X. *The Hyoid and Larynx of the Anura.*

By Ethelwynn Trewavas, *B.Sc.*

(*Communicated by* C. Tate Regan, *F.R.S.*)

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FOREWORD.

Some years ago Dr. TATE REGAN suggested to me that a study of the hyoid region of the tailless Amphibia would be of value. This paper is the outcome of that suggestion. It was begun when I was Gilchrist Research Scholar in Zoology at King's College of Household and Social Science (1925–26 and 1927–28), working under Dr. P. C. ESDAILE, to whom I am very grateful for her help during my two and a half years in her department. At this time I was also assisted by a Government Grant from the Royal Society. Since March, 1928, I have held a post at the British Museum (Natural History), and the work on frogs has been relegated to spare time.

My main purpose has been to discover and make known the structures of the hyolaryngeal apparatus in a large and representative series of the Anura, in order that an idea may be gained of the range of diversity of these organs in the group, and of the extent to which resemblances in their structure are indicative of relationship. In all, I have studied sixty species, belonging to thirty-six genera ; in fifty of these species and twenty-three of the genera the larynx is now described for the first time.

HISTORICAL SUMMARY.

DUGÈS (1835) made some comparative studies on the hyoid and larynx in European species, but the foundation of comparative work from the point of view adopted here was laid by HENLE (1839) in his "Beschreibung des Kehlkopfs," in which twenty-one Anuran species are dealt with, some in more detail than others. One of his most striking statements was that the cartilago cricotrachealis of *Discoglossus pictus* consists of separate right and left halves and thus represents a condition found in the larvæ of other Anura. This statement has been accepted by subsequent authors (GOEPPERT, WILDER), but has not been confirmed by later work, and HENLE was probably dealing with another species (perhaps a very young common toad ?).

GOEPPERT (1895 and 1898) and WILDER (1892 and 1896) were chiefly concerned in tracing the homologies of the skeletal and muscular parts of the larynx in Urodela, Anura and (GOEPPERT) Reptilia. EDGEWORTH (1920) had the same aim, extended to the whole vertebrate series, and adduced developmental evidence. GOEPPERT referred to HENLE'S and (1898) WILDER'S work for most of his comparative Anuran data, but himself described fully the larynx of *Rana temporaria*, and had sections of young stages of this species and of *Xenopus* and *Bombina bombina*. WILDER (1896) and his pupil, Miss FRAZIER (1924), examined the laryngeal skeleton in twenty-one species of Anura, and the muscles (WILDER) in some of these. They discovered in the Anuran larynx a greater diversity than had been expected, and recognized that further study was required before generalizations could be made.

A useful contribution to the study of the comparative histology of the skeletal parts of the Anuran larynx was published in 1930 by BLUME, who also made reconstruction-models from his serial sections. He studied twenty-eight representative species, and, still finding his knowledge not extensive enough to estimate the phylogenetic value of these structures, summarized his results by describing a number of larynx-types.

These are the chief works leading up to the present study, and others are referred to in the text. Among these, of special importance are those of BEDDARD (1907 *a* and *b* and 1911) on Pelobatidæ, and of GRÖNBERG (1894) and RIDEWOOD (1897 *a* and 1900) on Aglossa. GAUPP'S (1896, 1899 and 1901) thorough and accurate account of the larynx of *Rana esculenta* is the standard work of reference on the subject.

SCOPE AND METHODS.

Members of every family of the Anura have been studied, except the Aglossa, which have been omitted because good descriptions of their hyolaryngeal apparatus already exist, [HENLE (1839), RIDEWOOD (1897 *a* and 1900), and GRÖNBERG (1894, p. 636)], and also because their position in the system is isolated and comparatively well established, and can hardly be improved by further study of the parts in question.

The hyolaryngeal apparatus has been studied as a whole, that is, the hyoid, the muscles attached to it, the laryngeal cartilages and muscles. *Musculus intermandibularis* is also reported upon, since it is so closely associated with *m. interhyoideus*, and had to be dissected away. Histological study has not come into the purpose of the investigation, and the interior of the larynx and the minute cartilages of the vocal chords are, therefore, usually not described, unless they can be seen in dissection.

The hyoid and larynx, with their muscles, were dissected out and studied under a binocular dissecting-microscope. This was sometimes followed by staining with toluidin blue and clearing in oil of wintergreen, but this method was used sparingly, as it leaves the muscles in a condition unsuitable for further study or reference. A few larynxes were sectioned for the determination of special points.

Where possible, two or more specimens of a species, or, failing this, of a genus, were dissected, preferably representing both sexes, but some species are so rare in the collections available to me that this was impossible. Where it could be checked, however, the amount of individual variation was very slight, and the allowances to be made for sexual differentiation, where only one sex is known, can usually be judged by comparison with other species. *Rana esculenta* shows some individual variation in the shape of the anterior process of the hyoid. In *Pelobates fuscus*, KOTHE (1910) has shown variation to exist in the amount of disintegration of the hyale, which is always reduced in this species, and apparently there may or may not be some reduction of the hyale in *Bufo marinus* (see* p. 457). BIGALKE (1927) found, in *Bufo vulgaris*, that the omohyoid muscle, usually present, was exceptionally absent, and that the second posterior petrohyoid was exceptionally present, but on one side only. Otherwise the muscles are subject to very little individual variation.

Sexual differentiation is usually expressed in size of the larynx, and may also involve a difference in the development of the œsophageal process of the cricoid. Certain sesamoid cartilages of the larynx may be present in the male and absent in the female, notably in the Hylidæ.

MATERIAL.

I am indebted for my material to the following persons and institutions :—

THE BRITISH MUSEUM (Natural History) [B.M.N.H.] ; THE ZOOLOGICAL SOCIETY OF LONDON [Zool. Soc.] ; THE PERCY SLADEN TRUST FUND collection of Professor J. P. HILL [SLADEN] ; Professor J. P. HILL, F.R.S. (for specimens from his private collection) ; Dr. MALCOLM SMITH ; Mr. G. ARCHEY of the Auckland Museum, New Zealand ; Miss P. C. ESDAILE, D.Sc. ; Mrs. A. S. CORBET, B.Sc. (my sister).

To all of whom I give my sincere thanks, and also to Mr. H. W. PARKER of the British Museum (Natural History), not only for allowing me to use Museum material, but also for identifying some of the specimens obtained from other sources, and for several profitable suggestions. The sources of the specimens are acknowledged in square brackets at the head of each description, the first three abbreviated as shown above.

TERMINOLOGY.

The terminology used in this paper is based on that found in GAUPP'S (1896 and 1901) edition of ECKER'S and WIEDERSHEIM'S "Anatomie des Frosches." The terms are used either in their original (Latin) form or in their English form. Certain exceptions and additions have been made and are given below, with reasons.

1. *Musculus intermandibularis anterior* and *posterior* of this paper are *m. submentalis* and *m. submaxillaris* of GAUPP. *M. interhyoideus* of this paper is *m. subhyoideus* of GAUPP.

These names have already been used by other authors and their use brings the terminology of these muscles into line with that of other vertebrates.

GAUPP'S names have, however, been retained for the *mm. petrohyoidei*, although it is known that they represent the *levatores arcuum branchialium*, for the old name is more descriptive of their relations in Anura (as long as the word " hyoid " is retained for the whole hyobranchial skeleton), and does not suggest any false homologies.

2. *Laryngeal muscles.* GAUPP'S names have been retained for *m. dilatator laryngis*, and for its parts when it is subdivided, but new names are used for the remaining laryngeal muscles.

In this Paper.	GAUPP.
m. constrictor laryngis externus	m. hyolaryngeus.
m. constrictor laryngis anterior	m. sphincter laryngis anterior.
m. constrictor laryngis posterior	m. sphincter laryngis posterior.

EDGEWORTH (1920) states that, in Amphibia, two sets of intrinsic laryngeal muscles are met with, the *laryngei*, surrounding the arytænoids in front of the dilatator, and the *constrictor laryngis*, behind the dilatator. GOEPPERT (whose terminology is adopted by GAUPP) considered that in Anura the " *hyolaryngeus* " represents the *laryngei* and the " *sphincteres anterior* and *posterior* " the *constrictor*, which he calls " *sphincter laryngis.*" EDGEWORTH, however, points out that, as all three muscles in Anura are behind the insertation of the *dilatator*, the probability is that they are all derived from the *constrictor* and that the *laryngei* are absent. WILDER (1896) had previously suggested, on comparative anatomical grounds, that the "hyolaryngeus" of GOEPPERT was derived from the constrictor, and EDGEWORTH brought forward developmental evidence in support of this hypothesis.

In this paper, therefore, EDGEWORTH'S term *constrictor laryngis* (= *constrictor aditus laryngis* of HENLE and other authors ; see EDGEWORTH 1920, p. 127) is used to denote all the (primitively) intrinsic laryngeal muscles of the Anura. The diversity of forms and functions of the parts of the constrictor in the group has induced me to discard the word " sphincter," and to use the term " constrictor " in a morphological sense. EDGEWORTH called GOEPPERT'S " hyolaryngeus " " constrictor laryngis posterior," but the adjective posterior is suitable only in the early developmental stages, and I have therefore applied it to the muscle which bears it in GOEPPERT'S terminology, and have used " externus " to indicate the extra-laryngeal attachment of the " hyolaryngeus."*

3. *Orientation of the Larynx.*—The tilt of the larynx is so various, even in different species of the same genus, that the terms " dorsal," " ventral," " anterior," and " posterior "

* The terminology of the laryngeal muscles was decided upon in consultation with Professor EDGEWORTH, to whom, for this and for his continued interest in the work, I wish to express my warm thanks.

are not always easily applied. They are used in this paper, except where ambiguity may result, when the terms "pharyngeal" and "cardiac," as introduced by WILDER, are substituted.

4. *Skeleton of the Larynx.*

In this Paper.	GAUPP.
cricoid	cartilago crico-trachealis.
œsphageal process (of cricoid)	spina œsophagea.
articular process (of cricoid)	processus articularis posterior.
cardiac process (of cricoid)	processus articularis anterior.
muscular process (of cricoid)	processus muscularis.
bronchial process (of cricoid)	processus trachealis + proc. pulmonalis.
lateral process (of cricoid)	(not named).

BLUME (1930) has already noticed that the term "spina" is not always applicable to the œsophageal process, and has replaced it by "processus." "Articular," "cardiac" and "bronchial processes" are terms used by WILDER, and are adopted here for the reason given under (3) above, and for the sake of brevity. For the sake of brevity also WILDER'S term for the muscular process is not used. The lateral process is very small in *Rana*, and is described, but not named, by GAUPP; it is better developed in some other Anura, and is the process by which the cricoid articulates with the end of the postero-medial process of the hyoid, either directly or by means of a ligament; it is named "tuberculum hyoideum" by BLUME.

5. *Thyroid membrane.*—This membrane spans the gap between the postero-lateral and postero-medial processes of the hyoid, and often includes or surrounds the thyroid gland. It is described, but not named, by GAUPP.

The following description of the hyolaryngeal apparatus of *Leptodactylus ocellatus* is intended to introduce the terminology, and to supply a standard of comparison for other species.

Leptodactylus ocellatus.

Hyolaryngeal apparatus described in detail as a generalized Anuran type.

Male, 97 mm., and female, 80 mm. from snout to vent, from South America. [ZOOL. SOC. and B.M.N.H.]

Hyoid and laryngeal skeleton.—The width of the hyoid plate is about one and a half times its median length. The hyoglossal sinus is deep, extending behind the level of the alary processes; these are lobes with narrow bases. The hyale is slender with the anterior process represented by a blunt expansion. The postero-lateral processes are slender. Each postero-medial process is composed of a slim bony shaft, expanding posteriorly to end in a short cartilaginous epiphysis.

The *arytænoid* is more deeply concavo-convex in the male than in the female; its pharyngeal apex is acute and somewhat produced; small *pulvinaria vocalia* cap the corners to which the vocal chords are attached. There are no *apical cartilages*, and if the vocal chords possess *basal cartilages* no trace of them is visible in dissection.

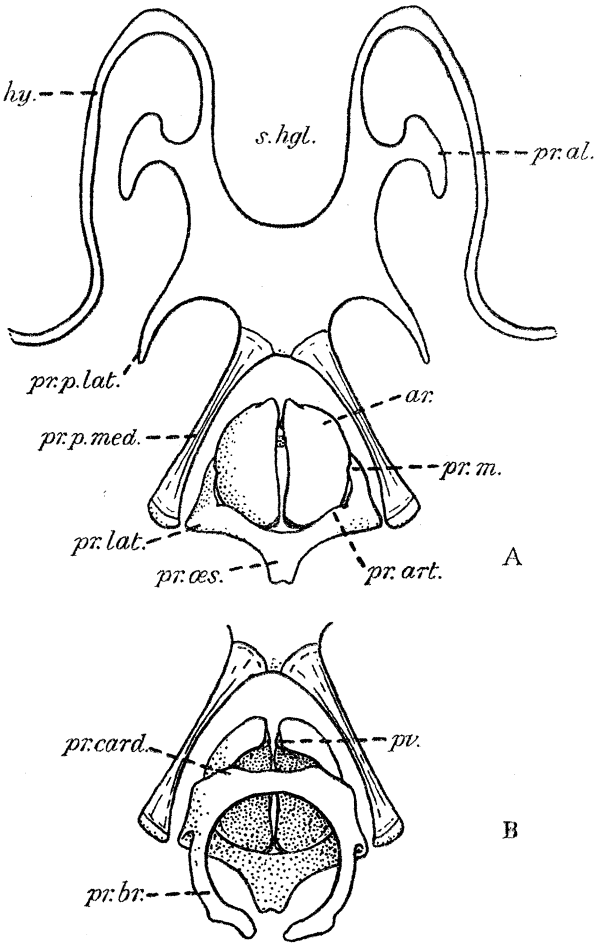

FIG. 1.—*Leptodactylus ocellatus*. A. Hyoid and laryngeal skeleton, dorsal view. B. Laryngeal skeleton, ventral view. × 2⅔. For key to lettering in this and subsequent figures see p. 525.

