although the width is notably larger. Although variation is great, the ratio of snout width/skull length shows a curve similar to that of snout length/skull length. The ratio of snout length/snout width gives the following figures for the terminal stages: .44, pretiosa; .45, cascadae; .46, aurora.

Maxillary Gap

The maxillary gap, the distance between the anterior tips of the maxillae, was measured to give an indication of the shape of the anterior tip of the snout. This measurement (see Appendix) decreases slightly from S-42-46 due to ossification of the maxillae; postmetamorphic growth shows a steady increase of similar rate in all species. *R. cascadae* is intermediate between the others at S-51.

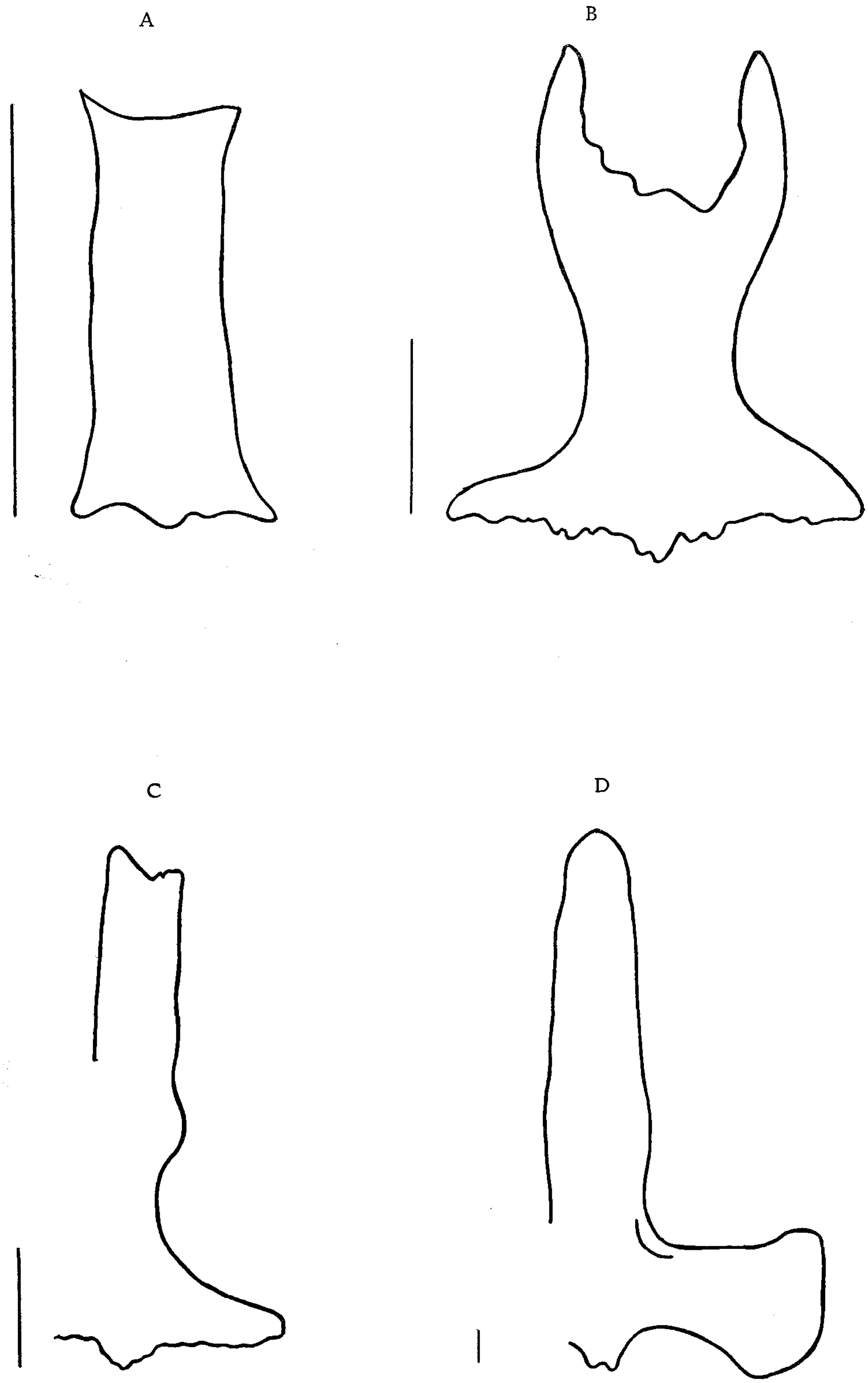
## Development of Bones

### Parasphenoid

*Descriptive.* The parasphenoid, forming the brain case floor, appears earlier in *R. pretiosa* and *aurora* than in *cascadae*, but development in the larger species is slow so that by S-38-39 all three show a similar configuration. Development from this point is similar in all species.

Figure 3 shows the developmental pattern of the parasphenoid; at first appearance (S-32-33, 36) it is a faint rectangular ossification in the longitudinal section of the bone just anterior to the alary processes. The anterior end is usually even, with the posterior border crenulate. By S-37 the bone is wider anteriorly and posteriorly than in the middle, and lateral processes extend anteriorly with an unossified area between. The posterior margin is still crenulate and often has a median projection; the anteromedial portions of the alary processes are present. By S-41-42 the adult

Figure 3. Developmental pattern of the parasphenoid exemplified by R. pretiosa S-33 (A); S-36 (B); S-37 (C); S-53 (D). Each line equals one millimeter. The right alary process is omitted on (C) and (D).


A
B
C
D

shape of the bone is evident although the posterior border and anterior tips may be jagged and cancellous areas may occur throughout the bone. A shallow lateral notch, followed anteriorly by a lateral bulge, occurs directly anterior to the alary processes.

By S-45-46 the bone is stronger with complete margins posteriorly. The posteromedial process remains, often with a median notch.

Further growth entails size increase and general strengthening of the bone. The posterior border of the alary process is concave, and the anterior border is nearly straight and projects slightly posteriorly. The lateral notch in the blade remains, the lateral tips of the alary processes enlarge where they underlie the otic capsules, and a semicircular ridge delimiting a recessed area occurs at the angle of the blade and alary process.

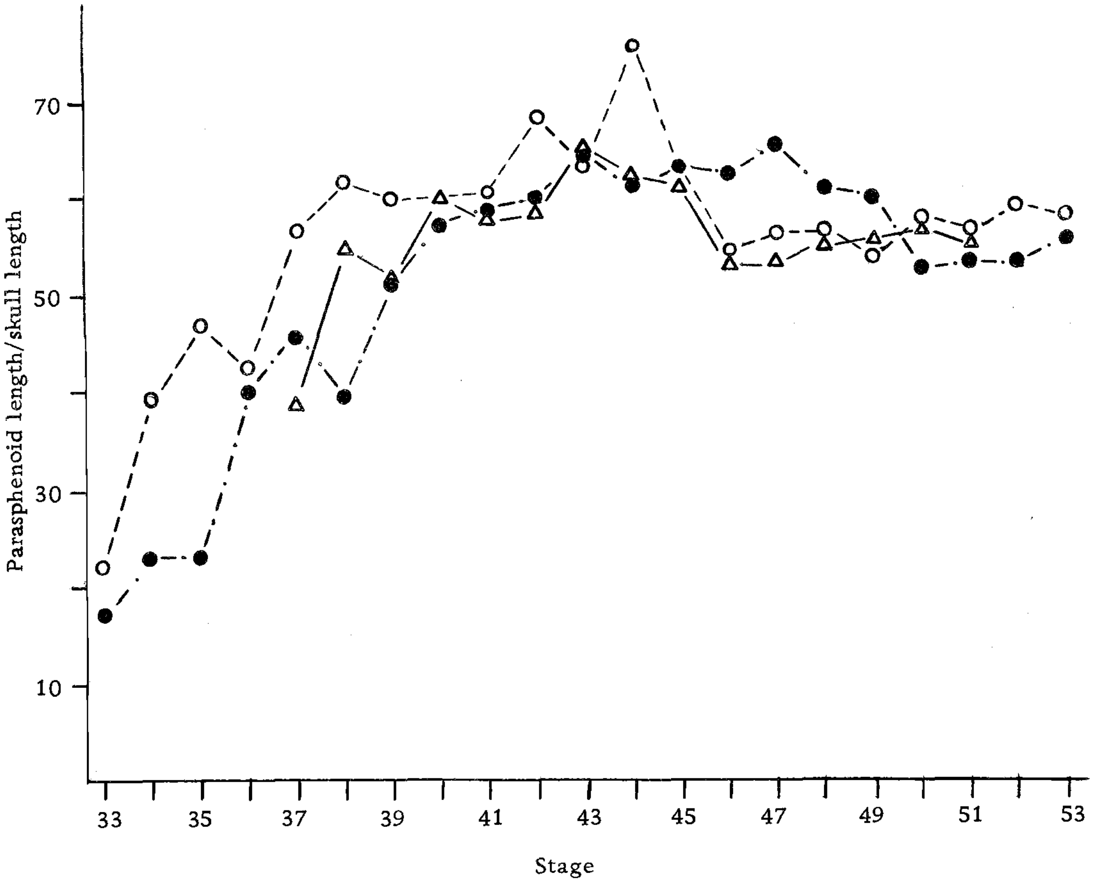
Meristic. Graphs 5-A and B show the growth pattern of the parasphenoid; there is an allometric increase through about S-44 when the rate decreases in relation to the skull. During the adult stages the parasphenoid grows at the same rate as the skull. Graph 3-B shows paraphenoid length/width for *pretiosa* only.

## Exoccipital

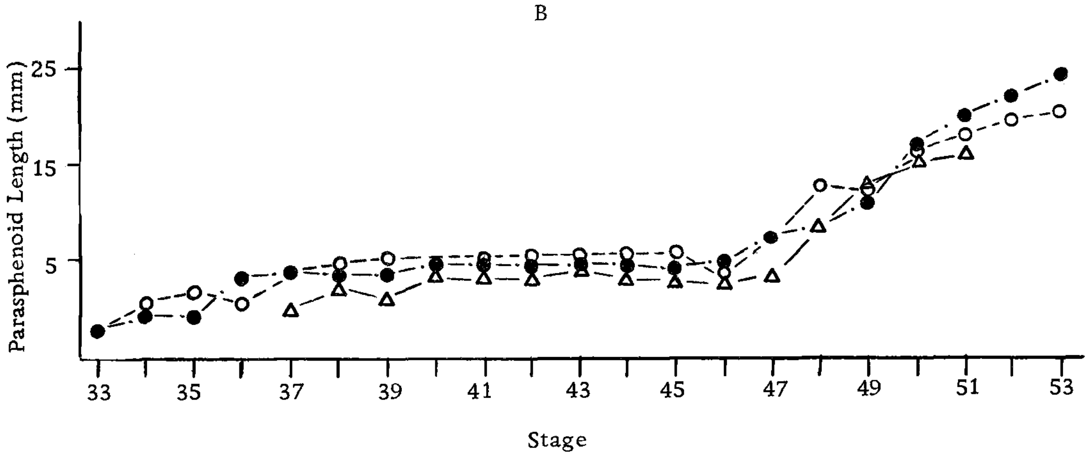
Descriptive. The paired exoccipitals surround the foramen magnum and support the skull on the spinal column. The exoccipital

Graph 5. The ratio of parasphenoid length/skull length (A) and parasphenoid length (B) vs. stage of development in *R. pretiosa*, *R. cascadae*, and *R. aurora*. See Graph 1 for legend.

A


Parasphenoid length/skull length
70
50
30
10
33
35
37
39
41
43
45
47
49
51
53
Stage

B


Parasphenoid Length (mm)
25
15
5
33
35
37
39
41
43
45
47
49
51
53
Stage

appears (S-33 and 36) as a small curved cylinder in the lateral walls of the foramen magnum and far posterior to the frontoparietal or parasphenoid. Early development includes a height increase so the dorsal tips lie closer together and the ventral tips reach below the spinal cord to enlarge as the basal sections. The basal section is evident by S-47 and the anterolateral edge of the exoccipital fuses with the posterior otic ossification by S-48. The articular condyles are definitely evident at S-48.

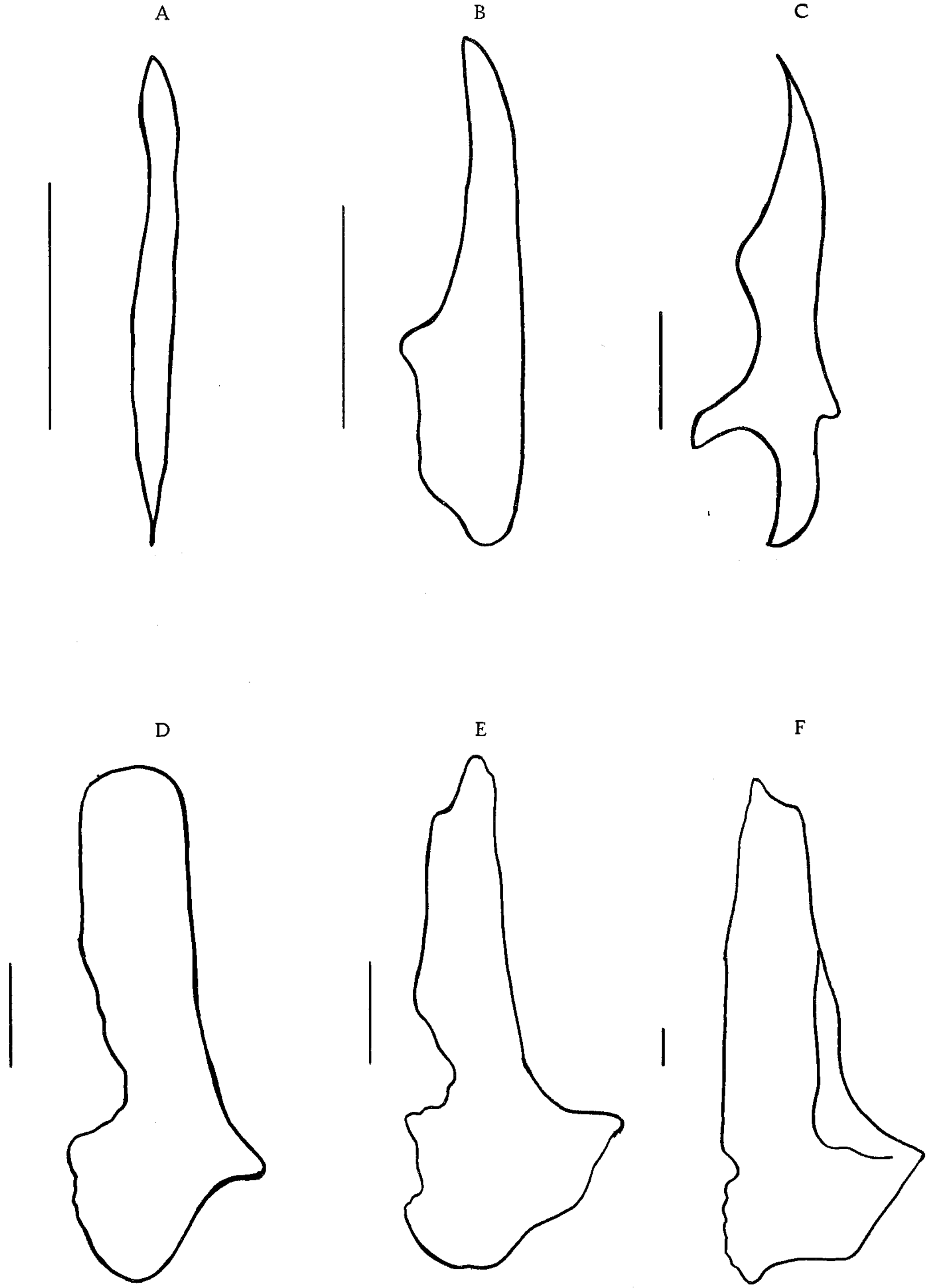
The basal portion enlarges and is underlain by the parasphenoid, but the two exoccipitals never contact each other dorsally and ventrally; calcification appears between the two bones. The posterior face of the vertical section becomes concave where muscles attach and the dorsal edge abutts against the posterior face of the frontoparietal.

Frontoparietal

Descriptive. The paired frontoparietals form the roof to the brain case; Figure 4 shows the developmental pattern of the right frontoparietal.

The frontoparietal appears (S-33-34, 36) as a small bar at the dorsolateral edge of the brain and even with the middle of the eye; it spreads rapidly to the anterior margin of the eye and to the junction of the brain and otic capsule without a change in shape. When 2-3 mm

Figure 4. Developmental pattern of the right frontoparietal exemplified by Rana pretiosa S-36 (A); S-37 (B); S-38 (C); S-45 (D); S-42 (E); and S-53 (F). Each line equals one millimeter.

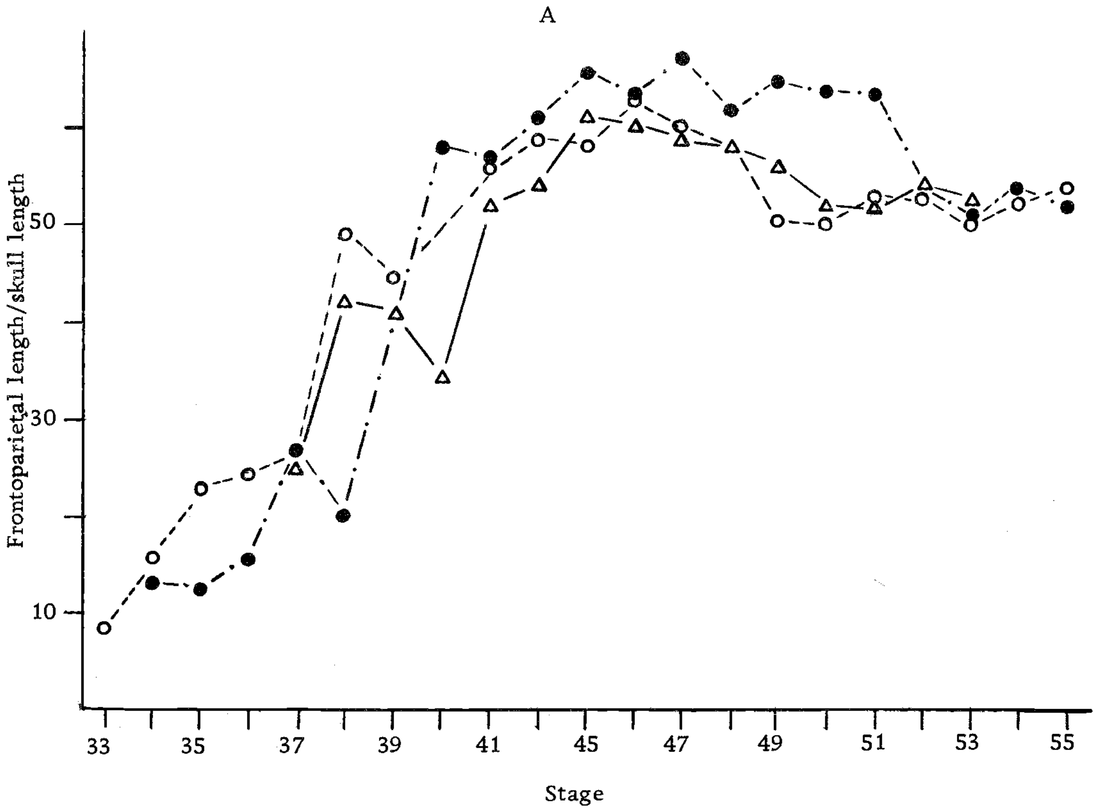

A
B
C
D
E
F

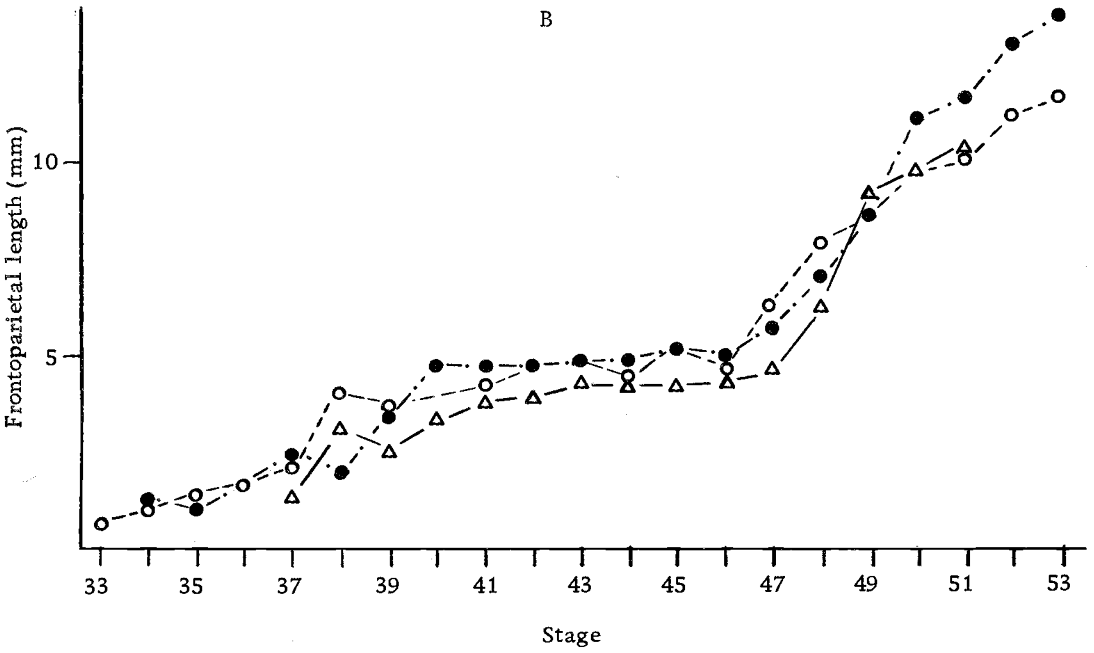
long it begins to spread medially, a medial projection where the two bones first contact is evident, and frontal and parietal areas are noticeable. By S-38 the otic process at the anterior end of the otic capsule is evident; at the same time lateral and medial parietal projections are present with the former being larger. The space between these processes fills in so that by S-42, at the start of metamorphosis, the frontoparietal has a near adult configuration. Development through metamorphosis consists primarily of size increase so that by S-46 the bone slightly overlaps the otic capsule while a medial fontanelle persists.

During postmetamorphic growth, the margin between the otic process and the posterior tip of the bone fills in, and the medial fontanelle is reduced to a narrow slit that often remains throughout life; some large frogs have an open suture, and a small aperture, at the bottom of a shallow depression, always remains between the two bones at the junction of the frontal and parietal areas. The bone is convex in cross-section throughout development, but by S-50 a triangular area of the bone projects over the lateral surface of the brain; this area is higher near the otic capsule and narrows anteriorly. The blunt tips, reaching about to the anterior margin of the eye, overlap the sphenethmoid and often diverge from each other anteriorly. The lateral borders of the brain case converge anteriorly.

Meristic. Graph 6-A and B shows the growth pattern of the

Graph 6. The ratio of frontoparietal length/skull length (A) and frontoparietal length (B) vs. stage of development in *R. pretiosa*, *R. cascadae*, and *R. aurora*. See Graph 1 for legend.


A
Frontoparietal length/skull length
10
30
50
33
35
37
39
41
45
47
49
51
53
55
Stage


B
Frontoparietal length (mm)
5
10
33
35
37
39
41
43
45
47
49
51
53
Stage

frontoparietal, which is similar to that of the parasphenoid. As with the parasphenoid, the reduction in relative size of the frontoparietal in aurora does not come until several stages after pretiosa and cascadae.

Prootic

Descriptive. Due to the complex bilaminar design of the otic capsule that requires sectioning techniques for a complete examination, the present data are not detailed. Miyawaki (1929) followed the development of the ear capsule of Hyla arborea japonica.

The prootic first appears (S-38-39) as diffuse external perichondral centers in the capsule wall just anterior to the parasphenoid alary process and around the prootic foramen. Soon the internal lamella of each area appears, and by S-48 the exoccipital fuses with the posterior center. These two centers enlarge slowly; by S-43 the posteroventral and anterior regions of the capsule are ossified, but the two centers are separate as are the lamellae.

At S-45-46 the columella ossifies and at that time diffuse ossification appears in the capsule wall near the columella. About S-48 diffuse ossification appears throughout the capsule, both internally and externally. The lamellae appear fused in some areas, and the exoccipital-otic complex abutts against the posterior edge of the parasphenoid alary process. By S-50 the capsule is essentially complete although considerable variation occurs; the two centers still may not be in contact ventrally and other areas of weak ossification are present.

*R. aurora* and *cascadae* follow a similar pattern although adult *cascadae* may have weakly ossified capsules.