The *cricoid* forms a complete ring, articulating with the arytænoid by inconspicuous *articular* and low, broad *cardiac processes*, and with the epiphysis of the postero-medial process by a ligament (the *hyocricoid ligament*) attached to a well-marked *lateral process*. There is a short *muscular process* on each side. The *œsophageal process* is short, bluntly bifid distally. Each *bronchial process* curves over the ventral side of the root of the lung, almost to the middle line.

Muscles.—M. intermandibularis anterior extends from right to left ramus of the lower jaw immediately behind the symphysis. *M. intermandibularis posterior* forms a thin sheet of muscle across the floor of the mouth, for the whole extent of the lower jaw,

with a median linea alba. Its fibres are approximately transverse. The small anterior region lying below m. intermandibularis anterior is aponeurotic.

M. interhyoideus appears as a posterior continuation of m. intermandibularis near the middle line, but laterally takes its origin from the up-curved part of the hyale.

M. sternohyoideus (paired) is one of the ventral body-muscles supplied by the hypoglossal nerve. Its greater part is a continuation of the rectus abdominis from the latter's last tendinous inscription, but its ventral strip and its *pars dorsalis* arise from the sternum. The *pars dorsalis* crosses the rest of the muscle obliquely, and is the most posteriorly inserted part, being attached to the ventral surface of the thyroid membrane, outside the thyroid gland. The rest of the muscle is attached to the lateral part of the ventral surface of the hyoid plate from the alary to the postero-medial process, the ventral slip being the most anteriorly inserted.

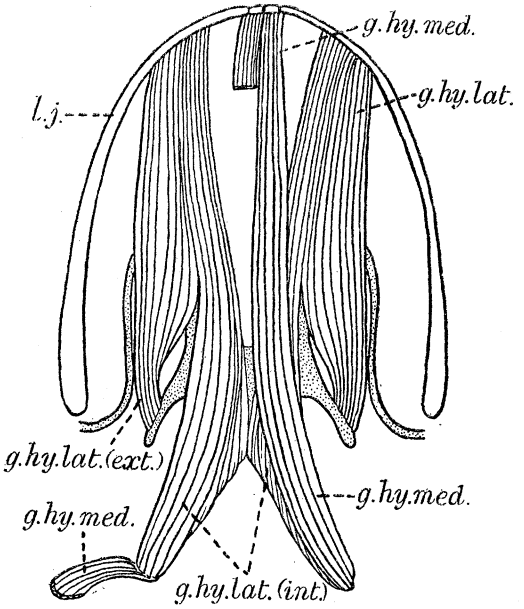

FIG. 2.—*Leptodactylus ocellatus*. M. geniohyoideus, showing its attachments to lower jaw and hyoid. × 1⅘. M. medialis is shown complete on one side only.

M. omohyoideus (paired) is one of the same series of muscles. Its origin is on the ventral end of the scapula, and its insertion on the edge of the hyoid between the postero-lateral and postero-medial processes.

M. hyoglossus originates in two halves from the ventral surface of the posterior end of the postero-medial process; the halves join below the hyoid plate and the single muscle runs into the tongue. The hyoglossal sinus is spanned by a membrane which is a specialized part of the sheath of this muscle.

M. geniohyoideus (paired) is also supplied by the hypoglossal nerve. It consists of two parts, a ventral, superficial *m. geniohyoideus medialis*, and *m. geniohyoideus lateralis*. Both are attached in front to the lower jaw, m. medialis adjacent to its fellow

near the middle line, and m. lateralis more laterally. The attachments of both may be partly on the tendon or sheath of m. intermandibularis anterior. M. lateralis divides into two posteriorly, the *external* part passing outside the hyoid end of the sternohyoid to an insertion on the postero-lateral process of the hyoid, the *internal* part extending inside the sternohyoid, spreading over the hyoglossal muscle, to be inserted round the edges of the paired part of the latter, that is, at the end of the postero-medial process and on its inner edge or, in part, on the hyo-arytænoid membrane. M. medialis is not divided, but lies on the ventral side of the internal part of m. lateralis, and is attached to the end of the postero-medial process.

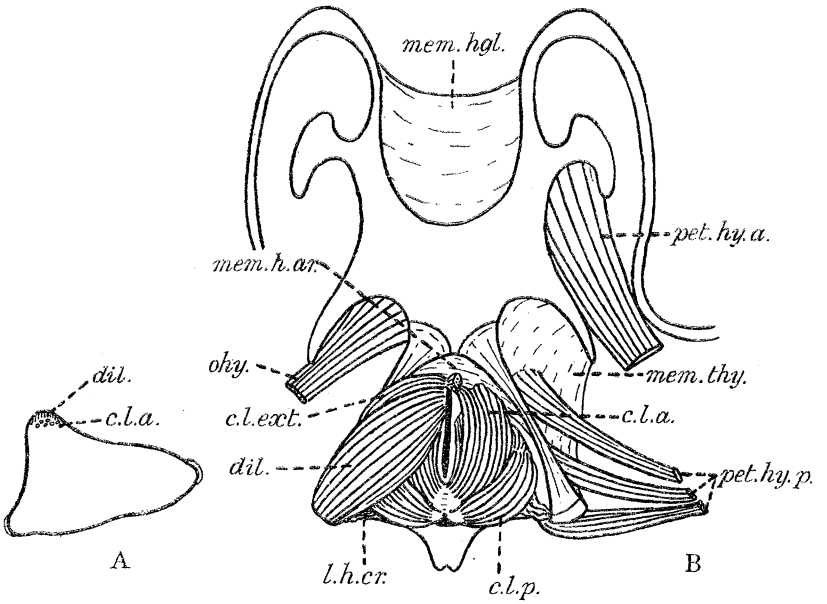

FIG. 3.—*Leptodactylus ocellatus*. Hyoid and larynx, dorsal. × 2⅔. On the right the hyoid muscles are shown, m. dilatator laryngis is removed and m. constrictor lar. externus is cut short. On the left the thyroid membrane is removed to show the attachment of m. omohyoideus. A. Lateral view of left arytænoid, showing muscle-insertions.

GAUPP thought that m. medialis also divided to go to both insertions. It may be that this sometimes occurs in *Rana esculenta*, but in some specimens of that species I have found it as here described, and this is certainly the usual Anuran condition. It has been accurately described by BIGALKE (1927) in *Bufo vulgaris*.

M. petrohyoideus anterior originates on the otic region of the skull, and is inserted on the lateral edge of the hyoid plate. It is supplied by the glossopharyngeal nerve.

There are three *mm. petrohyoidei posteriores*, arising on the skull adjacent to m. anterior; the first two are inserted on the lateral edge of the bony shaft of the postero-medial process, the last on its cartilaginous epiphysis, and on the hyo-cricoid ligament. All three are supplied by branches of the vagus nerve.

M. dilatator laryngis has its origin on the dorsal surface of the postero-medial process, and its insertion on a narrow area at the pharyngeal apex of the arytænoid.

M. constrictor laryngis externus is attached to the postero-medial process immediately in front of the dilatator and meets its fellow in a narrow raphe in front of the arytænoid.

M. constrictor anterior ends in front partly in the raphe of the constrictor externus, partly on the hyo-arytænoid membrane. Behind, it is attached, with its fellow, to a membrane crossing both arytænoids. A specialized fibrous tract of this membrane extends postero-laterally on each side to the cricoid. It is the inter-cricoid ligament, and is continuous on each side with the hyo-cricoid ligament, which joins the cricoid to the end of the postero-medial process.

A few fibres of the constrictor anterior which are adjacent to the arytænoid, end on the apex of this cartilage, close to the dilatator. This, however, is exceptional in the group.

M. constrictor posterior is attached at each end by a minute tendon to a pulvinar vocale, the fibrous cap at the corner of the arytænoid. Midway it is interrupted by an attachment to the muscular process of the cricoid.

The *vocal chord* has a prominent posterior lip; it is attached by a basal membrane to the base of the arytænoid. The membrane is strengthened by a median frenulum, as in *Rana esculenta*.

The larynxes of male and female are alike in structure, but that of the male is larger, filling the laryngeal sinus, whereas that of the female is considerably smaller than the sinus.

Liopelmidæ.

Liopelma hochstetteri, Fitzinger.

Range, North Island, New Zealand.

Female, 30½ mm. from snout to vent, from North Island, New Zealand. [Mr. G. Archey.]

Hyoid and Laryngeal Skeleton.—Width of hyoid plate a little greater than its median length. A median flat parahyoid bone, shaped like a pair of thick arcs united by their convex edges, inseparably fused to the ventral surface of the hyoid plate. Hyale with a slight expansion in place of an anterior process. Alary process absent; postero-lateral process short, simple; postero-medial process stout, hour-glass shaped, with triangular cartilaginous epiphysis.

Arytænoid strongly concavo-convex, with produced, acute pharyngeal corner projecting forwards. No pulvinaria vocalia or apical cartilage. *Cricoid* a complete ring, with no well-marked processes, except the bronchial processes, of which the right is simple, the left forked distally.

Muscles.—*M. intermandibularis anterior* relatively small, *posterior* typical. *M. interhyoideus* typical.

M. sternohyoideus inserted in its entirety on an oval area on the ventral surface of the hyoid plate, well separated from its fellow.

M. omohyoideus well developed, with insertion on the hyoid adjacent to m. sternohyoideus.

M. geniohyoideus lateralis and *medialis* inserted together on the antero-lateral part of the hyoid plate, immediately in front of m. sternohyoideus, not divided into external and internal portions.

M. hyoglossus originating from the ventral surface of the posterior part of the bony postero-medial process and its cartilaginous end.

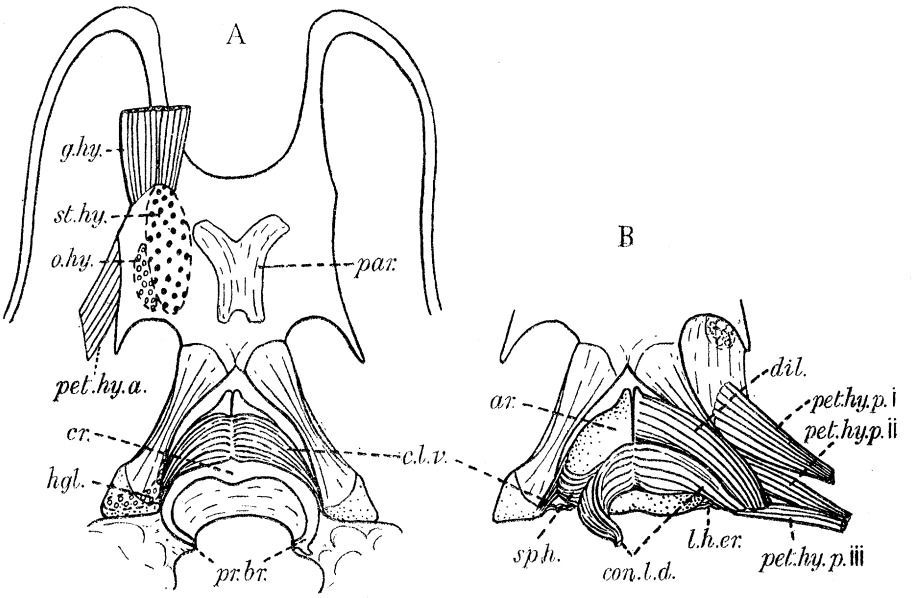

FIG. 4.—*Liopelma hochstetteri*. A. Hyoid and larynx, ventral. B. Larynx, dorsal, with dilatator removed on the left. × 8½. *c.l.v.* and *c.l.d.* ventral and dorsal hyoid slips of m. constrictor laryngis; *sph.* " sphincteric " portion of this muscle.

M. petrohyoideus anterior small, attached to the edge of the hyoid plate.

Three *petrohyoidei posteriores*, the first ending on the thyroid membrane near the middle of the postero-medial process, the second and third distinct only at their attachments to the lateral and posterior edges respectively of the epiphysis of the postero-medial process.

M. dilatator laryngis with a broad attachment to the arytænoid. *Constrictor* musculature consisting of a deep thin layer, which is a sphincter with dorsal and ventral raphes, and a superficial layer divided into a pair of dorsal constrictors, extending from the end of the postero-medial process to the dorsal raphe of the sphincter, and a pair of ventral constrictors extending from the same place on the postero-medial process to the ventral raphe of the sphincter.

A second specimen, a young female, 26 mm. from snout to vent, was also dissected, and resembles the specimen described above in all essentials: the hyale, however, is

relatively broader and stronger, a juvenile character; small alary processes, not expanded, are present; the os parahyoideum is relatively broader and is more asymmetrical in shape; the attachment of the hyoglossus is continued round the inner edge of the shaft of the postero-medial process on to its dorsal surface, more on the right than on the left side; the sphincteric portion of m. constrictor laryngis is very feeble and consists of only a few, deep, posterior fibres.

Discoglossidæ.

Discoglossus pictus, Otth.

Range, Western Mediterranean region.

Female, 56½ mm. from snout to vent. [Zool. Soc.]

Hyoid and Laryngeal Skeleton.—Median length of hyoid plate less than one-third its width, in which are included large alary processes occupying the whole lateral edge of the hyoid with the exception of short postero-lateral processes; hyoglossal sinus

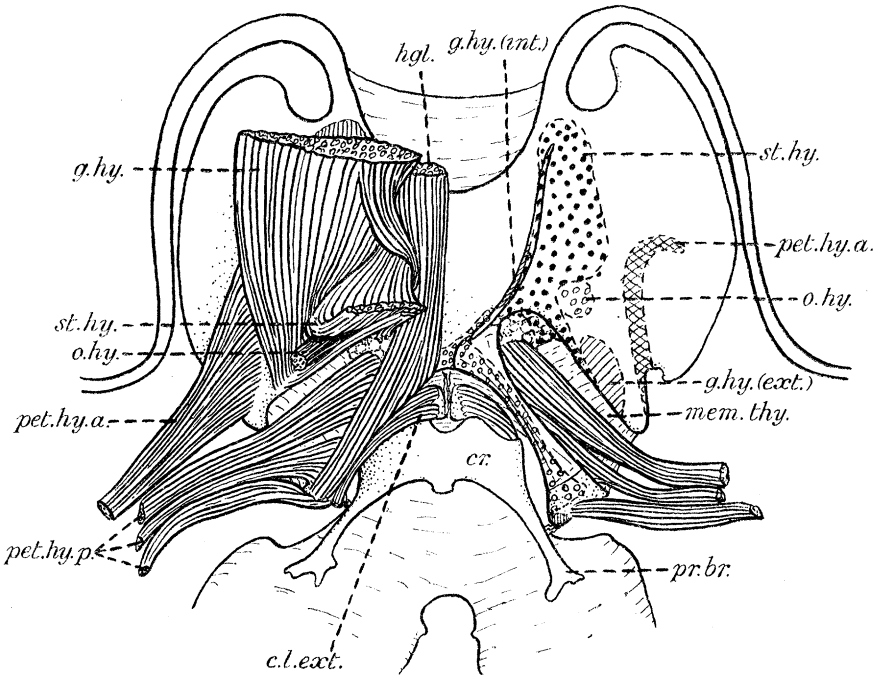

Fig. 5.—*Discoglossus pictus*. Hyoid and larynx, ventral. × *ca.* 6. Most of the muscles of the left side are removed, including m. constrictor laryngis externus. The insertions of hyoid muscles are shown by diagrammatic shading; three of these extend on to the parahyoid bone, which is not labelled.

fairly deep. A pair of splint bones (*parahyoids*) attached to ventral surface of hyoid plate. *Hyale* without anterior process. Postero-medial process typical, with expanded cartilaginous end.

Arytœnoid with produced, acute pharyngeal corner, without apical cartilages or pulvinaria. *Cricoid* a complete ring; œseophageal process represented by a broad plate

with a small median fenestra; no lateral or muscular processes; a paired cardiac process and a short median posterior cardiac process present; bronchial process expanded distally with short digitform branches.

Muscles.—Mm. intermandibularis and *interhyoideus* typical.

M. sternohyoideus inserted on a broad area on the hyoid, its inner fibres on the parahyoid bone, well separated from its fellow; *pars dorsalis* distinct, with insertion continuous with that of main muscle, on inner edge of postero-lateral process.

M. omohyoideus inserted at the angle between postero-lateral and postero-medial processes.

Mm. geniohyoideus lateralis and *medialis* forming a single muscle the bulk of which passes outside the sterno-hyoid to the external insertion on the postero-lateral process, a small superficial slip turning inwards between sterno-hyoid and hyoglossal muscles to be inserted on the parahyoid bone.

M. hyoglossus originating from ventral surface of whole length of postero-medial process, and a few fibres from posterior end of parahyoid bone.

M. petrohyoideus anterior rather small, inserted on ventral surface of hyoid at base of alary process.

Three *petrohyoidei posteriores*, the first two inserted on the lateral edge of the bony shaft of the postero-medial process, the last on the posterior edge of its cartilaginous tip.

M. dilatator laryngis with typical attachments to postero-medial process and arytænoid. *Constrictor* musculature consisting of a broad sphincter with dorsal and ventral raphes, and a *constrictor externus*, extending on each side from the ventral raphe of the sphincter to the posterior end of the postero-medial process.

Previous Work on Discoglossus.—HENLE'S account of the larynx (1839, pl. I, fig. 39) differs so much from the above that it must refer to a young specimen or to a different species. He stated that the cricoid is incomplete dorsally and ventrally, consisting of a pair of lateral cartilages, each with a posterior out-growth, the bronchial process. The " compressor " of the larynx was said to be like that of *Bufo*.

The hyoid figured by W. K. PARKER (1881, Plate xx, fig. 10), and ascribed to this species, is so different from the above that it must belong to a different genus.

FUCHS (1929) correctly described the hyoid and parahyoid, and BLUME (1930, p. 397, text-fig. 107) described and figured the skeleton of the larynx. His specimens agree closely with mine in the structure of the cricoid, but his figure, from a model reconstructed from sections, does not adequately show the shape of the arytænoids.

No complete description of the hyolaryngeal muscles has heretofore been given.

Alytes obstetricans (Laurenti).

Range, middle and western Europe.

Two females, 38 and 40 mm. from snout to vent. [ZOOL. SOC.]

Hyoid and Laryngeal Skeleton.—Hyoid like that of *Discoglossus*, but with the parahyoid bones united by a cross bar near their posterior ends. It has been figured and described by HENLE (1839, Plate 2, fig. 24), W. K. PARKER (1881, Plate 24, fig. 4), and RIDEWOOD (1898), who also described its development.*

The *larynx* is very similar to that of *Discoglossus*, but with the œsophageal process represented by a loop of cartilage, open anteriorly, and with the whole ring more slender. It was described incompletely by HENLE (*loc. cit.*) and, thoroughly, by WILDER (1896, pp. 285–6 and 310, fig. 37). WILDER found the "annulus" (cricoid) incomplete ventrally, but this is not so in my specimens, nor in those recently described by BLUME (1930, pp. 404–407, text-figs. 116–118), whose account agrees with my finding, with the addition that, in a male specimen, he found a minute nodule of cartilage in each vocal chord.

The laryngeal muscles have already been described by WILDER (*loc. cit.*), and are like those of *Discoglossus*.

Hyoid Muscles.—*M. sternohyoideus* inserted on the hyoid plate and on the parahyoid bone.

M. omohyoideus inserted on the hyoid plate, adjacent to m. sternohyoideus.

M. geniohyoideus arising anteriorly in two parts in the typical manner, but lying entirely outside m. sternohyoideus and with a single insertion on the medial side of the base of the postero-lateral process.

M. hyoglossus arising from the anterior half of the ventral surface of the postero-medial process, and from the parahyoid bone; inserted in the tongue.

A small *petrohyoideus anterior* and three typical *petrohyoidei posteriores* present.

Bombina.

Several authors, from DUGÈS (1835) onwards, have figured the hyoid of *Bombina*, which is like that of *Alytes* in shape, but with large paired endochondral ossifications. FUCHS (1929) found in *B. variegata* (= *pachypus*) a minute bone between the hyoglossal muscle and the posterior end of the hyoid plate, and believes this to represent the parahyoid of *Discoglossus* and *Alytes*. This ossicle is absent in *B. bombina* (=*igneus*), and is not always found in *B. variegata*. FUCHS found it by means of microscopical sections; my dissections fail to reveal it.

The skeleton of the larynx is also well known from the descriptions of HENLE (1839) and WILDER (1896)† and recently BLUME (1930) has redescribed it from sections in *B. bombina* and *B. variegata*.

Small arytænoids lie at the anterior end of a "resonance-box" (WILDER) formed of the greatly broadened cricoid, which, however, is narrower at the sides, where the

* DUGÈS' figure (1835) of the hyoid of *Obstetricans vulgaris* is evidently not of this species, but is more like that of *Bombina*.

† WILDER'S description (like his figure) is correct and has evidently been misunderstood by BLUME (1930, p. 400).

anterior parts of the dorsal and ventral cricoid shields are joined by muscle. This muscle is a backward continuation of the sphincter-like *constrictor laryngis* and its relations are best understood if the dorsal and ventral parts of the cricoid are imagined as growing forwards into the dorsal and ventral lineæ albæ of a broad *constrictor*. Not only, as in *Discoglossus* and *Alytes*, is there no *constrictor anterior*, but there is also no *constrictor externus* differentiated.

The *hyoid musculature* was briefly described by WALTER (1887, Plate 2, figs. 14, 15). The following description is based on dissections of two males (38 mm. from snout to vent) and a female (43 mm.) of *Bombina variegata*.

Mm. interhyoideus and *intermaxillaris* typical.

M. sternohyoideus with main insertion in a broad area on the hyoid plate, surrounding the hyoglossal sinus and nearly reaching the middle line behind it; insertion of *sterno-hyoideus dorsalis* separated from this by *m. omohyoideus*, on thyroid membrane, adjacent to anterior end of postero-medial process.

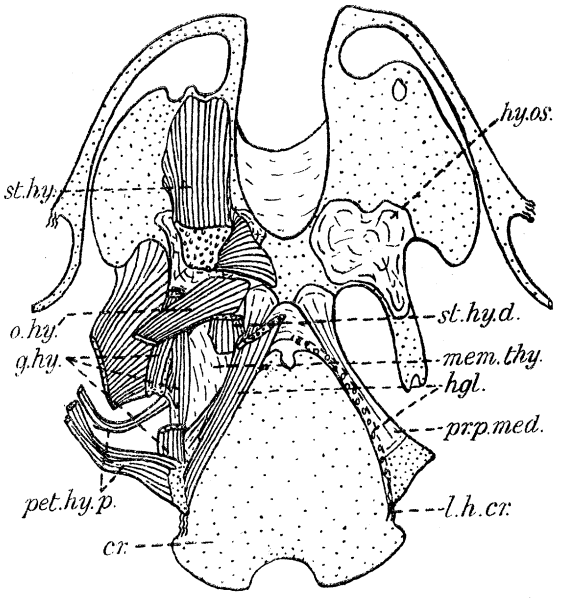

FIG. 6.—*Bombina variegata*. Hyoid and larynx of male, ventral. × 6⅔. Muscles of left side removed. *hy. os.* hyoid ossification.

M. geniohyoideus arising from the jaw in lateral and medial portions, the medial lying ventral to the lateral, both inserted, externally to the sternohyoid, in a narrow area extending, continuously or discontinuously, from the posterior end of the postero-lateral process, along the thyroid membrane to the end of the bony postero-medial process.

M. hyoglossus rather weak, with a linear area of origin extending along the inner edge of the postero-medial process and on the hyo-arytænoid membrane.

M. petrohyoideus anterior with the usual attachment to the edge of the hyoid plate

and to the skull and the hyale near the skull, but with many fibres from each end spreading over the wall of the pharynx and ending there.

Three *petrohyoidei posteriores*, the first slender, inserted on the dorsal side of the thyroid membrane, the second and third inserted close together on the cartilaginous end of the postero-medial process.

Bombina is a conspicuous example of the difference in relative size of the larynx in male and female. In the two males examined by me its length is 11 to 12% of the body length, in the female 8%.

Pelobatidæ.

Megalophrys robusta, Boulenger.

Range; India (Darjeeling).

Female, 99 mm., from snout to vent; from Darjeeling.

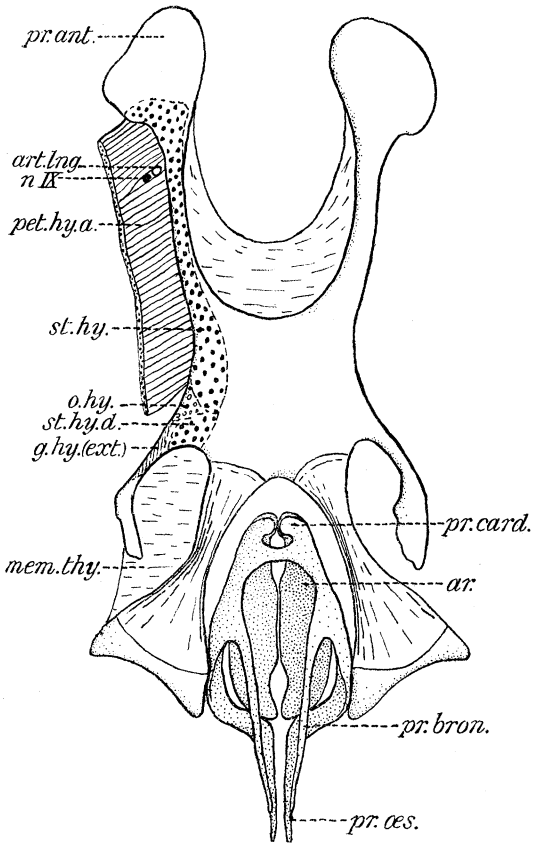

Fig. 7.—*Megalophrys robusta*. Hyoid and laryngeal skeleton of female; vent insertions of the right side shown.

Hyoid and Laryngeal Skeleton.—Hyoid plate about as broad as long. Manubrium hyoidei expanding anteriorly into a cartilaginous plate, which represents the hyale, of which the main portion is lacking. Alary process absent; postero-lateral process

long, distally expanded; postero-medial process stout, only slightly inclined to the plane of the hyoid plate, with broadly expanded posterior end.

Arytænoid elongated from its antero-ventral to its postero-dorsal end; with its edge at the aditus laryngis raised into a prominence corresponding to the " anvil-like process " in *M. boettgeri* (FRAZIER, 1924, Plate 2, fig. 15).

Cricoid incomplete mid-dorsally, with two long parallel œsophageal processes; no muscular or lateral processes; cardiac processes prominent, spoon-shaped, united by close syndesmosis with the arytænoid; bronchial processes long, slender, simple.

Muscles.—*M. intermandibularis* typical. *M. interhyoideus*, in the absence of hyalia, attached to otic region of skull with *mm. petrohyoidei*; on the right a small slip attached by a tendon to end of lower jaw, near depressor mandibulæ.

M. sternohyoideus with a long continuous area of insertion on the side of the ventral surface of the hyoid plate and on the manubrium.

M. geniohyoideus with typical external insertion at origin of postero-lateral process; internal portion typical, spreading on surface of hyoglossus and inserted on edge of laryngeal sinus.

M. omohyoideus typical, inserted on hyoid in front of external geniohyoid.

M. hyoglossus originating on ventral surface of epiphysis and bony shaft of postero-medial process, and (a few fibres) on hyo-arytænoid membrane.