## Premaxilla

*Descriptive*. The paired, dentigerous premaxillae form the anterior tip of the snout and upper jaw; the first evidence (S-38, 40) of this bone is a flat, cancellous ossification in the dorsal tip of the nasal process slightly anterior to the external nares. Growth anteriorly and ventrally completes the concave nasal process by S-43; immediately the dorsal edge of the dental process is evident. The dental process is essentially complete by S-44-45 when it contacts the dental process of the maxilla and unattached teeth may be present. During this development the medial tip of the dental process turns inward and the spine of the palatal process projects posteriorly from this point. Shortly the rest of the premaxillary palate appears and abutts against the similar development of the maxilla.

In the adult frog, the dorsally notched nasal process projects dorsally and then slightly laterally from near the medial tip of the dental process. The maxillary dental process overlaps the dental process of the premaxilla slightly. No sign of fusion between the

Table 3. Range and mean of the number of prevomerine, premaxillary, and maxillary teeth of Rana pretiosa, R. cascadae, and R. aurora stages 45 to 53.

| Stage and teeth | Species | | |
|---|---|---|---|
| | pretiosa | cascadae | aurora |
| 45-prevomerine | 2(2) | 0(0) | 0(0) |
| premaxillary | 0(0) | 0(0) | 0(0) |
| maxillary | 0(0) | 0(0) | 0(0) |
| 46-prevomerine | 0(0) | 0(0) | 0(0) |
| premaxillary | 0-8(3.9) | 1(1) | 2-5(3.5) |
| maxillary | 3-14(8.8) | 4-11(7.4) | 4-15(8.2) |
| 47-prevomerine | 6-8(7) | 7(7) | 1-5(3.5) |
| premaxillary | 14-17(15.4) | 0(0) | 8-17(12.4) |
| maxillary | 38-59(48.5) | 19(19) | 34-56(47.5) |
| 48-prevomerine | 5-8(6.7) | 2-4(3.0) | 1-4(2.6) |
| premaxillary | 12-23(18.5) | 13(13.0) | 12-14(12.8) |
| maxillary | 40-48(43.3) | 28-46(35.6) | 32-50(39.6) |
| 49-prevomerine | 8(8) | 4-11(7.4) | -- |
| premaxillary | 15(15) | 16-24(20.0) | -- |
| maxillary | 39(39) | 50-71(60.8) | -- |
| 50-prevomerine | 5-12(6.7) | 5-12(7.1) | 5-9(7.3) |
| premaxillary | 12-24(17.5) | 18-27(22.4) | 16-20(18.0) |
| maxillary | 30-58(46.5) | 50-83(68.8) | 52-78(64.0) |
| 51-prevomerine | 0-8(5.6) | 0-11(6.7) | 7-9(8.0) |
| premaxillary | 17-22(20.6) | 18-28(22.4) | 16-20(18.6) |
| maxillary | 35-52(45.4) | 55-84(67.7) | 61-89(72.4) |
| 52-prevomerine | 0-10(6.2) | -- | 7-11(10.3) |
| premaxillary | 11-21(16.6) | -- | 16-26(21.7) |
| maxillary | 41-70(52.5) | -- | 65-87(78.7) |
| 53-prevomerine | 0-8(6.3) | -- | 8-15(10.7) |
| premaxillary | 16-19(17.8) | -- | 20-27(23.4) |
| maxillary | 43-71(56.0) | -- | 77-97(83.7) |

maxilla and premaxilla or between the two premaxilla appears.

## Teeth

The premaxillae, maxillae, and prevomers are dentigerous; Table 3 gives the counts for each series in each species in S-45-53. Teeth first appear as unattached cusps adjacent to the bone; prior to their appearance, odontoid-like rugosities may be present on the dental processes of the maxilla and premaxilla. The dentigerous section of the prevomer is rugose before teeth appear.

Considerable individual variation was noted, but specific differences are present. Overlap in counts would probably include large females of the species with fewer teeth and small males of the species with a larger number of teeth. Notable differences include the separation of the adults of the two large frogs, *aurora* and *pretiosa*, on tooth counts and the large number of teeth in the smaller *cascadae*. Also, one *cascadae* (S-51) and three *pretiosa* (S-51-53) have no prevomerine teeth and the rugose pedicels are absent. In other respects the prevomers of these specimens are normal.

## Septomaxilla

*Descriptive*. Due to the small complex design, detailed notes were not taken on the septomaxilla; sectioning methods are required. Hasurkar (1956, *Rana tigrina*), Lapage (1928), Baldauf (1955, 1958, Bufo woodhousei), Barry (1956, Bufo angusticeps), and others have written extensively on this small bone. The septomaxilla surrounds the lachrymonasal duct (de Beer, 1937) and may aid in support and operation of the nares.

The septomaxilla is situated in the roof of the nasal capsule posterior to the external nares. Viewed dorsally the adult bone is divisible into anterior and posterior sections that are connected laterally. The first ossification (S-39-41) is a weak center in the anterior section; soon a similar center appears in the posterior section and by the end of S-42 the two are usually weakly fused. Further growth entails size increase and completion of the adult configuration.

## Dentary

Descriptive. The dentary forms the lateral and anterior margins of the mandible. At first appearance (S-42) the dentary is a thin strip of vertically oriented bone on the lateral side of Meckel's cartilage directly below the maxilla. It does not overlap the angular which usually appears at this stage. Growth is rapid and the bone soon arches around the anterior curvature of the jaw; the angle of curvature is considerably greater than in later stages. By S-45 the dentary and angular overlap and the dentary may be diffusely fused to the mentomeckelian. This fusion is complete by S-48 and although blade-like, the medial surface of the dentary is concave. Further growth entails size increase and general strengthening of the bone.

Maxilla

Descriptive. The paired, dentigerous maxillae form the greater part of the upper jaw; this bone first appears (S-40-42) as a small diffuse center in the facial process with an indication of the dental process appearing immediately. The dental process forms faster anteriorly and contacts the premaxilla by S-44-45; the facial process has its adult configuration. Unattached teeth are present at S-46 and the dental process is definitely concave. The palatal process is first evident at S-45 as an anteromedial enlargement. From this point it tapers posteriorly and terminates near the posterior margin of the eye. The maxilla overlaps the quadratojugal at S-46.

Except for size there is little difference in the maxillae of the three species, although the facial process is often distinctive. In pretiosa and cascadae the process is rectangular with a posterodorsal process; aurora often lacks this process. Also, aurora often has serrations in the facial process and nasal where the two bones are adjacent. Considerable calcification appears between these two bones in large specimens.

Nasal

Descriptive. The paired nasals form an incomplete roof on the nasal capsules; the adult configuration is roughly teardrop-shaped with the wide section medial and the tail projecting posterolaterally and ventrally in front of the eye.

The nasal appears as a diffuse, narrow sheet (S-41-42) situated laterally in front of the eye. Ossification is rapid along the central axis so that by S-43 the bone is a thin transverse spine; the medial end of the bone then enlarges so that the adult configuration is present by S-46 although weakly ossified. Further growth entails size increase and general strengthening of the bone.

The tail of the nasal, where it lies adjacent to the maxillary facial process is often serrate in large aurora; the body of the bone is often pierced by nerve foramina in all species.

Squamosal

Descriptive. The squamosal overlies the cartilagenous quadrate and serves as a connecting strut for the lower jaw. The squamosal first appears (S-42) as a cancellous strip of bone projecting at about a 40° angle posterodorsally from the lower jaw articulation. At S-44 the bone is longer and situated at about the middle of the eye; by the next stage the squamosal is vertically oriented and the otic section of the dorsal bar is well formed but cancellous. By the end of this stage or by S-46 the zygomatic section of the dorsal bar is evident; the whole bone is larger and stronger, and the vertical section is more convex to lie adjacent to the quadrate.

By S-48 the bone is usually fully formed and has attained an anteriorly slanted position of about 115°. The dorsal bar is fully formed and projects subparallel with the lateral margin of the frontoparietal. The zygomatic section is a vertically oriented blade and the otic section is a horizontally oriented blade that eventually contacts the otic capsule. Calcification appears at this point about S-50.

Angular

Descriptive. The angular is the other large bone in the mandible and forms the medial portion of the jaw. It first appears (S-42-43) as a cancellous sheet on the ventral surface of Meckel's cartilage close to the posterior end. By S-45 the axis of the bone has shifted more vertically with the posterior portion wider. The bone increases in length to overlap the dentary and is generally solidly constructed. By S-48 the angular extends anteriorly around the curvature of the jaw to end near the posterolateral edge of the mentomeckelian. The angular is more curved and adpressed to Meckel's cartilage by this stage. Further growth entails size increase and minor completion of the adult configuration; the anterior tip often fuses with the mentomeckelian.

Prevomer

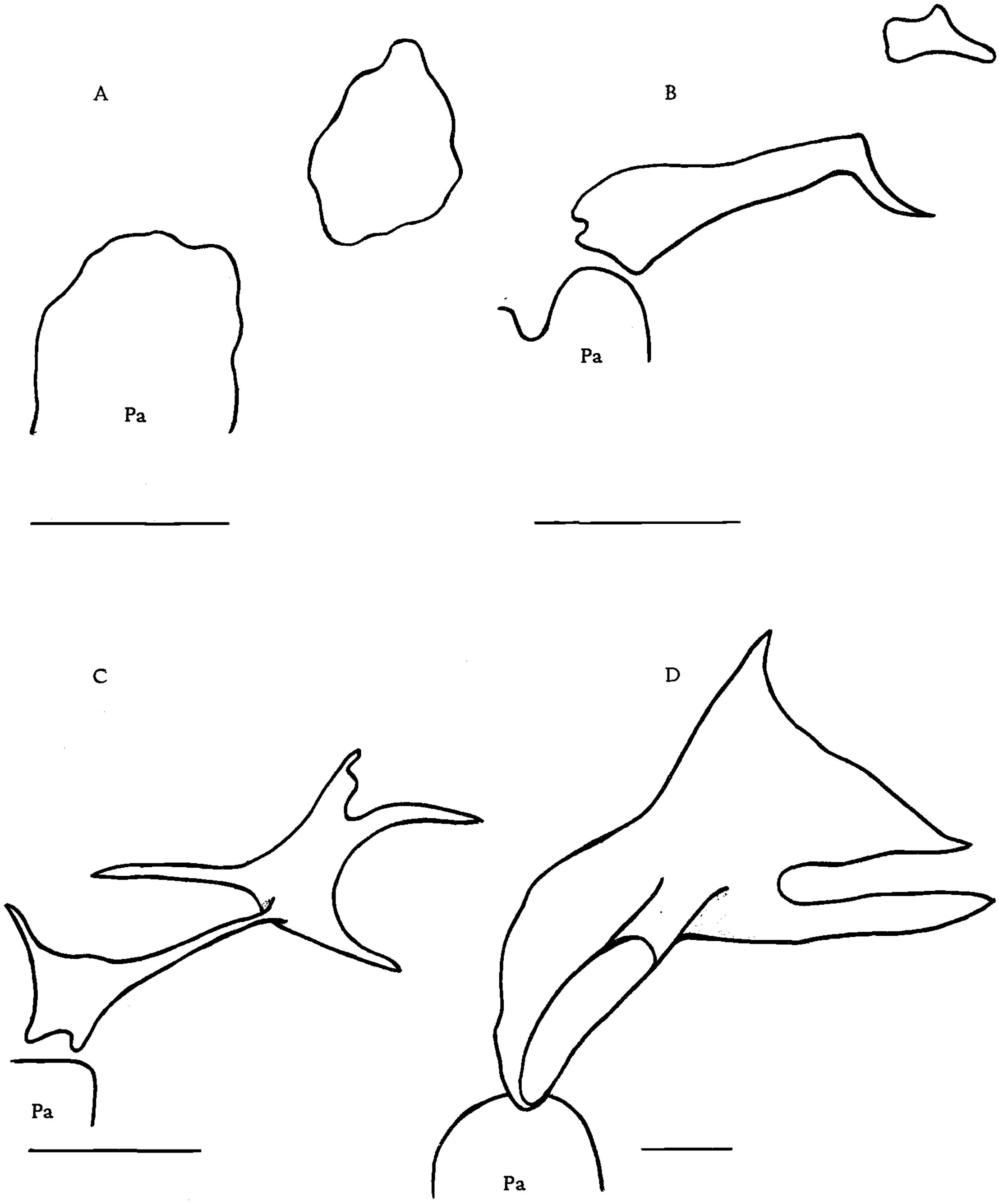
Descriptive. The paired prevomers are dentigerous palatal bones that form the floor of the nasal capsules. The development (Figure 5) and adult configuration is highly variable.

At first appearance (S-43-45) the prevomer is a small irregular plate situated anterolaterally to the anterior tip of the parasphenoid. Slightly later a narrow anterolateral process appears that terminates in a spinous posterior projection; at the same time a small trapezoid-shaped center appears anterolaterally to the tip of the above process. The concave posterior surface of this small center and the spinous projection of the first center roughly delimit the choana. The area adjacent to the parasphenoid appears rugose and unattached teeth may be present.