M. petrohyoideus anterior inserted on edge of hyoid plate and manubrium. The lingual artery and nerve pierce it as they pass from ventral to dorsal side of the hyoid apparatus.

Three *petrohyoidei posteriores*, the first two passing on the *ventral* side of the thyroid membrane (an unusual relation) to their insertion on the edge of the postero-medial

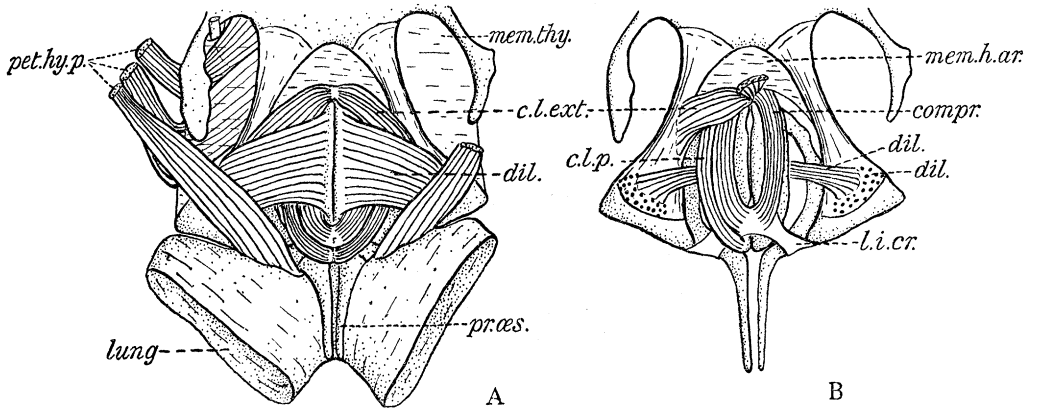

FIG. 8.—*Megalophrys robusta*. Larynx of female; dorsal. × 2⅔. A. With roots of lungs shown diagrammatically, and with all laryngeal muscles. B. With some muscles removed.

process and of the hyoid plate immediately in front of this; the third crossing the dorsal surface of the postero-medial process to be inserted on the inner corner of its cartilaginous epiphysis, close to the cricoid.

M. dilatator laryngis with origin on the postero-medial process, and with main insertion on the arytænoid at the aditus laryngis, but with also a small ventral slip inserted on

the membranous wall of the larynx, between arytænoid and cricoid, at the base of the vocal chord.

M. constrictor externus attached to middle of postero-medial process, meeting its fellow in front of arytænoids in a linea alba; *constrictor anterior* ending in front in the same linea alba, except a few fibres, which end near it on the hyo-arytænoid membrane; behind attached to the membrane which is continued laterally as the inter-cricoid ligament. *M. constrictor posterior* a continuous muscle, attached at pharyngeal end to a small fibrous pulvinar vocale, at the other end to the fibrous layer over the closely apposed cardiac process of the cricoid and cardiac end of the arytænoid.

LEPTODACTYLIDÆ.

Leptodactylus caliginosus, Girard.

Range: S. America.

Male, 39½ mm., and female, 45 mm. from snout to vent.

Hyoid and Laryngeal Skeleton.—Hyoid plate and its process with shape and proportions as in *L. ocellatus*, but with a broadening of the hyale representing anterior process, and with hyglossal sinus shallower.

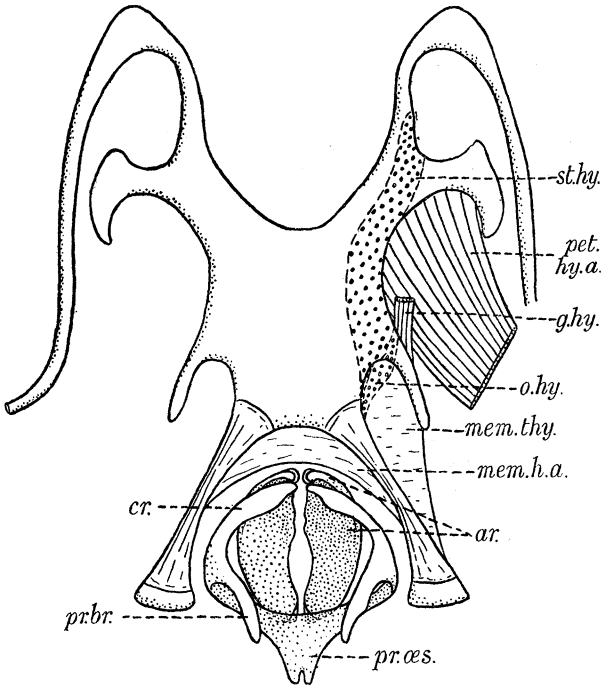

FIG. 9.—*Leptodactylus caliginosus*. Hyoid and laryngeal skeleton of female, with some muscle-insertions shown; ventral view; × 9.

Arytænoid with notched, broadly obtuse pharyngeal angle and with feeble pulvinaria vocalia. *Cricoid* incomplete ventrally, with low cardiac processes separated by a gap. Œsophageal process broad, notched posteriorly. No well-defined lateral or articular

processes. Muscular process present. Bronchial process simple, extending only halfway round ventral wall of laryngo-pulmonary opening.

Muscles.—Mm. intermandibularis and *interhyoideus* typical.

M. sternohyoideus with main portion as in *L. ocellatus ; pars dorsalis* as in *L. ocellatus* or with a few fibres attached to postero-medial process.

Mm. omohyoideus and *geniohyoideus* typical.

M. hyoglossus attached in part to ventral surface of epiphysis of postero-medial process, in part to posterior edge of hyoid plate.

M. petrohyoideus anterior inserted on edge of hyoid plate. Three *petrohyoidei posteriores*, inserted on postero-medial process, except a few fibres of the third which reach the larynx.

Mm. dilatator laryngis and *constrictor laryngis externus* typical. *M. constrictor anterior* attached to hyo-arytænoid membrane, except a few fibres, which are confluent with *m. constrictor externus* ; inter-cricoid ligament continuous with hyocricoid ligament. *M. constrictor posterior* present, partially interrupted by muscular process of cricoid.

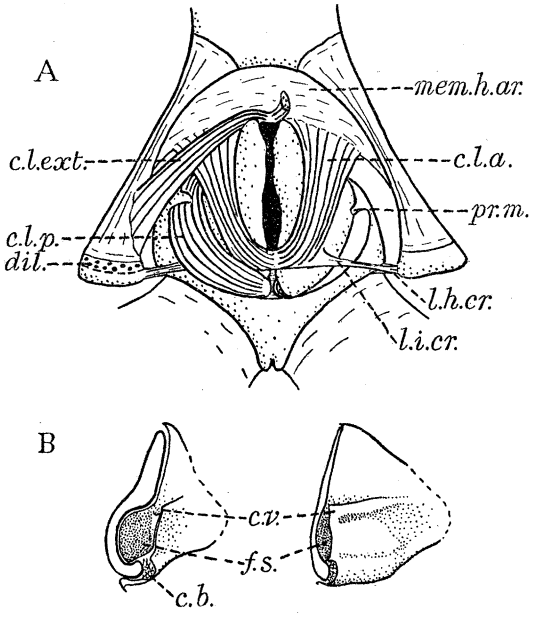

FIG. 10.—*Leptodactylus caliginosus*. A. Larynx of female, dorsal. × 9. Dilatator removed ; on the right constrictor posterior removed and constrictor externus cut short. B. Two views of anterior half of left arytænoid of male, with vocal chord in place. *c.b.* = fibrous pad, in position of cartilago basalis of other forms.

The male specimen is abnormal in lacking anterior and posterior laryngeal constrictors on the left side. Its larynx is relatively larger than that of the female, being 11% of the body length as compared with 9% in the female. A dense band of fibrous tissue, probably representing the *cartilago basalis*, lies along the incurved base of the arytænoid. The vocal chord has no frenulum, but its pars basalis is attached to the base of the

arytænoid and to the fibrous cartilago basalis, except at the ends, where it is attached to the upper border of the arytænoid concavity. The *fossa supralabialis* (see KRAUSE, 1920, Plate 20, fig. 1) is so excavated towards cardiac and pharyngeal ends as to form an oval chamber with a narrow opening towards the aditus laryngis, and having the appearance of a bubble imprisoned between the vocal chord and the arytænoid. In spite of the abnormality in the muscles, referred to above, this structure is the same on both sides and is probably normal. BLUME (1930, p. 387) describes a somewhat similar fossa supralabialis in *Chorophilus feriarum*. The larynx would repay microscopical study in another specimen.

Leptodactylus prognathus, Boulenger.

Range, Southern Brazil, Paraguay, Uruguay, Argentine.

Young male, 21 mm. from snout to vent. [B.M.N.H.]

The hyoid and larynx are like those of *L. ocellatus* except for juvenile characters, namely, the presence on the hyale of a lateral flange united by a ligament to the angle of the jaw, and the weak ossification of the postero-medial process of the hyoid. The pharyngeal pulvinaria vocalia appear to be cartilaginous.

Crossodactylus gaudichaudi, Duméril and Bibron.

Range, Eastern Brazil.

Male, 23 mm. from snout to vent. [SLADEN.]

Hyoid and Laryngeal Skeleton.—Length of hyoid plate three-quarters of its least width; hyoglossal sinus deep, spanned by membrane. A small ossification on each side in the narrow region behind the alary process. Hyale without anterior process. Alary process reduced to a narrow stalk with a slight distal expansion. Postero-lateral process long, curved, slender. Postero-medial process strong, with narrow epiphysis; laryngeal sinus wide.

Arytænoids simple, large, together dome-shaped, projecting into pharynx, tilted so that vocal chords are inclined at more than 45° to longitudinal axis of body. Pulvinaria vocalia small. *Cricoid* very narrow laterally, broad on cardiac and pharyngeal sides; œsophageal process short; articular and minute lateral processes present; no muscular process; bronchial process simple, slender; cardiac processes separated by a minute notch.

Muscles.—M. intermandibularis posterior with the anterior superficial fibres crossing the deeper ones at an angle, running backwards and medialwards (cf. *Rhinoderma*, BEDDARD, 1908 *b* and *Hyla aurea* and *H. cærulea*, pp. 442, 447).

M. interhyoideus typical.

M. sternohyoideus with a continuous lateral linear insertion on the hyoid, from base of alary process backwards on to thyroid membrane and edge of postero-medial process.

M. omohyoideus inserted at base of postero-lateral process, in part on cartilage, in part on thyroid membrane.

Mm. geniohyoideus and *hyoglossus* typical.

M. petrohyoideus anterior inserted on lateral edge of alary process and hyoid plate. Three *petrohyoidei posteriores* inserted in the typical way on the postero-medial process.

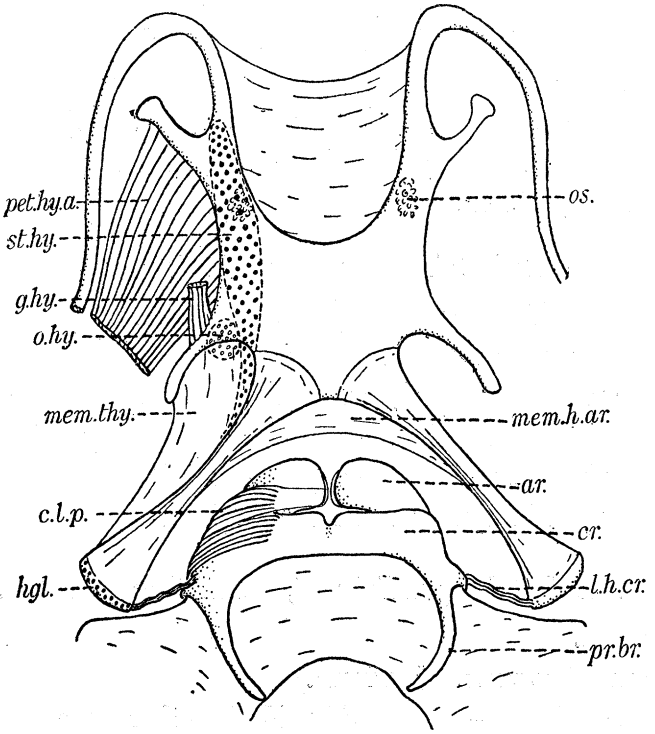

FIG. 11.—*Crossodactylus gaudichaudi*. Hyoid and larynx of male, ventral. × 15. Some of the muscles of the right side, or their insertions, shown. *os* = ossification or (?) calcified area in hyoid plate.

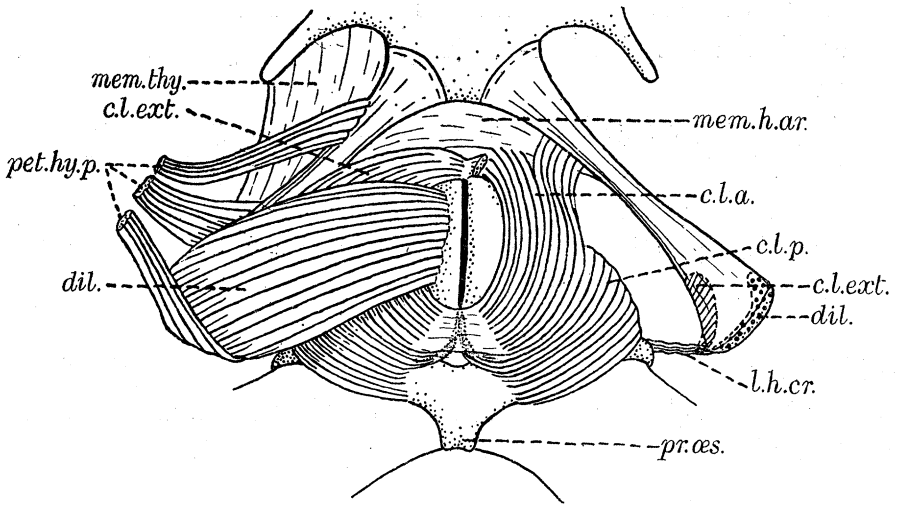

FIG. 12.—*Crossodactylus gaudichaudi*. Larynx of male, dorsal. × 15. On the right the dilatator is removed and m. constrictor externus is cut short, but their hyoid attachments are shown.

Mm. dilatator laryngis and *constrictor externus* typical. *M. constrictor anterior* attached in part to hyo-arytænoid membrane, but mainly to inner edge of postero-medial process.

M. constrictor posterior rather short, attached at each end partly to the narrow pulvinaria, but mainly to the cricoid.

Pleurodema bibroni, Tschudi.

Range, Chile, W. of Andes, between 30° and 44° S., and Eastern slope of Andes, in Argentina.*

Female, 41 mm. from snout to vent. [Zool. Soc.]

Hyoid and Laryngeal Skeleton.—Length of hyoid plate about equal to its width. Hyalia without anterior processes. Alary process a lobe with narrow base, arising from the manubrium. Postero-lateral and postero-medial processes long and slender.

Larynx not nearly filling the laryngeal sinus. *Arytænoid* with pharyngeal apex acute, projecting forwards: pulvinaria vocalia present, the cardiac pair being the

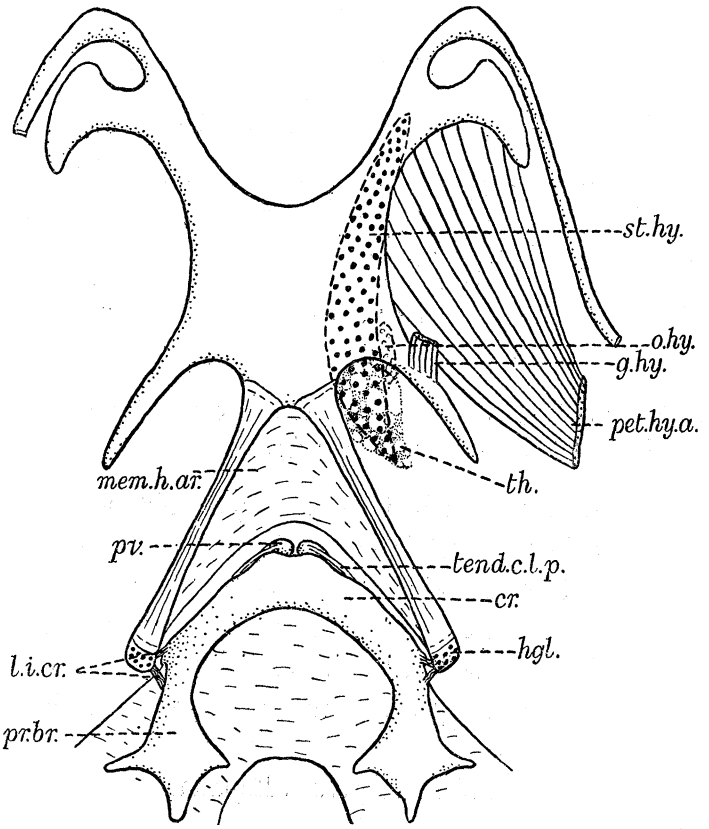

Fig. 13.—*Pleurodema bibroni.* Larynx and hyoid of female; ventral; × 9.

only parts of the arytænoids visible in a ventral view of the larynx. *Cricoid* a complete ring, rather broad except between articular and muscular processes, where it is so deeply notched as almost to be divided; œsophageal process short, broad; bronchial process stout, with broadly expanded, bluntly triradiate end; cardiac process low.

Muscles.—*Mm. intermandibularis* and *interhyoideus* typical.

* H. W. Parker, 1927.

M. sternohyoideus with hyoid insertion on the lateral part of the ventral surface of the hyoid plate, extending backwards on the thyroid membrane under the thyroid gland.

M. omohyoideus typical.

M. geniohyoideus with typical insertions, the part covering the hyoglossus becoming aponeurotic near its insertion.

M. hyoglossus attached to ventral surface of epiphysis of postero-medial process.

Petrohyoideus anterior attached to lateral edge of hyoid plate.

Three *posterior petrohyoids*, with typical insertions on the postero-medial process, and crossing the thyroid membrane on its dorsal side.

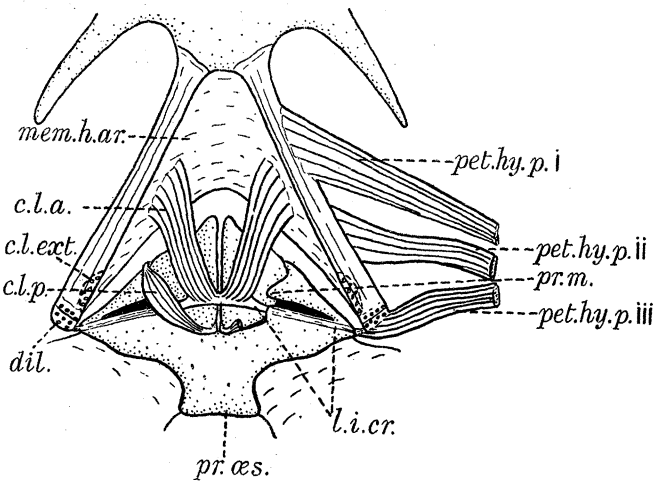

FIG. 14.—*Pleurodema bibroni*. Larynx of female, dorsal; × 9. Dilatator and constrictor externus removed, and constrictor posterior cut short on the right.

M. dilatator laryngis simple, attached to the arytænoid near its pharyngeal apex. *M. constrictor externus* typical; *constrictor anterior* ending anteriorly on hyo-arytænoid membrane, posteriorly on the intercricoid ligament, which is continuous with the hyo-cricoid; *constrictor posterior* semitendinous, not attached to muscular process.

The hyoid of this species was figured by W. K. PARKER (1881, Plate 18, fig. 3). He shows a blunt lobe behind the alary process, but in my specimen there is none.

Edalorhina perezi, Espada.

Range, Ecuador.

Female, 41½ mm. from snout to vent, from Ecuador. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Hyoid plate slightly longer than wide. Hyale with anterior process; other hyoid processes typical, the postero-medial relatively short. On each side, two small areas of calcified cartilage, one in the hyoid plate, the other midway in the length of the hyale.

Arytænoid well rounded, its basal axis steeply inclined to the plane of the postero-medial processes, its antero-ventral end conspicuously projecting on the cardiac side

of the larynx. Pharyngeal pulvinar vocale cartilaginous; no cardiac pulvinar. Cricoid stout, except for a deep, narrow notch between articular and muscular processes, where it is impossible to determine by dissection whether the cartilage is continuous or not.

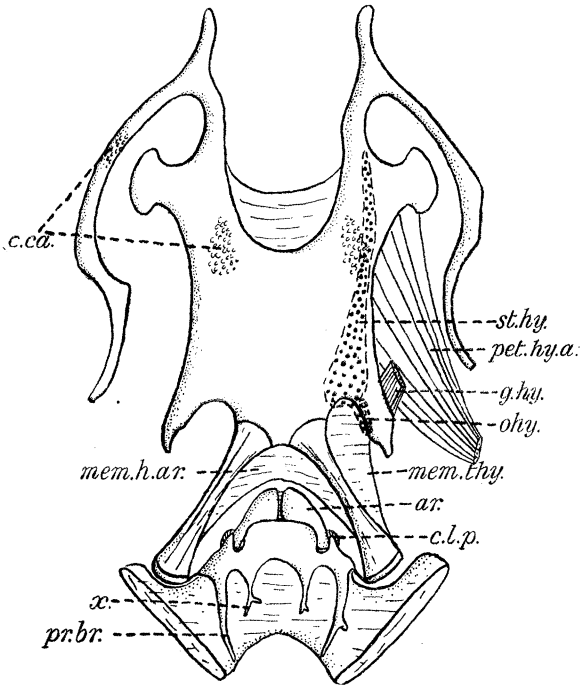

FIG. 15.—*Edalorhina perezi*. Hyoid and larynx of female; ventral; × $6\frac{2}{3}$. Roots of lungs shown diagrammatically.

Muscular process strong, appearing in a cardiac view of the larynx. Cardiac processes united to form a single cardiac expansion, the edge of which is closely applied to the edges of the arytænoids. Bronchial processes slender, one with a minute branch; between them a pair of short, distally bifid *posterior cardiac processes*, forming additional support to the ventral wall of the larynx.

Muscles.—M. intermandibularis posterior with a superficial portion with fibres running obliquely forwards and medialwards (fig. 16, A, and cf. *Brachycephalus* and the Brevicipitidæ). *M. interhyoideus* small, typical.

M. sternohyoideus inserted on the lateral part of the ventral surface of the hyoid plate, widely separated from its fellow; insertion of *m. dorsalis* continuous with this, on the thyroid membrane, at the edge of the postero-lateral process.

M. omohyoideus inserted on the base of the postero-lateral process.

M. geniohyoideus with typical external and internal insertions, the internal part forming a thin aponeurosis over the hyoglossus.

M. hyoglossus typical, attached to the ventral surface of the epiphysis of the postero-medial process.

Mm. dilatator laryngis and *constrictor externus* typical. *Constrictor anterior* attached in front to the postero-medial process, behind to the inter-cricoid ligament, which is

continuous on each side with the hyo-cricoid. *Constrictor posterior* extending on each side from the pharyngeal end of the arytænoid (not the cartilaginous pulvinar) to the muscular process, where it ends, its cardiac half being absent.

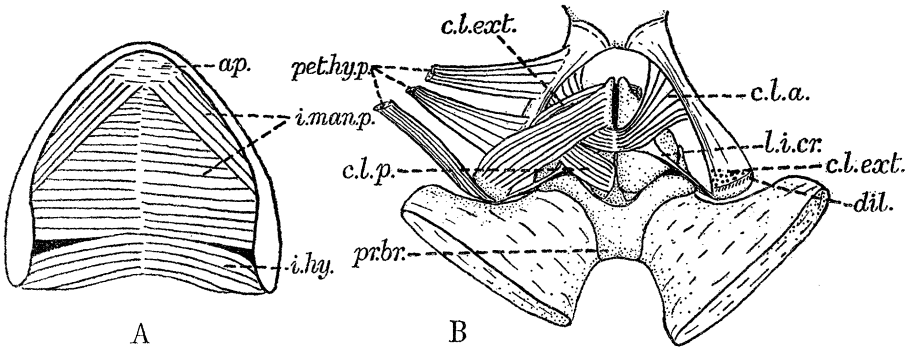

FIG. 16.—*Edalorhina perezi*. A. Superficial muscles of throat. *ap.* = anterior aponeurosis of intermandibularis posterior, hiding intermand. anterior. B. Larynx, dorsal. On the right, all muscles removed except constrictor anterior. Roots of lungs shown diagrammatically.

Eupemphix nana, Boulenger.

Range, Brazil.

Male, 25 mm. from snout to vent, from Therezopolis, Brazil. [SLADEN.]

Hyoid and Laryngeal Skeleton.—Length of hyoid plate nearly double its least width. Hyale with no anterior process. Alary process large, with broad base; postero-lateral process simple; postero-medial process relatively short, diverging widely from its fellow.

Larynx large, almost globular. *Arytænoids* composed of rather thin cartilage, having an inflated appearance. Pharyngeal pulvinaria present, but the cardiac much reduced, composed of looser, more faintly-staining tissue than in *Physalæmus* (see p. 428). *Cricoid* forming a complete ring; its pharyngeal half a narrow band, without processes; its cardiac half broader, bearing the muscular process and a straight, simple bronchial process on each side. Cardiac processes united, their edges closely applied to those of the arytænoids, with which they are, at one point, continuous; a minute notch in the middle of their anterior border, continuing the division between the arytænoids; behind this notch, cricoid forming a median, blunt, beak-like projection.

Muscles.—*M. intermandibularis posterior* typical. *M. interhyoideus* relatively large, coarse, and pouched, in relation to the enormous vocal sac, which extends into the ventral abdominal lymph-spaces.

M. sternohyoideus with a long hyoid insertion, which meets its fellow in the middle line. *M. dorsalis* inserted on thyroid membrane, near postero-lateral process.

M. omohyoideus absent.

M. geniohyoideus with typical external and internal divisions, the internal aponeurotic over the paired part of *m. hyoglossus*.

M. hyoglossus inserted on the ventral surface of the epiphysis of the postero-medial process.

M. petrohyoideus anterior inserted on the ventral surface of the hyoid plate, the area of insertion sloping inwards from the anterior end of the alary process and extending backwards, adjacent to the sternohyoid.

Only two *petrohyoidei posteriores*, the middle one being absent.