By S-45 the two centers have joined as in Figure 5-C. The anterior center has four processes: anterolateral and posterolateral processes delimiting the choana, anterior process projecting toward the premaxilla, and a medial process. The posterior center, besides the bridge connecting the two centers, has an anteromedial process.

Later development is varied; some adult frogs have prevomers similar to the above, while in others the areas between the processes fill in so that the prevomer appears as in Figure 5-D. Often there are

Figure 5. Developmental pattern of the left prevomer exemplified by _R. pretiosa_ S-45 (A); S-45 (B); S-45 (C); S-53 (D). The scale line equals 3 mm (A), 2 mm (B and C), or 1 mm (D). Legend: Pa, parasphenoid.


A
B
Pa
Pa
C
D
Pa
Pa

indentations so that the connecting bridge may be quite narrow, the anterior process of the second center prominent, etc. The internal nares is a narrow, posteroventrally facing slit. After S-47 there is a vertical spine on the dorsal surface of the anterior center extending from the anterior tip posteriorly and then laterally to the tip of the posterior choanal process.

The prevomer is not a flat sheet; it projects in a gentle curve anteriorly and ventrally from the level of the parasphenoid to the premaxilla. Due to variation, no specific differences were noted. The prevomers often overlap the tip of the parasphenoid, especially in pretiosa and aurora.

Palatine

Descriptive. The paired palatines project transversely along the posteroventral border of the orbitonasal lamina and act as bracing struts for the maxilla and pterygoid. The palatine first appears (S-43-45) as a diffuse lateral center. Growth is rapid so that an adult configuration is attained by S-47 when the bone is concave to lie adjacent to the lamina and the ends are flared wider than the middle. The lateral tip, where it contacts the maxilla and pterygoid, is usually wider than the medial tip that overlaps the sphenethmoid. Viewed ventrally, the bone is slightly arched in front of the eye.

Mentomeckelian

Descriptive. The paired mentomeckelians form the sagittal symphysis of the mandible. Each bone is a small cylinder fused to the posterior surface of the dentary, and the two mentomeckelians never fuse.

The bone first appears (S-44-46) as a small splint in the posterior wall of the bone and separate from the dentary. Further growth entails size increase and completion of the cylinder to effect fusion with the dentary.

Pterygoid

Descriptive. The pterygoid is a triradiate bracing strut for the lower jaw articulation, otic capsule, and maxilla. The pterygoid appears (S-43-45) as a small center in the maxillary process just anterior to its junction with the other two processes. After slight enlargement, at S-46 the quadratic process appears separate from the first center. At this time both processes are spine-like, but by S-47 the two centers join and their shape is more of a vertically oriented blade. The maxillary process projects anteriorly and then curves laterally to contact the medial surface of the maxilla; it eventually extends anteriorly as far as the palatine.

At S-47 the otic process is evident and gradually enlarges to be loosely associated with the otic capsule. This process of the pterygoid is a horizontally oriented blade, and, along with the quadratic process, never makes solid connection with adjacent bones.

Quadratojugal

Descriptive. The quadratojugal is a small, L-shaped connecting strut between the posterior tip of the maxillary dental process and the medial surface of the squamosal. It appears (S-43-45) as a small triangular ossification situated anteriorly to the ventral tip of the squamosal; a spike soon extends anteriorly toward the maxilla. By S-45-46 the quadratojugal overlaps the tip of the maxilla medially and the dorsal point lies against the medial surface of the squamosal. During early development the longitudinal axis of the bone is slanted posteroventrally, but shifts to a near horizontal position due to the posterior migration of the squamosal.

Sphenethmoid

Descriptive. The sphenethmoid forms the anterior and anterolateral walls of the brain case; Figures 6 and 7 show the developmental pattern of the sphenethmoid.

The bone first appears as two, small, cancellous centers (S-47-48) situated in the lateral wall of the brain case near the anterior tip of the frontoparietals. This center is the external perichondral

Figure 6. Developmental pattern (dorsal view) of the sphenethmoid exemplified by *R. pretiosa* S-49 (A); S-50 (B); S-52 (D); and *R. cascadae* S-51 (C). Each line equals one millimeter. Dotted lines indicate extent of frontoparietal overlap.

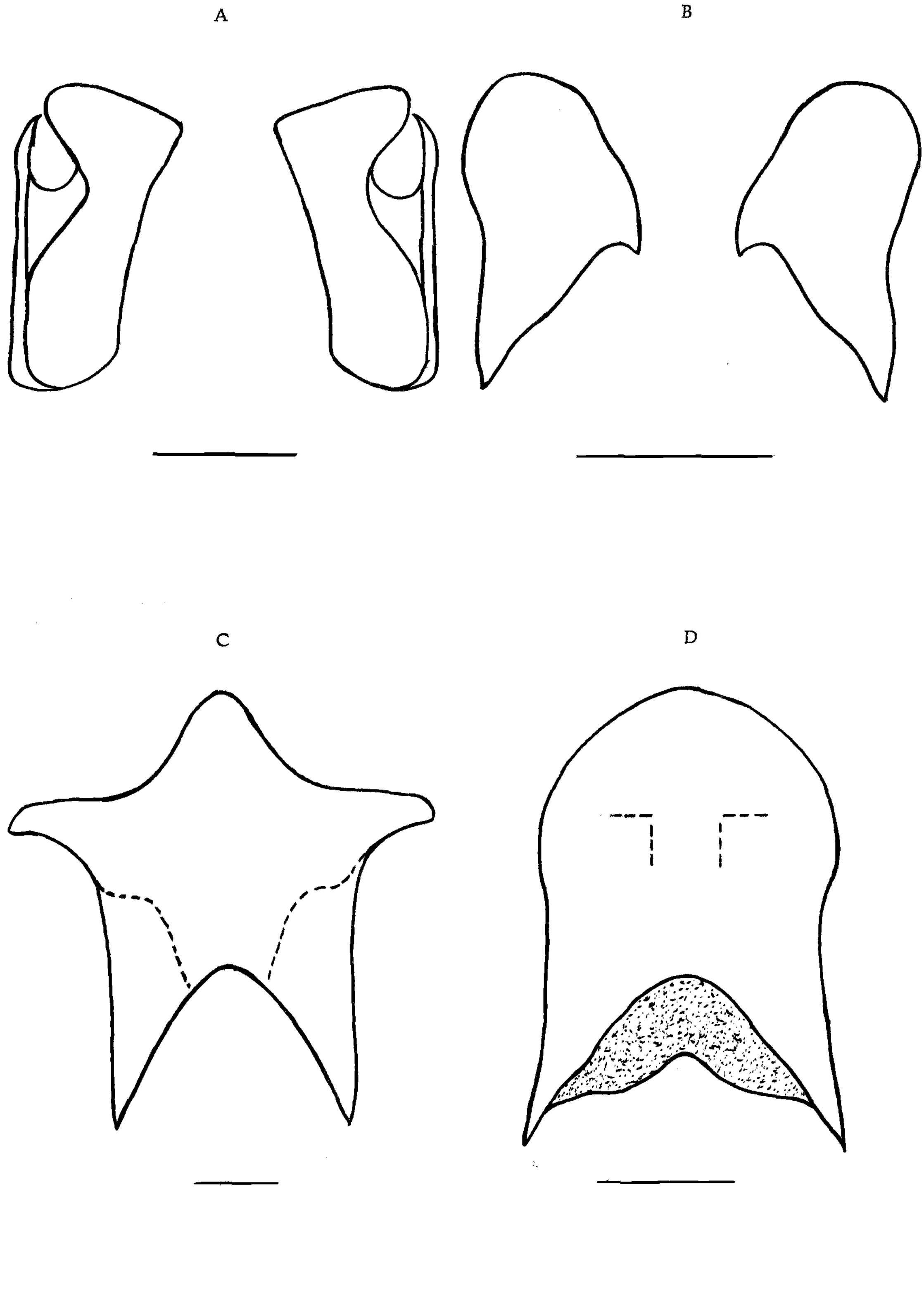
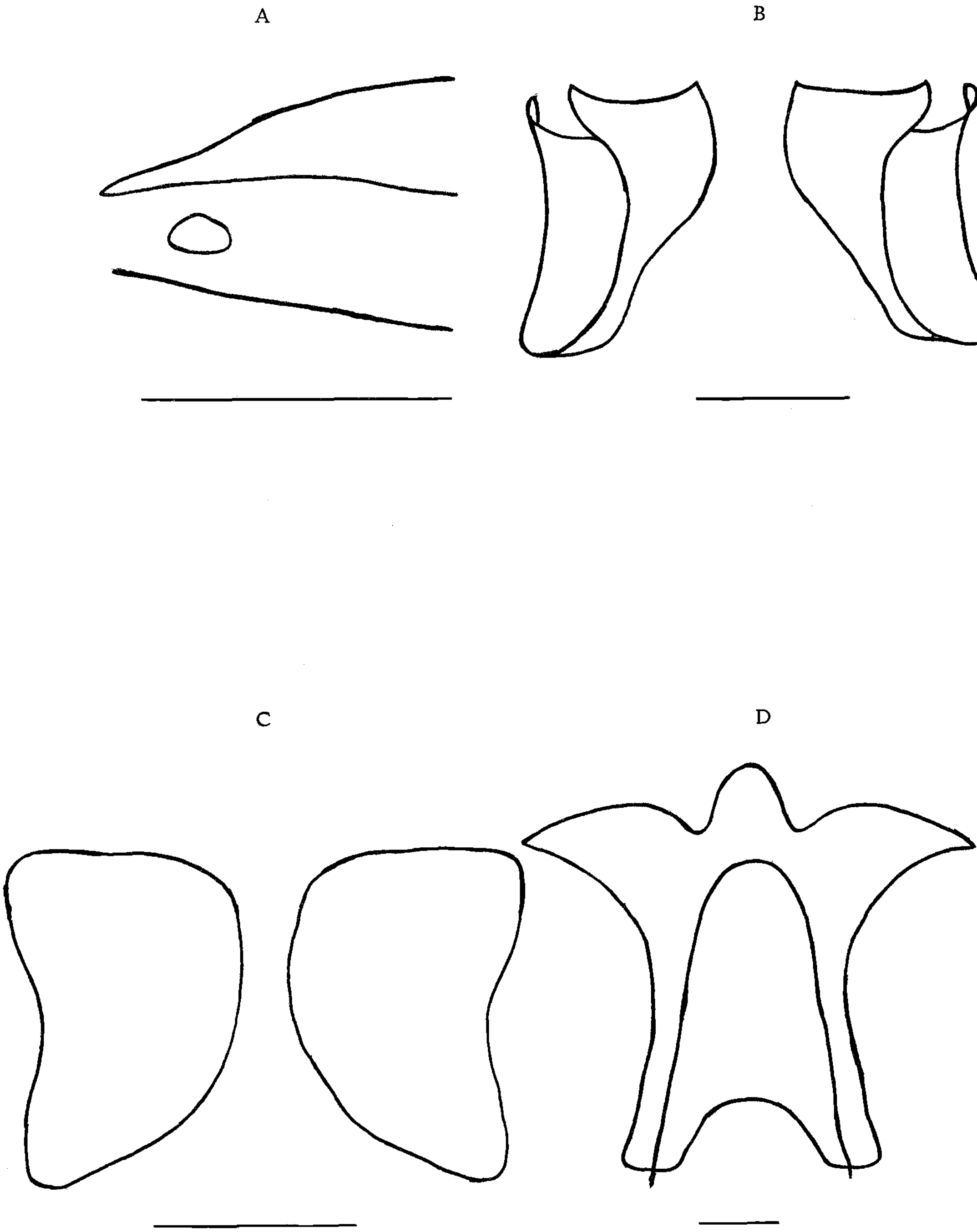

A
B
C
D

Figure 7. Developmental pattern (ventral view) of the sphenethmoid exemplified by *Rana aurora* S-48 (A), lateral view from left side; *R. pretiosa* S-49 (B); S-50 (C); S-52 (D). The scale line equals 1 mm (B, C, D) or 2 mm (A). The extent of parasphenoid overlap is indicated on (D).


A
B
C
D

lamella of this bilaminar bone; soon the internal lamella appears and the two fuse ventrally and posteriorly. Dorsally and anteriorly the two sheets do not fuse, and the inner lamella flexes medially over the brain while the outer sheet remains vertical. The two lamellae slowly fuse throughout their length and by S-49-50 the sphenethmoid consists of two separate elements of solid construction. Each half is a vertical saddle curving medially around the brain. About S-50 the two halves fuse ventrally and then dorsally to complete the cup around the anterior end of the brain. Posteriorly, there is a dorsal and ventral sagittal notch.

Later the bone starts to spread laterally as vertical bilaminar wings; the palatine overlaps these extensions. These wings extend only a short distance laterally and eventually become solid. Heavy calcification in the nasal septum may appear as a bilaminar anterior projection from the sphenethmoid. Further growth entails size increase and general strengthening of the bone although it never appears solidly ossified.

No specific differences were found, although the anterior tip tends to be more truncate in pretiosa than aurora and cascadae. In aurora the nasals often overlap the sphenethmoid dorsally and the parasphenoid, prevomers, and palatines underlie the sphenethmoid in all species. R. pretiosa can often be distinguished since the parasphenoid often extends to or beyond the anterior margin of the sphenethmoid.

Columella

Descriptive. The rod-shaped columella appears (S-45-46) as a small transversely oriented cylinder in the angle between the vertical and otic sections of the squamosal. In a given individual, the columella does not appear until the squamosal is nearly vertical; the rest of the squamosal migration consists primarily of a posterior pivoting of the vertical section around the columella. Further growth entails increase in size and completion of the cylindrical shape.

Hyoid

Descriptive. The thyrohyal process of the hyoid is a flattened dumbbell-shaped bone projecting from the posterolateral corner of the hyoid plate lateral to the larynx. It first appears (S-46) as a small cylinder in the center of the bone; by the end of the next stage the adult configruation has been attained so that further growth entails only a size increase.

Although a true parahyoid is absent in Rana (Trevawas, 1933), there is considerable calcification in the posteromedial and anterolateral sections of the hyoid plate.

## Extraneous Calcification

Descriptive. Diffuse calcification occurs in various places in adult specimens, such as the hyoid plate, eye ball, nasal capsule, junction of pterygoid, maxilla, nasal and palatine, between the dorsal and ventral tips of the exoccipitals, between the squamosal, pterygoid and otic capsule, tympanic ring, etc. The most extensive area involves the nasal capsule, as the nasal septum and all walls of the capsule are often quite heavily calcified in large specimens.

# DISCUSSION

Rana pretiosa, R. cascadae, and R. aurora are three closely related species within Orton's (1952) wood frog group that are primarily limited to the Pacific Northwest; only pretiosa ranges into the Great Basin and Rocky Mountain areas. R. cascadae is limited to four disjunct areas: Olympic Mountains of Washington, Cascade Mountains of Washington and Oregon, Mt. Lassen area of Northern California. As adults, pretiosa and aurora reach lengths of 90 mm while cascadae gets no larger than 70 mm. R. pretiosa metamorphose at 17-20 mm. All the tadpoles are typical pond tadpoles occurring in permanent and semipermanent water; metamorphosis occurs in one summer. The tadpoles of pretiosa are the largest followed by aurora and then cascadae.

The growth and metamorphic formation of the anuran skull is a dynamic process that would best be illustrated by animated moving pictures. Through metamorphosis there is no increase in length of the skull, but the major part of bone formation and changes in configuration occur during this period.

Before metamorphosis the skull consists of paired elements (except the parasphenoid), situated along the longitudinal axis, that serve primarily to protect the brain. The premaxillae and septomaxillae appear before the start of metamorphis but are small until following stages. At the start of metamorphosis, indicated by the eruption of the front legs, the adult mouth starts to form which necessitates several new bones to form and support the jaw. The dentary and angular of the lower jaw and the maxilla and squamosal of the upper jaw and suspensorium appear. The lower jaw articulation lies far forward near the anterior margin of the eye which makes a schematic representation of the skull (Figure 2) appear diamond-shaped with a blunt anterior end. Soon the lower jaw articulation starts to migrate posteriorly and slightly medially. This action effects the angle of the squamosal and the growth of the maxilla, premaxilla and quadratojugal. The upper jaw becomes more acutely rounded and the nasal processes of the maxillae and premaxillae project dorsally from the dental processes.

By S-46 the skull is similar to the adult although considerable ossification continues. The lower jaw has reached a point near its definitive position, the squamosal stands near vertical, and the quadratojugal completes the upper jaw arch. The columella appears as the squamosal reaches the vertical position. The supportive palatines and pterygoids are present, and at S-47-48 the sphenethmoid completes the anterior end of the brain case. The lateral wall of the brain case between the spehnethmoid and otic capsule, the nasal capsules, tympanic ring, and other areas become heavily calcified.

Further growth entails a general size increase, completion of bones, and general closure of the dorsal fontanelle.

Erdmann (1933) presents a listing of sequential appearance of cranial elements in Rana temporaria that differs somewhat from the present species. In the European species, the nasals and prevomers appear after metamorphosis rather than early during metamorphosis, the prootics appear during metamorphosis rather than early in bone formation, and other elements appear somewhat later in the sequence. A closer comparison cannot be made due to the lack of a common staging system.

Differences in the sequential appearance of bones in Eleutherodactylus nubicola (Lynn, 1942) are probably correlated with the necessity for the young frog to feed on macroscopic organisms immediately after hatching; in this frog the angular, squamosal, and parasphenoid are the first bones to appear at ten days prior to hatching. The premaxilla, dentary, exoccipital, and frontoparietals follow in three days. In Pseudacris nigrita triseriata, a small hylid (Stokely and List, 1954) the prootic and parasphenoid appear 14-22 days after S-42 and calcification in the nasal cartilage appears at S-42. Trueb's (1966) listing for Hyla septentrionalis, a large hylid, shows only the frontoparietals and septomaxillae present prior to metamorphosis. The prootics appear when the frog is about 18 mm long (metamorphic size is about 12 mm) and are among the last of the bones to appear.

The exoccipitals and parasphenoid appear immediately after metamorphosis, some time after the maxillae, premaxillae, and nasals. Duellman and Trueb (1966), working on Smilisca baudini, show the prootic as the last bone to appear. Ascaphus truei (Altig, unpublished data) has a sequence similar to Rana pretiosa except that the bones appearing during metamorphosis all appear at S-45-46; this may be a means of allowing the suctorial mouth to remain functional as long as possible.

Factors affecting the sequence of appearance of cranial bones may include size of the organism, feeding and locomotor mechanisms of the tadpole, developmental type, etc. Presently unknown factors may also be present to account for the differences between Rana pretiosa and temporaria and other species of similar development. More information is needed on developmental and functional anatomy as well as the ecology of tadpoles.

Skull length and the portion of snout-vent length contributed by the skull vary in R. pretiosa, cascadae, and aurora. R. cascadae are similar to S-51 pretiosa. The latter species has a small head compared to its snout-vent length (ca. 26%). R. aurora, which is comparable in size to pretiosa, has a larger head in actual measurements and in relation to its body.

Skull length shows a growth trend that appears in other measurements, i.e. R. pretiosa and cascadae have a faster growth rate immediately after metamorphosis than does aurora. In actual time, not stage, this occurs during the first two to three summers of life. This growth data based on measurement of head length agrees with that of Briggs (personal communications) based on an asymtotic growth regression of body length in R. cascadae. This difference in skull size is reflected in all skull measurements; using the area of schmatic skulls as in Figure 2 as a reference, S-51 cascadae and S-53 pretiosa and aurora have skulls covering 27.3, 33.0, and 51.2 $cm^2$ respectively. This makes the skull of cascadae slightly over half the size of aurora and pretiosa about two-thirds the size of aurora.

Except for the following short notations, there is almost no comparative material on developmental pattern of individual bones; the comparison with other frogs with bones of different configuration is not necessary at this time.

The embryological origin, composition, and development of the frontoparietal of anurans is debated. Parker (1871), Gaupp (1906), Erdmann (1933), de Jongh (1968), and Griffiths (1954) contend the frontal and parietal arise separately as individual bones that fuse during ontogeny. Gaupp (ibid.) states that they fuse early, Parker (ibid.) states that they are separate at a stage equivalent to S-42, and de Beer (1937) figures a skull near the end of metamorphosis with the bones still separate and rather fully formed.

Eaton (1939) states that these bones arise as single elements, including the European R. temporaria and R. esculenta, and that the above authors erred in observation. He (Eaton, 1942) also supports the idea that frontoparietals are actually only frontals with the parietals being absent in anurans. It is not within the bounds of this study to determine the homology of this bone; regardless of its composition, I found the frontoparietal arose as a single element in the three species studied, frontal and parietal areas are evident, but never separate.

Erdmann (ibid.) states that the first ossification in the maxilla occurs in the facial process and I agree, while de Beer (ibid.) states that the maxilla appears as a center that spreads to the facial process. This may be an interpretation error as he had Erdmann's paper as a reference.

In agreement with de Beer (ibid.) I found an ossification center in the quadrate of a reference specimen of R. temporaria; such ossification was not found in any of the present species.

In the European species (R. temporaria, Gaupp, 1906; R. esculenta, Ecker, 1889; R. agilis and arvalis, personal observation) the anterolateral edge of the nasal comes in solid contact with the posterodorsal projection of the maxillary facial process; this contact was not observed in the present species, but aurora does show an indication of possible contact as the nasal and maxilla are serrate at that point.

The above authors state that the prootic first appears as perichondral lamellae near the prootic foramen. I found this center, although considerably earlier in development than Erdmann (_ibid._), plus a second similar center at the anterior tip of the otic capsule. These two centers grow slowly and may not contact each other until S-50.

Teeth are not commonly used as taxonomic characters in anurans, but included data (Table 3) indicates such may be of use; the maxillary and premaxillary series would most likely be combined in intact specimens. The maxillary series appears the most consistently different throughout development, but all three types are diagnostic as adults. _R. pretiosa_ and _aurora_ can usually be determined on teeth counts, while _aurora_ and _cascadae_ overlap somewhat. The means are considerably different so that a larger sample may show a statistical difference. The high teeth counts of _cascadae_ may indicate an affinity to _aurora_, but Goin (1958) and Chantell (1968) found more premaxillary teeth in the smaller of a species pair in the hylid genus _Acris_. The difference in number of teeth appears to be due to the size of individual teeth, the length of the bone, and the proportion of the bone that bears teeth.

Intrageneric relationships of North American ranid frogs are relatively undetermined. Orton (1952) formed four groups based on larval and adult characteristics similar to those of Boulenger (1919). Zweifel (1955) has studied the systematics of the frogs in the _boylei_ group. Chantell (*ibid.*) postulated two groups, based on osteological measurements and ratios, that cross Orton's (*ibid.*) lines; until Chantell's work is complete, I think it should not be considered. Dumas (1966) used the terms pond frog (*pretiosa* and *cascadae*) and wood frog (*aurora* and *sylvatica*) and stated that all the North American and temperate Eurasian species could probably be placed in one of these two groups. He implies, by placing them all in the pond frog group, that *pretiosa* and *cascadae* are more closely related to *pipiens* than to *aurora*. Until the genus *Rana* is better known I do not agree with this arrangement and prefer Orton's (*ibid.*) four group arrangement.

Dunlap (1955) examined 40 specimens each of *R. pretiosa*, *cascadae*, and *aurora*; he concluded that *cascadae* should be considered a species with some indication of being closely related to *pretiosa* while being intermediate between *pretiosa* and *aurora* in other respects. Dumas (*ibid.*), using data on water relations, ecology, behavior, electrophoretic separation of blood protein, precipitin ring tests, artificial hybridization, coloration and morphology, concluded that the three were separate species and *cascadae* definitely is closely related to *pretiosa* and derived from it. He suggested a mode of speciation for *cascadae*.

From the literature data and the data included here, I agree that *cascadae* should hold a specific status and that it is a *pretiosa* type. From my data it appears as a dwarf species of montane derivation as discussed by Dumas (ibid.) and Noble (1954). Growth patterns of various measurements (eg. skull length; skull length/ snout vent length) of cascadae closely follow the pattern of pretiosa during postmetamorphic stages but stops short of the adult pretiosa condition. Adult cascadae resemble S-51 pretiosa quite closely as to size, proportions, and configuration. The maxillary facial processes are similar in the two, and the skull of cascadae is often less well ossified than adults of the other two species; this could be expected from a species formed by arrested development. This is especially noticeable in the otic capsule, extraneous calcification throughout the skull, closeness of the two exoccipitals, completeness of the prevomer, and other conditions that might be expected to be completed at the end of development. The number of teeth may be indicative of it being the smaller of a species pair as in Acris (Chantell, ibid.).

Dumas (ibid.) suggested that the pretiosa stock isolated west of the Cascade Mountains during the Wisconsin glacial maximum speciated to the cascadae type and followed the retreating glacier into the mountains. The result was four disjunct populations of cascadae. R. pretiosa then reinvaded western Oregon and Washington through low mountain passes and the Columbia River Gorge.