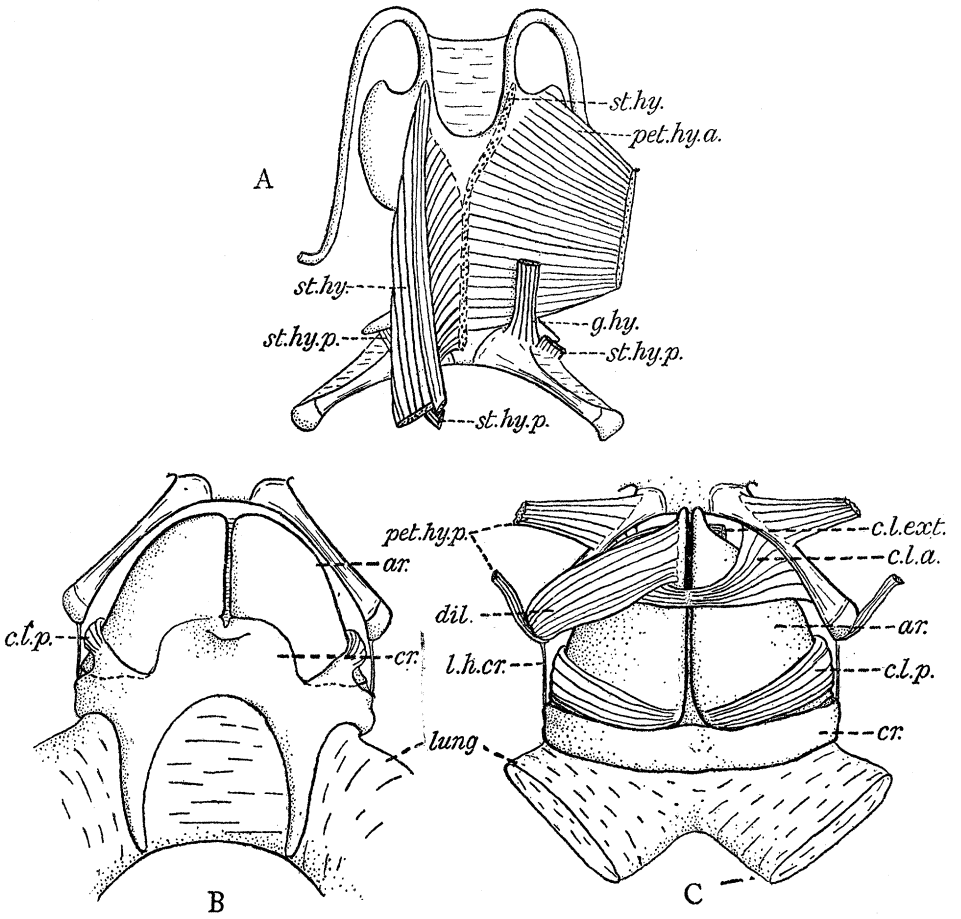

FIG. 17.—*Euphemphix nana*, male. A. Ventral view of hyoid, with different muscles shown on right and left sides. B. Larynx, ventral. C. Larynx, dorsal.

M. dilatator laryngis short and broad, with typical attachments. *Constrictor externus* typical; constrictor anterior spreading fan-wise from a narrow median raphe, to be attached to the inner edge of the postero-medial process; no inter-cricoid ligament; constrictor posterior separated from constrictor anterior by a wide gap, attached dorsally to a pulvinar, ventrally ending on the muscular process, and having no cardiac portion.

Physalæmus cuvieri, Fitzinger.

Range: Brazil, Uruguay, Paraguay, E. Bolivia and N. Argentina.

(*a*.) Male, 26 mm. from snout to vent. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Hyoid plate longer than broad, with all the typical processes. Hyale with an anterior process. Alary process a large lobe. In this specimen there is a tendency, more marked on the right, for fusion to occur between the base of the alary process and that of the postero-lateral process.

Larynx large, presenting an even more distended appearance than in *Eupemphix*. The *arytænoids* and *cricoid* have lost their normal shapes, and together form a thin flexible layer of cartilage over almost the whole of the wall of the larynx. On the pharyngeal side the large arytænoids and narrow cricoid, with its short œsophageal process, present a relatively normal appearance, but the cardiac side of the cricoid is

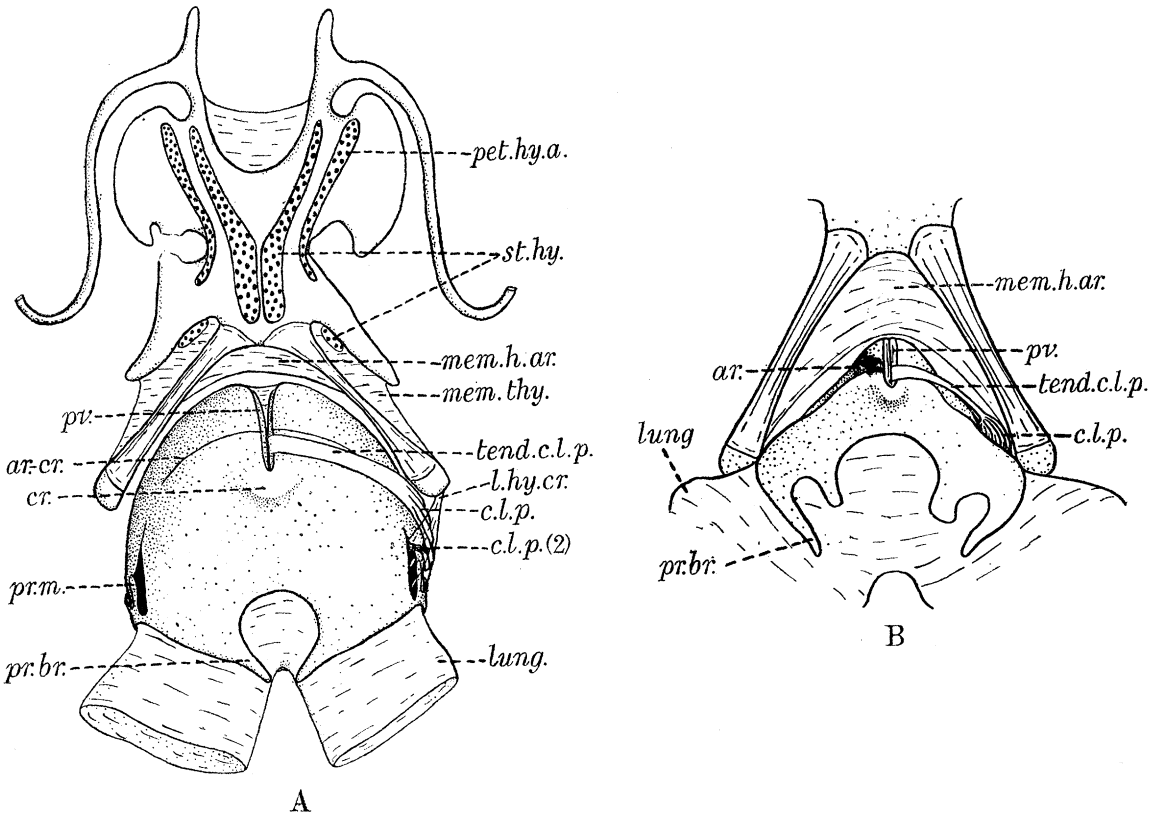

FIG. 18.—*Physalæmus cuvieri*. A. Hyoid and larynx of male; ventral; × 12. m. constrictor laryngis posterior of left side alone shown. Insertions of some hyoid muscles shown. *ar.-cr.* = arytænocricoid syndesmosis; *c.l.p.* (2) = lateral attachment of constrictor posterior. B. Larynx of female; ventral, × 12.

greatly expanded with its anterior edge applied accurately to that of the arytænoid, with which it is for some distance fused. A narrow median notch of the cricoid continues the space between the cardiac ends of the arytænoids and behind this the cartilage bulges outwards in a beak-like structure. The simple bronchial processes have broad bases. Laterally the cricoid becomes extremely narrow and gives off a minute slender process which seems to correspond to the muscular process, but does

not serve as a muscle attachment. The larynx extends backwards beyond the end of the postero-medial processes of the hyoid, and beyond the hyocricoid ligament, which is replaced by a triangular sheet of fibrous tissue attached to the edge of the arytænoid and to the pad of fibro-cartilage which, laterally, lies between it and the cricoid.

The cardiac pulvinar vocale of each side is continuous with the arytænoid. It extends along the edge of the notch of the cricoid, and although the transition between pulvinar and cricoid is rather abrupt, they do not appear to be separated by perichondrium.

Near the end of the notch of the cricoid a rod of cartilage, of the same type as that composing the pulvinar, runs into the vocal chord. It is continuous with the cricoid and also, for a short distance, with the pulvinar. It appears to correspond to the " processus vocalis des pars cricoidea " described by BLUME (1930) in the genus *Bufo*, and the fact of its union with the pulvinar vocale is a step towards the fulfilment of his prediction that an Anuran would yet be found in which the lip of the vocal chord

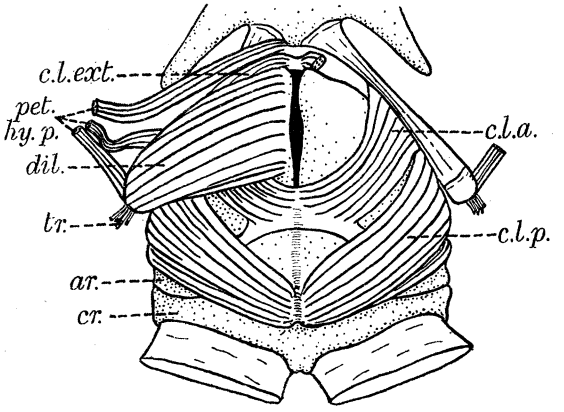

FIG. 19.—*Physalæmus cuvieri*. Larynx of male ; dorsal ; × 12 *tr* = fibres of m. transversus abdominis.

would be supported by a rod of cartilage united with the arytænoid via the pulvinaria and frenulum. (BLUME, *loc. cit.* p. 445.)

Muscles.—M. intermandibularis posterior typical ; *m. interhyoideus* broad and pouched, in relation to the large vocal sac, which, as in *Eupemphix nana*, extends into the ventral lymph sinuses.

M. sternohyoideus with the posterior part of its hyoid insertion meeting that of its fellow in the middle line. Dorsal portion inserted separately on the thyroid membrane, in the angle between postero-lateral and postero-medial processes of the hyoid.

M. omohyoideus present.

M. geniohyoideus with the usual external insertion at the base of the postero-lateral process ; internal part muscular throughout.

M. petrohyoideus anterior inserted along the base of the alary process and a short way behind this, near the insertion of the sternohyoid.

Three *posterior petrohyoids*, the first inserted near the middle line, the second very slender. All dorsal to the thyroid membrane.

M. hyoglossus typical.

M. dilatator laryngis attached in part to the edge of the arytænoid cartilage, in part to a fibrous rod between this and the aditus laryngis. *M. constrictor externus* with the usual relations. *M. constrictor anterior* attached laterally to the inner edge of the postero-medial process of the hyoid and, medially, with its fellow, to a fibrous membrane bridging the arytænoids; no inter-cricoid ligament. *M. constrictor posterior* appearing typical in a pharyngeal view, but on the cardiac side continued as a flat fibrous band attached to the pulvinar vocale, where this lies against the edge of the cricoid, in front of the beak-like process of the latter; a small slip of this muscle ending laterally on the fibro-cartilage filling the lateral gap between arytænoid and cricoid (*cf.* attachment of the whole muscle in *Eupemphix nana*).

(*b.*) Female, 33 mm. from snout to vent, from Paraña. [B.M.N.H.]

Hyoid and its *muscles* essentially similar to those of male, but without the irregular outgrowths of the right edge of the hyoid plate found in the male here described. Anterior process with angle between it and hyale partially filled by thin cartilage. Postero-medial processes less widely diverging than in male.

Anterior part of laryngeal sinus filled by hyo-arytænoid membrane. *Larynx* (fig. 18 B), much smaller than in male. Dorsal view essentially as in male, but with arytænoids less swollen, and muscles weaker. Inter-cricoid ligament continuous with hyocricoid. *Cricoid* narrow laterally; ventrally becoming suddenly broader, with its edge closely apposed to that of arytænoid, but apparently not fused with it; with a median, beak-like projection containing a notch for the continuation of the cardiac pulvinaria, as in male. Cartilage of cricoid less extensive than in male, but with a pair of *posterior cardiac* processes between the bronchial processes, as in *Edalorhina perezi*. *M. constrictor posterior* semitendinous, as in male, with a minute ligamentous union with the cricoid near the hyocricoid ligament.

Pseudopaludicola falcipes (Hensel).

Range, Southern Brazil.

Male, 15 mm. from snout to vent, from Rio Grande do Sul, Brazil. [B.M.N.H.]

The larynx was first dissected and drawn, then sectioned.

Hyoid and Laryngeal Skeleton.—Width of hyoid plate nearly double its median length, owing to the presence, on each side, of a broad lobe representing fused alary and postero-lateral processes. A median strip of more granular cartilage in the posterior half of the hyoid plate may have been calcified before preservation. Microscopic examination shows it to consist of smaller cells and denser matrix than the rest of the hyoid. Hyoglossal sinus shallow. Tip of anterior process rejoining the hyale, enclosing a small oval fenestra (*cf. Megalixalus*, p. 478, *Breviceps*, p. 492, etc.). Epiphysis of the postero-medial process fused with cricoid.

Arytænoids large ; their cardiac ends projecting somewhat and conspicuous in a ventral view of the larynx. Edge at aditus thick, with a produced, flattened apical region ;

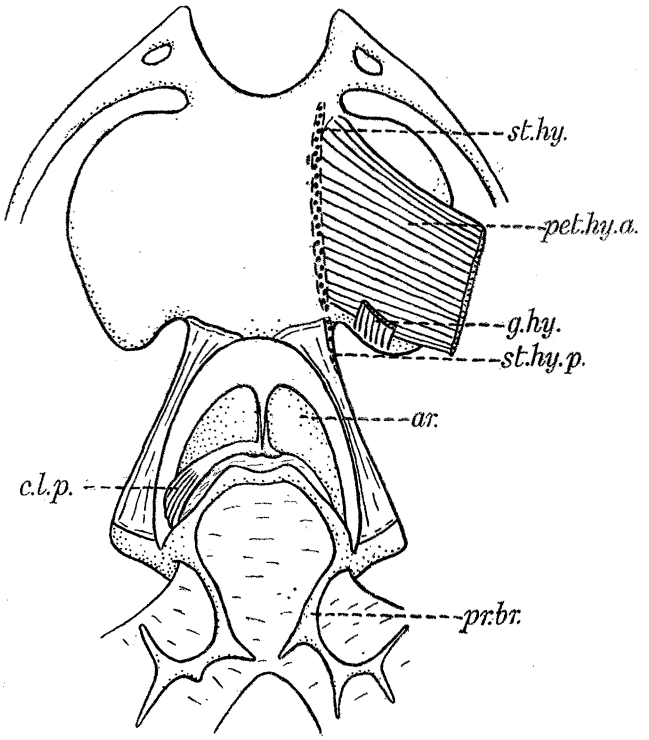

FIG. 20.—*Pseudopaludicola falcipes.* Hyoid and larynx of male ; ventral ; × 18. Some hyoid muscles of left side, and constrictor posterior of right side, shown.