This is a workable solution to the problem as presently understood, but a different picture might appear when this group, as well as the genus, is better known. None of these species has ever been subjected to a thorough examination using series from throughout the ranges. Chantell and his students (personal communication) are starting to examine the osteology and myology of various species in the genus *Rana*. Until more information is available on the North American *Rana*, it will not be possible to form intrageneric species groups as Tihen (1962, osteology) and Blair (1963, hybridization) have been able to do in the genus *Bufo*. No doubt certain members of the Eurasian fauna will have to be checked as some of them are quite similar to the North American wood frogs; Cope (1889) made the error of calling *pretiosa* and *aurora* subspecies of European species.

# SUMMARY

The developmental and growth patterns of the skull and its constituent bones were followed (110 *pretiosa*, 100 *cascadae*, 115 *aurora*) from the time bone appeared through the adult stages.

Skull length remains constant through metamorphosis and then increases at variable rates according to the species; *R. aurora* appears to consistently have a slower growth rate immediately after metamorphosis than the other two species. Skull width decreases through metamorphosis due to the migration of the lower jaw articulation; following metamorphosis it increases similar to the skull. *R. pretiosa* has a small head compared to *aurora* of similar size; *cascadae* resemble *pretiosa* at S-51. The sequence of appearance varies between species to a significant degree only during early stages; the parasphenoid, exoccipitals and frontoparietals appear three to four stages earlier in the large frogs. Over half the bones appear during metamorphosis, and only the sphenethmoid appears after metamorphosis.

The squamosal-exoccipital distance reduces through metamorphosis and is maintained at about 2 mm in the adult. All three species have skulls of similar shape and proportions.

The parasphenoid and frontoparietal show positive allometric growth in relation to the skull through S-45-46; this is followed by a reduction to a plateau.

Figures of the developmental pattern of the parasphenoid, frontoparietal, prevomer, and sphenethmoid are presented. The pattern of other bones is described; the frontoparietal was found to arise from one center on each side. The prootic ossified from two centers in contrast to only the one in some citations. The number of teeth, especially the maxillary teeth, could be used as a taxonomic characteristic in this group. Extraneous calcification appears in various places throughout the skull of large specimens, especially in the nasal capsule region.

I agree with Dumas (1966) that R. cascadae should be considered a full species of pretiosa derivation, but I do not agree with his division of the genus Rana into the wood frog and pond frog groups. I think this is unwarranted with present information. His explanation of speciation of R. cascadae is presently useful, but a different scheme might well arise when more information is available on geographic variation of these species.

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# APPENDIX

| Stage | pretiosa | cascadae | aurora |
|---|---|---|---|
| | **Skull length/body length** | | |
| 46 | ------------------- | .38 - .46 ( .41) | ------------------- |
| 47 | .36 - .42 ( .39) | .39 ( .39) | .32 - .40 ( .34) |
| 48 | .38 - .49 ( .42) | .22 - .32 ( .28) | .28 - .35 ( .32) |
| 49 | .36 ( .36) | .35 - .38 ( .36) | .33 ( .33) |
| 50 | .30 - .36 ( .33) | .29 - .36 ( .32) | .34 - .36 ( .35) |
| 51 | .29 - .33 ( .31) | .29 - .34 ( .31) | .32 - .35 ( .34) |
| 52 | .22 - .31 ( .28) | ------------------- | .26 - .34 ( .30) |
| 53 | .21 - .29 ( .25) | ------------------- | .30 - .34 ( .32) |
| | **Skull length** | | |
| 33 | 6.1 - 7.1 ( 6.6 ) | ------------------- | 8.6 - 9.6 ( 9.0 ) |
| 34 | 6.3 - 7.1 ( 6.7 ) | ------------------- | 8.9 - 9.7 ( 9.2 ) |
| 35 | 6.4 - 7.1 ( 6.8 ) | ------------------- | 8.6 - 9.3 ( 8.8 ) |
| 36 | 5.7 - 7.9 ( 6.6 ) | ------------------- | 9.3 - 11.1 ( 9.8 ) |
| 37 | 7.1 - 8.6 ( 7.8 ) | 5.7 - 6.4 ( 6.1 ) | 7.7 - 10.3 ( 9.2 ) |
| 38 | 7.6 - 8.6 ( 8.1 ) | 6.4 - 7.4 ( 6.7 ) | 8.6 - 10.3 ( 9.5 ) |
| 39 | 7.9 - 9.3 ( 8.4 ) | 5.7 - 6.1 ( 5.9 ) | 7.9 - 10.0 ( 8.7 ) |
| 40 | ------------------- | 7.1 - 7.7 ( 7.3 ) | 7.7 - 8.9 ( 8.1 ) |
| 41 | 7.3 - 8.9 ( 7.7 ) | 6.9 - 8.0 ( 7.2 ) | 7.9 - 8.6 ( 8.1 ) |
| 42 | 7.0 - 8.6 ( 7.7 ) | 7.0 - 7.3 ( 7.2 ) | 7.4 - 8.3 ( 7.9 ) |
| 43 | 7.9 - 8.6 ( 8.2 ) | 6.6 - 7.3 ( 7.0 ) | 7.1 - 7.7 ( 7.4 ) |
| 44 | 6.9 ( 6.9 ) | 6.1 - 7.6 ( 6.9 ) | 6.9 - 8.6 ( 7.8 ) |
| 45 | 8.3 - 8.6 ( 8.4 ) | 6.9 - 7.6 ( 7.0 ) | 7.4 ( 7.4 ) |
| 46 | 7.1 - 8.6 ( 7.9 ) | 6.4 - 8.3 ( 7.0 ) | 7.7 - 8.1 ( 7.9 ) |
| 47 | 10.0 - 11.7 (10.9 ) | 8.1 ( 8.1 ) | 8.0 - 12.1 ( 9.4 ) |
| 48 | 14.3 - 17.6 (15.9 ) | 17.1 - 22.6 (19.6 ) | 9.4 - 12.3 (10.9 ) |
| 49 | 16.1 (16.1 ) | 16.7 - 18.7 (17.6 ) | 13.4 (13.4 ) |
| 50 | 16.7 - 20.4 (18.7 ) | 16.3 - 22.6 (18.0 ) | 20.0 - 21.9 (20.7 ) |
| 51 | 18.0 - 23.4 (20.0 ) | 17.9 - 23.6 (19.6 ) | 21.9 - 24.4 (23.1 ) |
| 52 | 16.1 - 24.4 (21.0 ) | ------------------- | 20.1 - 27.1 (24.1 ) |
| 53 | 17.4 - 25.4 (21.5 ) | ------------------- | 24.6 - 28.9 (26.5 ) |
| | **Skull width** | | |
| 40 | ------------------- | 8.0 ( 8.0 ) | ------------------- |
| 41 | ------------------- | 6.4 - 7.1 ( 6.7 ) | ------------------- |
| 42 | 6.0 ( 6.0 ) | 5.7 - 7.4 ( 6.4 ) | 7.9 - 9.0 ( 8.5 ) |
| 43 | 6.6 - 7.1 ( 6.7 ) | 5.1 - 5.7 ( 5.5 ) | 6.1 - 7.6 ( 6.8 ) |
| 44 | 6.1 ( 6.1 ) | 5.7 - 6.0 ( 5.8 ) | 6.1 - 6.9 ( 6.5 ) |
| 45 | 6.3 - 7.3 ( 6.6 ) | 4.1 - 5.7 ( 5.2 ) | 5.3 ( 5.3 ) |
| 46 | 6.3 - 7.9 ( 7.1 ) | 5.4 - 7.4 ( 6.2 ) | 6.0 - 6.6 ( 6.2 ) |
| 47 | 9.7 - 11.7 (10.6 ) | 7.3 ( 7.3 ) | 8.4 - 11.1 ( 9.4 ) |

(continued)

Skull width (continued)

| | | | |
|---|---|---|---|
| 48 | 12.7 - 16.7 (14.8 ) | 11.3 - 13.0 (12.1 ) | 9.4 - 12.3 (10.9 ) |
| 49 | 13.7 (13.7 ) | 17.4 - 18.1 (17.7 ) | 14.0 (14.0 ) |
| 50 | 15.7 - 21.3 (18.0 ) | 17.1 - 27.1 (19.5 ) | 18.6 - 22.3 (20.1 ) |
| 51 | 17.4 - 24.4 (19.3 ) | 18.1 - 21.9 (20.2 ) | 21.6 - 25.9 (23.1 ) |
| 52 | 16.9 - 24.1 (21.6 ) | -------------------- | 22.8 - 27.6 (24.8 ) |
| 53 | 16.4 - 29.3 (21.4 ) | -------------------- | 25.9 - 31.6 (28.2 ) |

Skull length/width

| | | | |
|---|---|---|---|
| 42 | 1.1 - 1.2 ( 1.1 ) | .9 - 1.2 ( 1.1 ) | .8 - 1.0 ( .9 ) |
| 43 | 1.1 - 1.3 ( 1.2 ) | 1.2 - 1.5 ( 1.3 ) | .9 - 1.2 ( 1.0 ) |
| 44 | 1.1 ( 1.1 ) | 1.0 - 1.2 ( 1.1 ) | 1.0 - 1.3 ( 1.1 ) |
| 45 | 1.1 - 1.3 ( 1.2 ) | 1.2 - 1.7 ( 1.3 ) | 1.3 ( 1.3 ) |
| 46 | 1.0 ( 1.0 ) | 1.0 - 1.3 ( 1.1 ) | 1.2 - 1.3 ( 1.2 ) |
| 47 | 1.0 - 1.0 ( 1.0 ) | 1.1 ( 1.1 ) | .9 - 1.0 ( 1.0 ) |
| 48 | 1.0 - 1.1 ( 1.0 ) | .9 - 1.0 ( .9 ) | .9 - 1.0 ( .9 ) |
| 49 | 1.1 ( 1.1 ) | .9 - 1.0 ( .9 ) | .9 ( .9 ) |
| 50 | .9 - 1.1 ( 1.0 ) | .8 - 1.0 ( .9 ) | .9 - 1.1 ( 1.0 ) |
| 51 | .9 - 1.0 ( 1.0 ) | .8 - 1.0 ( .9 ) | .9 - 1.0 ( .9 ) |
| 52 | .9 - 1.0 ( .9 ) | -------------------- | .9 - 1.0 ( .9 ) |
| 53 | .8 - 1.0 ( 1.0 ) | -------------------- | .8 - 1.0 ( .9 ) |

Squamosal-exoccipital distance

| | | | |
|---|---|---|---|
| 42 | 4.6 - 5.4 ( 5.0 ) | 2.7 - 4.1 ( 3.4 ) | 4.6 - 5.9 ( 5.4 ) |
| 43 | 4.0 - 5.1 ( 4.4 ) | 3.0 - 3.9 ( 3.5 ) | 3.9 - 4.9 ( 4.2 ) |
| 44 | 3.4 ( 3.4 ) | 2.4 - 3.0 ( 2.7 ) | 2.1 - 3.3 ( 2.7 ) |
| 45 | 1.1 - 2.7 ( 1.9 ) | 1.9 - 2.6 ( 2.2 ) | 2.1 ( 2.1 ) |
| 46 | 1.4 - 1.9 ( 1.6 ) | 1.1 - 2.1 ( 1.6 ) | 2.1 - 2.6 ( 2.3 ) |
| 47 | 1.4 - 2.4 ( 2.0 ) | 1.6 ( 1.6 ) | .7 - 1.7 ( 1.1 ) |
| 48 | 2.0 - 3.9 ( 2.6 ) | 1.1 - 1.6 ( 1.4 ) | .6 - 1.9 ( 1.2 ) |
| 49 | 2.1 - ( 2.1 ) | .7 - 2.6 ( 1.7 ) | 1.4 ( 1.4 ) |
| 50 | 1.4 - 3.4 ( 2.5 ) | 0.0 - 2.6 ( 1.7 ) | 3.0 - 3.6 ( 3.3 ) |
| 51 | 1.9 - 3.6 ( 3.1 ) | 1.1 - 2.9 ( 2.2 ) | 2.7 - 3.6 ( 3.3 ) |
| 52 | 0.0 - 2.9 ( 1.7 ) | -------------------- | 1.3 - 4.6 ( 3.1 ) |
| 53 | 1.7 - 3.4 ( 2.5 ) | -------------------- | 1.9 - 3.6 ( 2.6 ) |

Snout length

| | | | |
|---|---|---|---|
| 40 | -------------------- | 1.9 ( 1.9 ) | -------------------- |
| 41 | 2.0 - 2.4 ( 2.1 ) | 1.7 - 1.9 ( 1.8 ) | -------------------- |
| 42 | 1.1 - 1.9 ( 1.8 ) | 1.7 - 2.0 ( 1.9 ) | 1.6 - 2.3 ( 1.9 ) |
| 43 | 1.6 - 2.1 ( 1.8 ) | 1.1 - 2.1 ( 1.7 ) | 1.3 - 2.1 ( 1.7 ) |
| 44 | .86 ( .86) | 1.6 - 2.1 ( 1.9 ) | 1.4 - 2.0 ( 1.7 ) |
| 45 | 1.3 - 1.4 ( 1.4 ) | 1.6 - 2.0 ( 1.7 ) | 1.6 ( 1.6 ) |
| 46 | 1.7 - 2.6 ( 2.3 ) | 1.4 - 2.4 ( 2.1 ) | 1.6 - 2.0 ( 1.9 ) |

(continued)

Snout length (continued)

| | | | |
|---|---|---|---|
| 47 | 4.9 - 5.6 ( 5.3 ) | 2.3 ( 2.3 ) | 2.1 - 4.3 ( 2.9 ) |
| 48 | 4.6 - 5.1 ( 4.9 ) | 4.0 - 4.4 ( 4.2 ) | 3.0 - 4.3 ( 3.5 ) |
| 49 | 4.7 ( 4.7 ) | 5.7 - 8.6 ( 6.6 ) | 4.4 ( 4.4 ) |
| 50 | 4.1 - 6.6 ( 5.2 ) | 5.3 - 7.6 ( 6.1 ) | 6.1 - 7.9 ( 7.0 ) |
| 51 | 5.3 - 6.0 ( 5.6 ) | 5.3 - 7.4 ( 6.7 ) | 6.4 - 7.4 ( 7.0 ) |
| 52 | 5.3 - 7.1 ( 6.1 ) | ------------------ | 6.4 - 11.4 ( 8.1 ) |
| 53 | 4.9 - 9.3 ( 6.7 ) | ------------------ | 7.1 - 9.7 ( 8.3 ) |

Snout width

| | | | |
|---|---|---|---|
| 40 | ------------------ | 5.4 ( 5.4 ) | ------------------ |
| 41 | ------------------ | 4.3 ( 4.3 ) | ------------------ |
| 42 | 4.0 - 4.6 ( 4.3 ) | 3.9 - 4.6 ( 4.2 ) | 4.7 - 6.7 ( 5.4 ) |
| 43 | 4.6 - 5.1 ( 4.7 ) | 3.0 - 3.9 ( 3.6 ) | 3.7 - 5.4 ( 4.5 ) |
| 44 | 4.3 ( 4.3 ) | 3.0 - 4.6 ( 3.9 ) | 4.0 - 4.6 ( 4.2 ) |
| 45 | 4.7 - 5.0 ( 4.9 ) | 3.3 - 4.1 ( 3.8 ) | 4.7 ( 4.7 ) |
| 46 | 4.4 - 5.4 ( 4.8 ) | 4.1 - 5.1 ( 4.5 ) | 4.0 - 5.4 ( 4.4 ) |
| 47 | 11.9 - 12.1 (12.0 ) | 5.6 ( 5.6 ) | 5.6 - 7.6 ( 6.4 ) |
| 48 | 8.9 - 11.4 (10.2 ) | 8.1 - 8.6 ( 8.3 ) | 6.0 - 9.3 ( 7.3 ) |
| 49 | 10.4 (10.4 ) | 12.4 - 13.3 (12.8 ) | 9.1 ( 9.1 ) |
| 50 | 11.4 - 15.0 (12.4 ) | 13.1 - 18.6 (14.0 ) | 12.6 - 15.3 (13.6 ) |
| 51 | 12.0 - 16.4 (13.4 ) | 12.0 - 15.7 (14.0 ) | 14.3 - 16.4 (15.3 ) |
| 52 | 11.4 - 17.1 (14.7 ) | ------------------ | 12.9 - 16.9 (15.1 ) |
| 53 | 10.7 - 19.1 (14.9 ) | ------------------ | 17.3 - 21.3 (18.8 ) |

Maxillary gap

| | | | |
|---|---|---|---|
| 42 | 2.6 - 3.0 ( 3.9 ) | 2.4 - 2.9 ( 2.7 ) | 2.3 - 3.0 ( 2.6 ) |
| 43 | 2.9 - 3.1 ( 3.0 ) | 2.1 - 2.6 ( 2.5 ) | 2.3 - 3.0 ( 2.7 ) |
| 44 | 2.4 ( 2.4 ) | 2.0 - 2.9 ( 2.4 ) | 2.1 - 2.6 ( 2.3 ) |
| 45 | 2.9 - 3.1 ( 3.0 ) | 2.1 - 2.6 ( 2.4 ) | 2.4 ( 2.4 ) |
| 46 | 2.6 - 2.9 ( 2.8 ) | 2.1 - 2.9 ( 2.5 ) | 1.7 - 2.6 ( 2.2 ) |
| 47 | 5.3 - 6.4 ( 5.8 ) | 4.3 ( 4.3 ) | 3.0 - 3.6 ( 3.3 ) |
| 48 | 4.4 - 5.3 ( 4.8 ) | 4.3 - 4.7 ( 4.4 ) | 3.3 - 4.7 ( 3.9 ) |
| 49 | 5.0 ( 5.0 ) | 5.7 - 6.0 ( 5.9 ) | 4.7 ( 4.7 ) |
| 50 | 5.0 - 6.1 ( 5.7 ) | 4.9 - 7.1 ( 6.2 ) | 6.0 ( 6.0 ) |
| 51 | 5.4 - 6.9 ( 6.1 ) | 5.4 - 7.3 ( 6.4 ) | 5.9 - 6.7 ( 6.5 ) |
| 52 | 5.4 - 7.1 ( 6.5 ) | ------------------ | 5.3 - 7.4 ( 6.7 ) |
| 53 | 5.4 - 7.6 ( 6.3 ) | ------------------ | 7.1 - 9.1 ( 7.6 ) |

Parasphenoid length

| | | | |
|---|---|---|---|
| 32 | .6 ( .6 ) | ------------------ | ------------------ |
| 33 | 1.0 - 2.1 ( 1.5 ) | ------------------ | 1.4 - 1.7 ( 1.6 ) |
| 34 | 2.1 - 3.3 ( 2.6 ) | ------------------ | 1.3 - 3.1 ( 2.1 ) |
| 35 | 1.7 - 4.0 ( 3.2 ) | ------------------ | 1.6 - 2.9 ( 2.0 ) |
| 36 | 1.7 - 3.6 ( 2.8 ) | ------------------ | 2.9 - 5.4 ( 4.0 ) |
| 37 | 3.9 - 4.7 ( 4.3 ) | 2.1 - 3.0 ( 2.5 ) | 2.4 - 5.6 ( 4.3 ) |
| 38 | 4.4 - 5.1 ( 4.9 ) | 2.7 - 4.3 ( 3.7 ) | 3.6 - 5.0 ( 4.4 ) |
| 39 | 4.4 - 5.7 ( 5.0 ) | 3.1 ( 3.1 ) | 2.9 - 5.0 ( 4.5 ) |

(continued)

Parasphenoid length (continued)

| | | | |
|---|---|---|---|
| 40 | ------------------- | 4.3 - 4.6 ( 4.4 ) | 4.1 - 5.7 ( 4.7 ) |
| 41 | 4.7 - 5.7 ( 5.2 ) | 4.0 - 4.4 ( 4.3 ) | 4.6 - 5.6 ( 4.8 ) |
| 42 | 4.9 - 5.7 ( 5.3 ) | 4.1 - 4.4 ( 4.3 ) | 3.7 - 5.4 ( 4.8 ) |
| 43 | 5.1 - 5.4 ( 5.2 ) | 4.3 - 4.7 ( 4.6 ) | 4.3 - 5.0 ( 4.7 ) |
| 44 | 5.3 ( 5.3 ) | 4.0 - 4.6 ( 4.3 ) | 4.4 - 5.1 ( 4.8 ) |
| 45 | 5.0 - 5.4 ( 5.1 ) | 4.0 - 4.3 ( 4.2 ) | 4.7 ( 4.7 ) |
| 46 | 4.1 - 4.7 ( 4.5 ) | 2.9 - 4.3 ( 3.9 ) | 4.3 - 5.7 ( 5.0 ) |
| 47 | 5.4 - 6.9 ( 6.1 ) | 4.3 ( 4.3 ) | 5.3 - 6.9 ( 6.2 ) |
| 48 | 8.3 - 10.0 ( 9.1 ) | 6.6 - 6.9 ( 6.8 ) | 6.3 - 7.7 ( 6.8 ) |
| 49 | 8.7 ( 8.7 ) | 9.4 - 10.3 ( 9.9 ) | 8.1 ( 8.1 ) |
| 50 | 10.0 - 12.3 (10.9 ) | 8.6 - 11.4 (10.1 ) | 10.3 - 12.4 (11.0 ) |
| 51 | 10.0 - 13.6 (11.4 ) | 9.3 - 11.9 (11.0 ) | 12.1 - 13.3 (12.6 ) |
| 52 | 10.0 - 14.3 (12.5 ) | ------------------- | 11.7 - 14.6 (13.1 ) |
| 53 | 9.7 - 15.6 (12.6 ) | ------------------- | 14.3 - 15.9 (14.9 ) |

Parasphenoid width

| | | | |
|---|---|---|---|
| 33 | .71 - 1.6 ( 1.1 ) | ------------------- | .71 - 1.0 ( .86) |
| 34 | 1.4 - 2.4 ( 2.0 ) | ------------------- | .71 - 3.0 ( 1.7 ) |
| 35 | 1.3 - 3.1 ( 2.1 ) | ------------------- | 1.0 - 2.4 ( 1.6 ) |
| 36 | 1.4 - 2.9 ( 2.1 ) | ------------------- | 1.1 - 3.0 ( 2.3 ) |
| 37 | 2.4 - 3.0 ( 2.7 ) | 1.6 ( 1.6 ) | 2.3 - 4.1 ( 3.0 ) |
| 38 | 3.3 - 3.6 ( 3.4 ) | 2.0 - 3.7 ( 2.5 ) | 2.0 - 2.6 ( 2.4 ) |
| 39 | 3.4 - 4.3 ( 3.8 ) | 3.1 ( 3.1 ) | 2.4 - 3.3 ( 2.8 ) |
| 40 | ------------------- | 3.1 - 3.7 ( 3.5 ) | 3.0 - 4.0 ( 3.5 ) |
| 41 | 3.4 - 4.4 ( 4.0 ) | 3.0 - 3.6 ( 3.2 ) | 2.9 - 4.3 ( 3.5 ) |
| 42 | 3.9 - 5.0 ( 4.4 ) | 3.1 - 3.6 ( 3.4 ) | 2.9 - 3.6 ( 3.4 ) |
| 43 | 4.0 - 4.4 ( 4.3 ) | 3.1 - 3.7 ( 3.5 ) | 2.9 - 3.6 ( 3.5 ) |
| 44 | 5.3 ( 5.3 ) | 2.9 - 3.6 ( 3.4 ) | 3.0 - 3.9 ( 3.6 ) |
| 45 | 4.4 - 4.9 ( 4.6 ) | 3.4 - 3.7 ( 3.6 ) | 3.6 ( 3.6 ) |
| 46 | 3.7 - 4.3 ( 4.1 ) | 3.1 - 4.4 ( 3.7 ) | 2.9 - 4.0 ( 3.6 ) |
| 47 | 5.4 - 6.4 ( 5.8 ) | 4.3 ( 4.3 ) | 4.9 - 6.9 ( 5.4 ) |
| 48 | 7.3 - 9.6 ( 8.3 ) | 6.0 - 6.4 ( 6.4 ) | 6.0 - 7.1 ( 5.7 ) |
| 49 | 12.6 (12.6 ) | 9.1 - 9.4 ( 9.3 ) | 7.4 ( 7.4 ) |
| 50 | 8.7 - 11.7 ( 9.5 ) | 8.9 - 10.8 ( 9.6 ) | 7.3 - 10.6 ( 9.3 ) |
| 51 | 7.9 - 14.3 (10.6 ) | 8.6 - 11.4 ( 9.7 ) | 9.9 - 11.1 (10.6 ) |
| 52 | 9.3 - 13.3 ( 9.7 ) | ------------------- | 9.7 - 12.3 (11.4 ) |
| 53 | 8.9 - 12.9 (11.1 ) | ------------------- | 12.3 - 15.0 (12.9 ) |