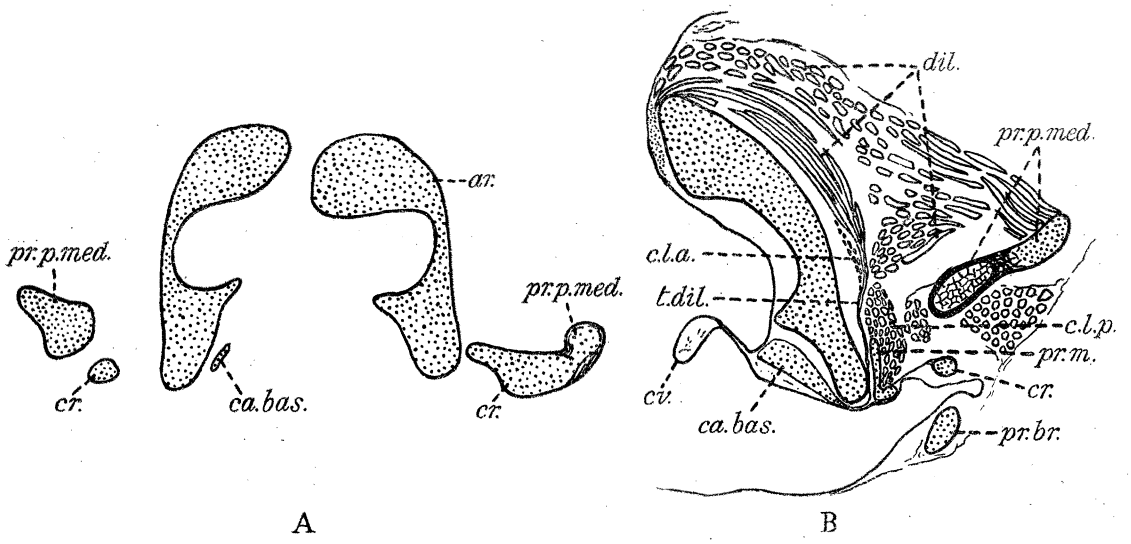

FIG. 21.—*Pseudopaludicola falcipes*, male. A. Transverse section of laryngeal skeleton near posterior end, showing hyo-cricoid union on the right, which is a little more posterior than the left side. B. Transverse section of right half of larynx, showing divisions of m. dilatator. The section is taken immediately in front of the frenulum of the vocal chord.

basal region thick, with a ledge projecting inwards and upwards for attachment of vocal chord ; intermediate region divided into two areas of thin cartilage by a transverse ridge. A distinct *cartilago basalis* along the border of the arytænoid to which the vocal chord is attached. Pharyngeal and cardiac pulvinaria present, the cardiac united to each other posteriorly. Pharyngeal pulvinaria perhaps united (but the sections are not good enough in this region to be certain).

Cricoid slender and complete. A short œsophageal process ; a very small muscular process, detected only by microscopic examination of sections. Cardiac processes low, not overlapping the ends of the arytænoids. Bronchial processes long, slender, giving off three branches where they curve over the root of the lung. Hyo-cricoid union cartilaginous.

Muscles.—M. intermandibularis typical. *M. interhyoideus* pouched over the vocal sac.

M. sternohyoideus with a linear insertion on hyoid plate, along the base of the large lateral lobes ; insertion of its dorsal portion continuing this line backwards for a short

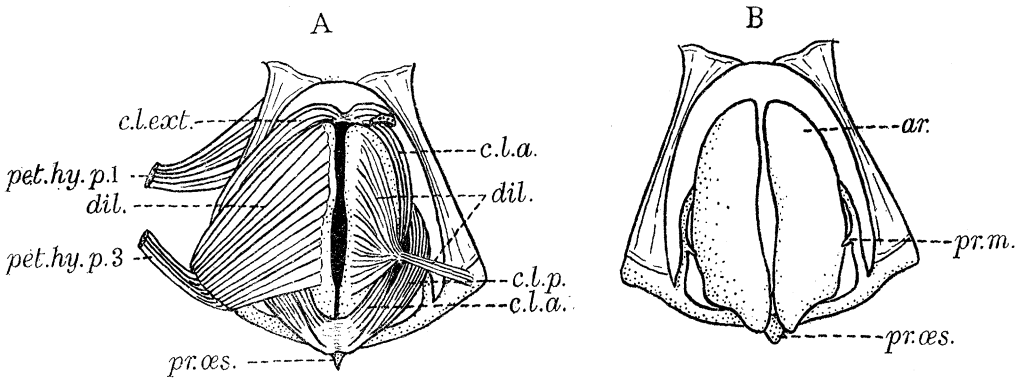

FIG. 22.—*Pseudopaludicola falcipes*, male. Larynx, dorsal ; × 18. A. With muscles ; constrictor externus and superficial part of dilatator removed on the right. B. Skeleton ; pulvinaria not shown.

distance along the outer edge of the postero-medial process. The insertions of right and left muscles widely separate.

M. omohyoideus typical.

M. geniohyoideus with the usual internal insertion with the hyoglossus ; its external portion attached to posterior edge of lateral lobe of hyoid.

M. petrohyoideus anterior with a linear insertion parallel and adjacent to that of main portion of the sterno-hyoid. Only two *posterior petrohyoids*, which in their attachments and their position relative to arteries correspond to the first and third of most Anura ; both dorsal to the thyroid membrane.

M. hyoglossus attached to ventral surface of epiphysis of postero-medial process.

M. dilatator laryngis consisting of a main portion with usual attachments, and two deep slips attached to a tendon between anterior and posterior constrictors at the level of

the small muscular process of the cricoid, but apparently not attached to it. One of these slips spreading fan-wise over anterior constrictor and arytænoid, and attached with the main part of the dilatator along the pharyngeal border of the arytænoid; the other attached with the other end of the dilatator on the epiphysis of the postero-medial process of the hyoid. Fibres of the tendon traceable beneath the posterior constrictor to the cartilago basalis of the vocal chord. Main part of dilatator attached in part to the thickened membranous lip of the aditus, in part directly to the arytænoid.

External constrictors attached anteriorly to a cushion of procartilaginous tissue on either side, the two cushions being joined by fibrous tissue.* *M. constrictor anterior* attached in part to these cushions, but with a few fibres passing to bony postero-medial process; muscle strongly compressed mid-way by fan-shaped slip of dilatator; no inter-cricoid ligament.

M. constrictor posterior passing outside muscular process, which interrupts a few of its deep fibres; attached by a short aponeurosis at each end to the pulvinaria vocalia.

Helioporus albopunctatus, Gray.

Range: Eastern, Northern and Western Australia.

Male, 54 mm., and female, 56 mm. from snout to vent; from Australia. [Dr. P. C. ESDAILE.]

Hyoid and Laryngeal Skeleton.—Length of hyoid plate about one and a half times its width; hyoglossal sinus extending well behind origin of alary processes. Hyale with anterior process directed inwards and expanding into a plate of thin cartilage, which almost reaches the middle line, ventral to the hyoglossal muscle. Alary and postero-lateral processes also expanded distally, with irregular and sometimes indefinite edges. Postero-medial processes with large cartilaginous ends.

Vocal chords inclined at about 30° to the horizontal. Apex of *arytœnoid* angular and entire; no apical or basal cartilages; but in both sexes a nodule of cartilage in the vocal chord at its attachment to the cardiac pulvinar, which is smaller than the pharyngeal. Cricoid a complete ring; œsophageal process short, slender; on each side two broad expansions, a pharyngeal and a cardiac, between which the cricoid is very slender; bronchial processes simple, of moderate length; slender lateral part of the cricoid lying close to the end of the postero-medial process, to which it is connected by fibrous tissue.

Muscles.—M. intermandibularis posterior completely hiding *m. intermandibularis anterior* in a ventral view, being muscular instead of, as is usual, aponeurotic where they overlap.

M. sternohyoideus inserted along lateral edge of hyoid from in front of base of alary process to base of postero-lateral process, and, without interruption, on the thyroid membrane, along the inner border of the postero-lateral process.

* It was in the position of these cushions that WILDER found sesamoid nodules in the males of *Acris gryllus, Chorophilus feriarum,* and *Hyla versicolor.*

M. omohyoideus inserted on the postero-lateral process.

M. geniohyoideus typical.

M. petrohyoideus anterior with a long insertion on the lateral edge of the hyoid. Three *posterior petrohyoids*, all lying dorsal to the thyroid membrane, the first inserted on the

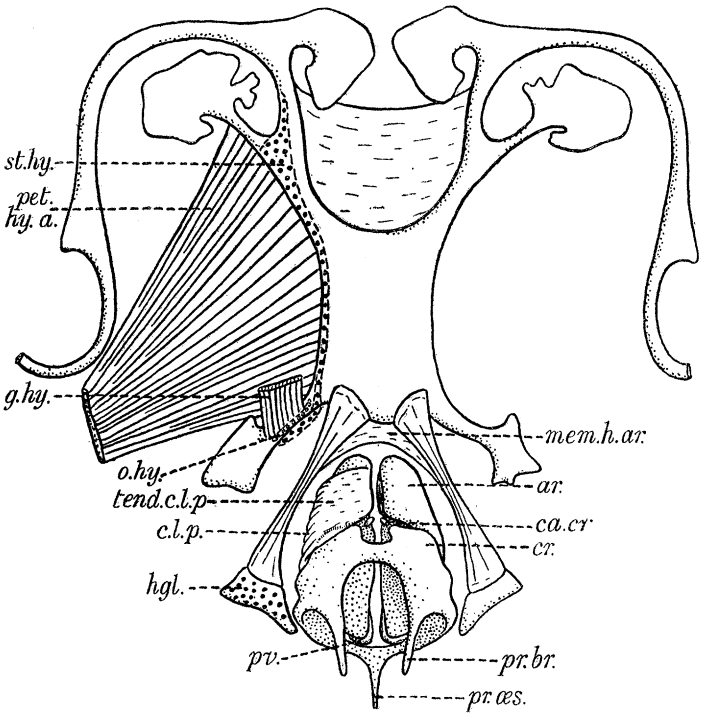

FIG. 23.—*Helioporus albopunctatus*.—Skeleton of hyoid and larynx, with some muscles; × 6. *ca. cv.* = cartilage of vocal chord.

dorsal surface of the postero-medial process, the second on its lateral edge, and the third partly on its cartilaginous end, and partly on the cricoid.

M. hyoglossus attached to ventral surface of end of postero-medial process.

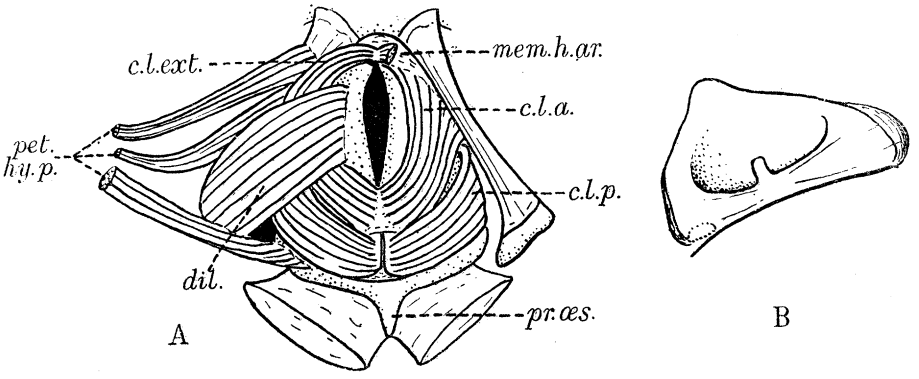

FIG. 24.—*Helioporus albopunctatus*.—A. Larynx, dorsal, × 6. B. Inner view of right arytænoid, with vocal chord.

Mm. dilatator laryngis and *constrictor laryngis externus* typical; dilatator attached directly to arytænoid. *M. constrictor anterior* attached, in front, in part to hyo-arytænoid membrane, in part to postero-medial process; no well-differentiated inter-cricoid ligament; *constrictor posterior* with ventral half aponeurotic, not interrupted by cricoid.

The vocal chord has well-marked anterior and posterior lips, and a fibrous frenulum. In addition, in the male, a fibrous appendage juts forward from the middle of the anterior lip.

Limnodynastes peronii (Duméril and Bibron).

Range: Eastern Australia, Tasmania.

Female, 51 mm. from snout to vent. [ZOOL. SOC.]

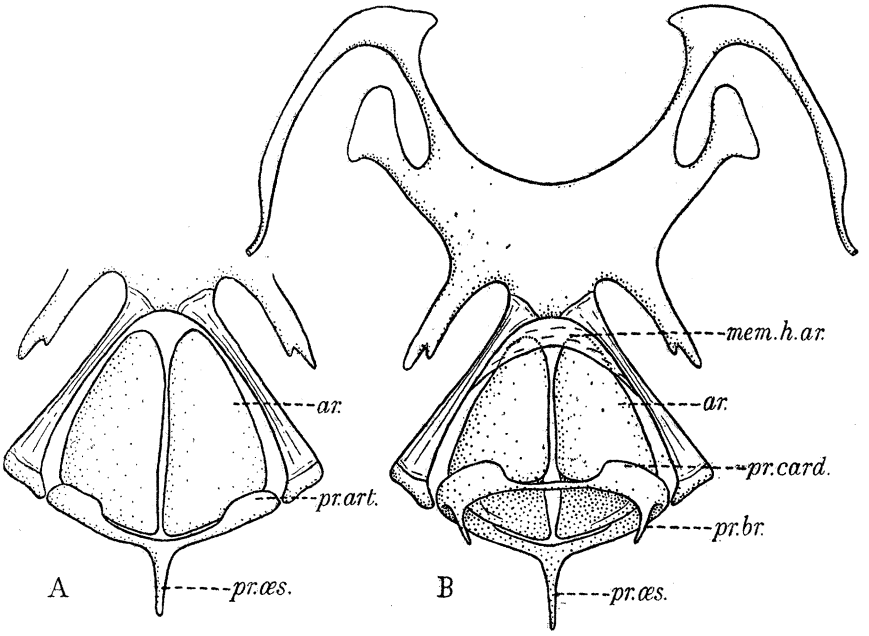

FIG. 25.—*Limnodynastes peronii*, female. A. Skeleton of larynx, dorsal. B. Hyoid and laryngeal skeleton, ventral. × 5.