Parasphenoid length/width

| | | | |
|---|---|---|---|
| 33 | .7 - 1.9 ( 1.5 ) | ------------------- | 1.7 - 2.0 ( 1.8 ) |
| 34 | 1.0 - 1.7 ( 1.4 ) | ------------------- | .8 - 1.9 ( 1.4 ) |
| 35 | 1.2 - 2.2 ( 1.6 ) | ------------------- | 1.1 - 1.6 ( 1.3 ) |
| 36 | 1.2 - 1.6 ( 1.4 ) | ------------------- | 1.3 - 2.6 ( 1.7 ) |
| 37 | 1.5 - 1.6 ( 1.6 ) | 1.3 ( 1.3 ) | 1.0 - 1.6 ( 1.4 ) |
| 38 | 1.3 - 1.5 ( 1.4 ) | 1.2 - 1.3 ( 1.2 ) | 1.4 - 2.2 ( 1.8 ) |
| 39 | 1.2 - 1.5 ( 1.3 ) | 1.1 - 1.1 ( 1.1 ) | 1.0 - 2.1 ( 1.6 ) |
| 40 | ------------------- | 1.2 - 1.4 ( 1.3 ) | 1.2 - 1.4 ( 1.3 ) |

(continued)

Parasphenoid length/width (continued)

| | | | |
|---|---|---|---|
| 41 | 1.2 - 1.4 ( 1.3 ) | 1.2 - 1.4 ( 1.3 ) | 1.2 - 1.6 ( 1.4 ) |
| 42 | 1.1 - 1.3 ( 1.2 ) | 1.2 - 1.3 ( 1.2 ) | 1.2 - 1.9 ( 1.4 ) |
| 43 | 1.2 - 1.3 ( 1.2 ) | 1.2 - 1.5 ( 1.3 ) | 1.2 - 1.6 ( 1.4 ) |
| 44 | 1.0 ( 1.0 ) | 1.2 - 1.4 ( 1.3 ) | 1.2 - 1.5 ( 1.3 ) |
| 45 | 1.1 - 1.2 ( 1.1 ) | 1.2 - 1.2 ( 1.2 ) | 1.3 ( 1.3 ) |
| 46 | 1.1 - 1.2 ( 1.1 ) | .9 - 1.3 ( 1.0 ) | 1.3 - 1.5 ( 1.4 ) |
| 47 | 1.0 - 1.2 ( 1.1 ) | 1.0 ( 1.0 ) | 1.0 - 1.2 ( 1.1 ) |
| 48 | 9.3 - 1.1 ( 1.1 ) | 1.0 - 1.1 ( 1.1 ) | .9 - 1.2 ( 1.1 ) |
| 49 | 1.4 ( 1.4 ) | 1.0 - 1.1 ( 1,1 ) | 1.0 ( 1.0 ) |
| 50 | 1.0 - 1.2 ( 1.1 ) | .9 - 1.2 ( 1.0 ) | 1.0 - 1.4 ( 1.2 ) |
| 51 | .9 - 1.3 ( 1.1 ) | 1.0 - 1.4 ( 1.1 ) | 1.2 - 1.2 ( 1.2 ) |
| 52 | .9 - 1.2 ( 1.1 ) | ------------------- | 1.0 - 1.3 ( 1.2 ) |
| 53 | .9 - 1.2 ( 1.1 ) | ------------------- | 1.1 - 1.3 ( 1.2 ) |

Parasphenoid length/skull length

| | | | |
|---|---|---|---|
| 32 | 8.9 ( 8.9 ) | ------------------- | ------------------- |
| 33 | 15.4 - 32.8 (22.3 ) | ------------------- | 14.6 - 18.9 (17.2 ) |
| 34 | 31.3 - 51.5 (39.5 ) | ------------------- | 14.0 - 34.8 (23.1 ) |
| 35 | 25.7 - 59.7 (46.7 ) | ------------------- | 17.2 - 33.7 (23.2 ) |
| 36 | 29.8 - 57.1 (42.8 ) | ------------------- | 29.9 - 58.1 (40.1 ) |
| 37 | 49.3 - 65.0 (56.3 ) | 32.8 - 52.6 (39.4 ) | 25.8 - 56.7 (46.1 ) |
| 38 | 58.0 - 64.5 (60.7 ) | 42.1 - 64.0 (55.4 ) | 35.0 - 52.1 (39.7 ) |
| 39 | 54.6 - 70.3 (59.9 ) | 50.8 - 54.3 (52.2 ) | 47.3 - 52,1 (39.7 ) |
| 40 | ------------------- | 57.1 - 64.7 (60.3 ) | 51.8 - 64.0 (57.8 ) |
| 41 | 49.4 - 68.4 (61.3 ) | 51.3 - 62.8 (58.3 ) | 49.3 - 69.1 (59.3 ) |
| 42 | 66.2 - 71.6 (68.8 ) | 56.1 - 62.9 (59.6 ) | 50.0 - 68.3 (59.9 ) |
| 43 | 61.6 - 65.0 (63.5 ) | 61.4 - 69.6 (64.8 ) | 57.1 - 70.4 (64.1 ) |
| 44 | 76.8 (76.8 ) | 60.2 - 65.5 (62.6 ) | 56.6 - 72.4 (61.6 ) |
| 45 | 60.2 - 65.0 (62.6 ) | 57.1 - 64.1 (61.1 ) | 63.5 (63.5 ) |
| 46 | 54.6 - 62.0 (54.8 ) | 45.3 - 62.5 (54.4 ) | 53.0 - 70.3 (62.8 ) |
| 47 | 53.2 - 58.4 (55.8 ) | 53.0 (53.0 ) | 57.0 - 71.1 (65.9 ) |
| 48 | 55.1 - 58.3 (54.8 ) | 55.0 - 57.9 (56.6 ) | 60.3 - 66.3 (61.4 ) |
| 49 | 54.0 (54.0 ) | 54.3 - 57.3 (55.7 ) | 60.4 (60.4 ) |
| 50 | 53.4 - 63.9 (58.0 ) | 50.2 - 61.9 (56.9 ) | 50.7 - 56.6 (53.1 ) |
| 51 | 55.5 - 58.1 (56.8 ) | 51.9 - 59.2 (55.8 ) | 51.6 - 55.5 (54.0 ) |
| 52 | 55.2 - 65.0 (59.3 ) | ------------------- | 48.4 - 58.6 (54.2 ) |
| 53 | 52.7 - 61.4 (58.4 ) | ------------------- | 54.1 - 58.2 (56.0 ) |

Frontoparietal length

| | | | |
|---|---|---|---|
| 33 | .6 - .7 ( .6 ) | ------------------- | ------------------- |
| 34 | .7 - 1.4 ( 1.0 ) | ------------------- | .7 - 1.6 ( 1.2 ) |
| 35 | .9 - 2.0 ( 1.4 ) | ------------------- | 1.1 ( 1.1 ) |
| 36 | 1.0 - 2.1 ( 1.6 ) | ------------------- | 1.1 - 2.1 ( 1.6 ) |
| 37 | 1.6 - 2.3 ( 2.1 ) | 1.1 - 1.9 ( 1.5 ) | 1.7 - 4.0 ( 2.5 ) |
| 38 | 3.7 - 4.3 ( 4.0 ) | 2.4 - 4.3 ( 3.2 ) | 1.4 - 2.3 ( 1.9 ) |
| 39 | 3.1 - 4.3 ( 3.7 ) | 2.1 - 2.9 ( 2.5 ) | 2.0 - 4.4 ( 3.4 ) |
| 40 | ------------------- | 2.4 - 4.1 ( 3.4 ) | 4.4 - 4.9 ( 4.7 ) |
| 41 | 3.9 - 4.4 ( 4.2 ) | 3.6 - 3.9 ( 3.8 ) | 4.1 - 5.3 ( 4.7 ) |

(continued)

Frontoparietal length (continued)

| | | | |
|---|---|---|---|
| 42 | 4.3 - 5.0 ( 4.6 ) | 3.6 - 4.0 ( 3.9 ) | 4.6 - 5.1 ( 4.8 ) |
| 43 | 4.4 - 5.4 ( 4.8 ) | 4.1 - 4.7 ( 4.3 ) | 4.7 - 5.1 ( 4.9 ) |
| 44 | 4.4 ( 4.4 ) | 3.7 - 4.6 ( 4.2 ) | 4.7 - 5.1 ( 4.9 ) |
| 45 | 5.0 - 5.4 ( 5.1 ) | 4.0 - 4.3 ( 4.2 ) | 5.1 ( 5.1 ) |
| 46 | 4.3 - 4.9 ( 4.6 ) | 4.1 - 4.6 ( 4.3 ) | 4.7 - 5.1 ( 5.0 ) |
| 47 | 5.7 - 6.9 ( 6.3 ) | 4.6 ( 4.6 ) | 5.7 - 6.9 ( 5.7 ) |
| 48 | 6.6 - 9.0 ( 7.9 ) | 6.0 - 6.7 ( 6.3 ) | 6.4 - 8.6 ( 7.0 ) |
| 49 | 8.6 ( 8.6 ) | 8.6 - 9.9 ( 9.3 ) | 8.6 ( 8.6 ) |
| 50 | 8.9 - 10.7 ( 9.6 ) | 8.9 - 13.1 ( 9.8 ) | 10.7 - 12.1 (11.3 ) |
| 51 | 8.9 - 12.9 (10.0 ) | 8.9 - 11.4 (10.4 ) | 10.3 - 12.6 (11.8 ) |
| 52 | 8.0 - 13.9 (11.2 ) | -------------------- | 11.7 - 14.3 (13.1 ) |
| 53 | 9.6 - 14.6 (11.7 ) | -------------------- | 13.1 - 16.0 (13.8 ) |

Frontoparietal length/skull length

| | | | |
|---|---|---|---|
| 33 | 8.0 - 10.0 ( 8.7 ) | -------------------- | -------------------- |
| 34 | 11.2 - 19.7 (15.5 ) | -------------------- | 8.0 - 18.0 (13.0 ) |
| 35 | 13.4 - 30.3 (23.1 ) | -------------------- | 12.8 (12.8 ) |
| 36 | 16.6 - 31.7 (24.2 ) | -------------------- | 11.8 - 20.3 (15.6 ) |
| 37 | 20.2 - 32.3 (26.4 ) | 17.1 - 33.3 (25.2 ) | 18.3 - 40.0 (27.1 ) |
| 38 | 48.1 - 53.0 (49.8 ) | 37.5 - 58.1 (47.7 ) | 13.6 - 26.7 (20.2 ) |
| 39 | 36.0 - 54.4 (44.6 ) | 35.0 - 47.5 (41.5 ) | 20.0 - 55.6 (40.4 ) |
| 40 | -------------------- | 33.8 (33.8 ) | 55.0 - 62.0 (58.1 ) |
| 41 | 48.3 - 58.9 (54.3 ) | 46.3 - 56.5 (52.3 ) | 51.2 - 65.4 (57.4 ) |
| 42 | 53.4 - 67.5 (59.5 ) | 51.4 - 56.4 (54.3 ) | 58.7 - 64.5 (61.0 ) |
| 43 | 53.0 - 68.3 (58.5 ) | 57.7 - 67.1 (61.6 ) | 61.0 - 70.4 (66.1 ) |
| 44 | 63.7 (63.7 ) | 57.9 - 65.6 (60.6 ) | 58.1 - 68.1 (63.4 ) |
| 45 | 58.1 - 65.0 (61.1 ) | 56.5 - 62.3 (59.3 ) | 68.9 (68.9 ) |
| 46 | 55.4 - 64.7 (58.2 ) | 51.8 - 67.2 (58.1 ) | 61.0 - 62.9 (62.0 ) |
| 47 | 53.2 - 60.5 (57.3 ) | 56.8 (56.8 ) | 57.0 - 71.2 (65.1 ) |
| 48 | 46.1 - 54.8 (50.0 ) | 50.0 - 55.3 (52.2 ) | 56.3 - 73.4 (64.8 ) |
| 49 | 53.4 (53.4 ) | 50.9 - 53.9 (52.4 ) | 64.1 (64.1 ) |
| 50 | 48.6 - 68.9 (53.2 ) | 48.1 - 61.3 (54.3 ) | 50.6 - 59.6 (54.4 ) |
| 51 | 46.8 - 55.1 (50.0 ) | 46.7 - 61.0 (53.0 ) | 47.0 - 51.9 (50.8 ) |
| 52 | 44.7 - 58.9 (52.7 ) | -------------------- | 49.5 - 64.1 (54.3 ) |
| 53 | 42.2 - 62.6 (53.0 ) | -------------------- | 49.8 - 55.3 (52.2 ) |