Hyoid and Laryngeal Skeleton.—Width of hyoid plate greater than its length; hyoglossal sinus very wide. Hyale with a short inwardly directed anterior process; alary and postero-lateral processes present, the latter unequally bifurcated distally; postero-medial processes widely diverging.

Arytænoids disposed so that the vocal chords make an even greater angle with the longitudinal axis of the body than in *Helioporus*. *Cricoid* as in *Helioporus*, but more slender and with relatively shorter bronchial processes.

The state of preservation of the specimen is not suitable for a study of the muscles.

Crinia signifera (Girard).

Male, 26 mm., and female, 21½ mm. from snout to vent, from Upper Manning River, New South Wales. [Professor J. P. Hill.]

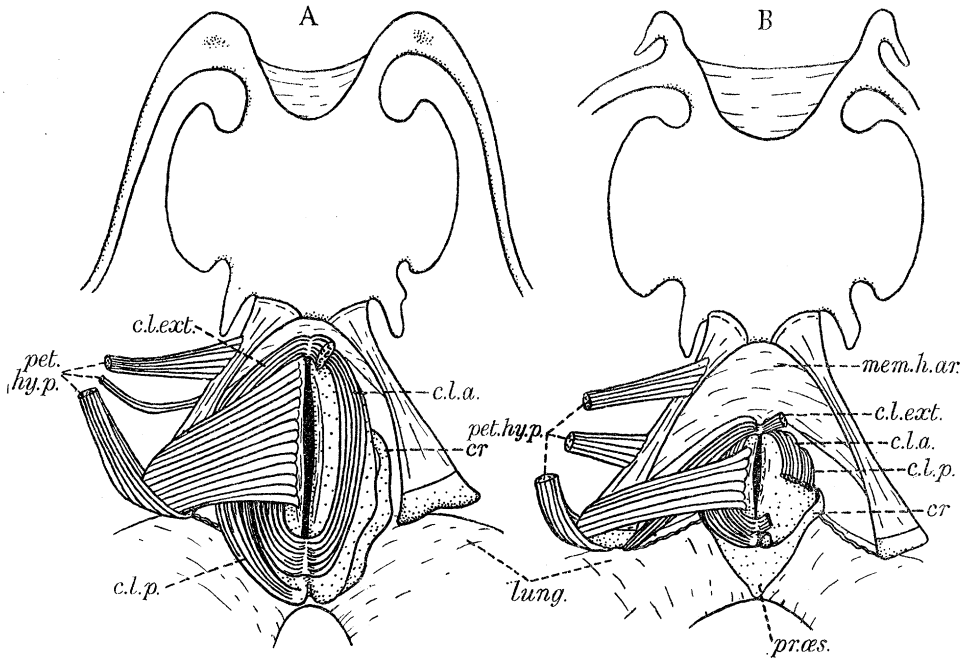

Fig. 26.—*Crinia signifera*. Hyoid and larynx, dorsal; A. Male; B. female; × 12. Some of the muscles of the right side removed or cut short. Pulvinaria vocalia not shown in male.

Hyoid and Laryngeal Skeleton.—Length of hyoid plate greater than its least width; hyoglossal sinus shallow. Base of alary process occupying most of lateral edge of hyoid plate. In the smaller specimen, hyale with an anterior process, which is recurved so as almost to meet hyale again; in the larger specimen this union is complete, with the enclosed space filled by thinner cartilage. Postero-lateral process simple; postero-medial process long, straight, expanded distally; cartilaginous tip bilobed in male.

Arytænoids in male almost filling laryngeal sinus, extending to posterior limit of air-passage, their length contained about seven and a half times in the body-length; in female small, one-sixteenth of the body-length, neither filling the laryngeal sinus nor extending over the whole length of the median air-passage. In both sexes, edge of arytænoid at aditus laryngis fibrous. Pulvinaria present. Cricoid incomplete mid-ventrally; lateral region narrow, without muscular or lateral processes; bronchial processes short, simple; œsophageal process broad in female, minute and hidden in dorsal view in male.

Muscles.—*M. intermandibularis* and *m. interhyoideus* typical.

M. sternohyoideus inserted on ventral surface of hyoid, from manubrium to base of postero-medial process, reaching the middle line in the posterior part of this insertion;

sternohyoideus dorsalis attached to edge of postero-medial process about midway in its length.

M. omohyoideus absent.

M. geniohyoideus with external insertion, in the male, on edge of anterior end of postero-medial process, in the female, on inner edge of postero-lateral process. In both sexes *m. geniohyoideus medialis* inserted on anterior part of edge of postero-medial process (in the male adjacent to the external insertion), and internal part of *m. geniohyoideus lateralis* alone continued as an aponeurosis over paired part of hyoglossus.

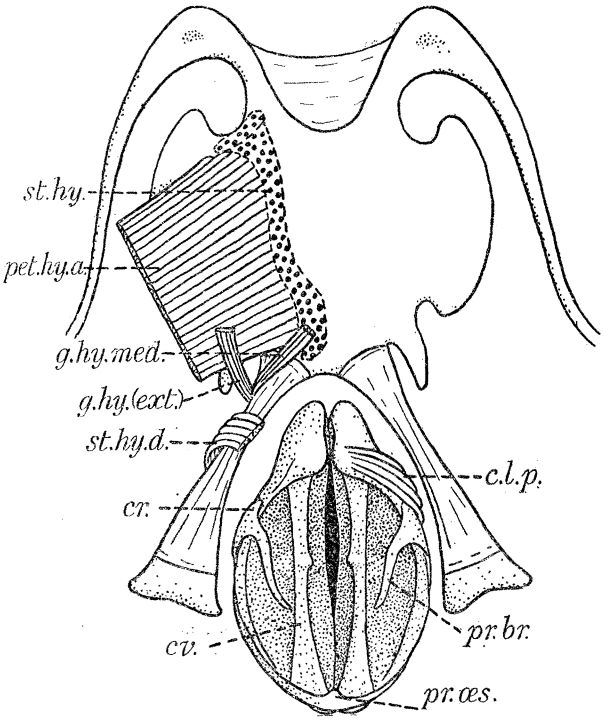

FIG. 27.—*Crinia signifera*, male. Hyoid and larynx, ventral; × 12. Membranous wall of larynx removed, but vocal chords left in place.

M. hyoglossus attached to ventral surface of end of postero-medial process.

M. petrohyoideus anterior inserted on ventral surface of hyoid plate, adjacent to m. sternohyoideus.

Three *petrohyoidei posteriores*, the first two on the lateral edge, the third on the posterior edge of the postero-medial process; the second very slender in the male.

M. dilatator laryngis typical, broader in male than in female; *constrictor externus* typical; *constrictor anterior* in part confluent with *constrictor externus* in front, in part ending near to this and to the posterior constrictor in connective tissue in front of arytænoids; inter-cricoid ligament continued outwards, in male ending in fibrous tissue between lung and œsophagus, in female, continuous with hyocricoid ligament; *M. constrictor posterior* muscular throughout, uninterrupted.

Mixophyes fasciolatus Günther.

Female (young), 28 mm. from snout to vent; from New South Wales. [Professor J. P. HILL.]

Hyoid and Laryngeal Skeleton.—Width of hyoid plate greater than its length. Hyale relatively well developed (a juvenile character) with a small blunt anterior process. Alary process small, not expanded; postero-lateral process fairly long, slender; postero-medial process relatively broad, weakly ossified, and with an expanded, rounded, cartilaginous end.

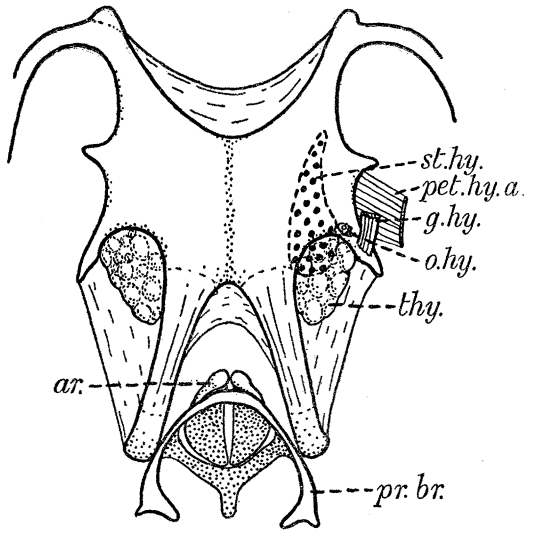

FIG. 28.—*Mixophyes fasciolatus.*—Hyoid and laryngeal skeleton, ventral; × 12.

Arytænoid rounded, approximately equilateral. *Cricoid* a complete ring, wider dorsally than ventrally, curving outwards laterally to meet the ends of the postero-medial processes, with which it is united by fibrous tissue; œsophageal process short, rectangular; bronchial processes well developed each ending in two blunt branches on ventral surface of entrance to lung.

Muscles.—*Mm. intermandibularis posterior* and *interhyoideus* typical.

M. sternohyoideus attached to a continuous area on lateral part of ventral surface of hyoid plate and on anterior part of thyroid gland, which, as might be expected in a young frog, is relatively large.

Mm. omohyoideus and *geniohyoideus* typical.

M. hyoglossus attached to ventral surface of distal end of postero-medial process.

M. petrohyoideus anterior inserted on lateral edge of hyoid plate, between alary and postero-lateral processes.

Mm. petrohyoidei posteriores primus and *secundus* inserted in the typical manner on the edges of the bony postero-medial process, and *m. tertius* upon its cartilaginous end.

M. dilatator laryngis simple. *M. constrictor externus* typical; *m. constrictor anterior* confluent with it in front, attached to the inter-cricoid ligament behind; *m. constrictor posterior* muscular throughout, uninterrupted.

Previous Work on Leptodactylidæ.

The larynx of the Leptodactylidæ was previously known only in the genus *Ceratophrys*, and the muscles have never been described.

HENLE'S figure (1839) of the laryngeal skeleton of *C. boiei* (= *granosus*) shows a cricoid with a minute, blunt œsophageal process, and with well developed, straight bronchial processes expanded at the ends.

BLUME (1930) described the hyoid and laryngeal skeleton in *C. cornuta*. The hyoid is broader than long, without anterior or alary processes, and with long postero-medial processes. The arytænoid is large (in a male specimen), with pulvinaria. The cricoid ring is complete, there are strong lateral processes, syndesmotically united with the postero-medial process; the œsophageal process is blunt; articular and cardiac processes are not prominent; the bronchial process is stout with the end expanded.

The same author investigated, by means of sections, the larynx of a female of *C. boiei*. In it the arytænoids have the pharyngeal apex acute. There is no cartilago basalis. Pulvinaria vocalia of the Ranid type are not present, but they are represented by fibrous pads between and inside the corners of the arytænoid. It is not clear, from BLUME'S description whether they are paired or median. The description of the cricoid agrees with HENLE'S account; the shaft of the bronchial process is longer and more slender than in *C. cornuta*.

HYLIDÆ.

Hyla rubra, Daudin.

Range: Brazil, Guiana, Ecuador.

Male, 42 mm. from snout to vent, from Therezopolis, Brazil. [SLADEN.]

*Hyoid and Laryngeal Skeleton.**—Width of hyoid plate double its median length; hyoglossal sinus deep and wide, extending backwards behind the level of the alary processes. Hyale without anterior process. Alary process small, with narrow base; postero-lateral process simple, tapering; postero-medial processes widely diverging, each with the bony shaft rather abruptly incurved at its distal end, and with a long, tapering cartilaginous epiphysis, closely apposed to the larynx.

Arytænoid long, more than one-seventh of the body length, with a corner projecting forwards into the pharynx; its inner concave surface with a transverse ridge (as in *H. aurea* and *H. cœrulea*); a short rod of cartilage supporting each end of the vocal chord and a process of the arytænoid supporting the frenulum; no cartilago basalis; pulvinaria vocalia small. *Cricoid* complete, broad ventrally; œsophageal process represented by a slight expansion; bronchial processes short, simple; no muscular processes; hyo-cricoid union close, fibrous.

Muscles.—M. intermandibularis posterior typical. *M. interhyoideus* thin, pouched over the vocal sac (which is described as " external ").

Hyoid insertions of right and left *sternohyoidei* widely separate; *M. sternohyoideus dorsalis* attached to the shaft of the postero-medial process.

M. omohyoideus well developed, typical.

M. geniohyoideus with external insertion on the postero-lateral process; internal part aponeurotic over the paired part of *m. hyoglossus*.

* W. K. PARKER (1881, p. 179, pl. 33, fig. 9) finds in the hyoid of his *H. rubra* a small median posterior ossification, and a pair of anterior processes, neither of which is present in my specimen.

M. hyoglossus attached comparatively far forwards on the bony shaft of the postero-medial process.

M. petrohyoideus anterior with a long insertion on the lateral edge of the hyoid plate.

Three *petrohyoidei posteriores*, the first slender, attached to the edge of the middle region of the postero-medial process, the second and third larger, attached close together on the edge of the broad part of the bony postero-medial process; only a few fibres of the third attached to its cartilaginous epiphysis.

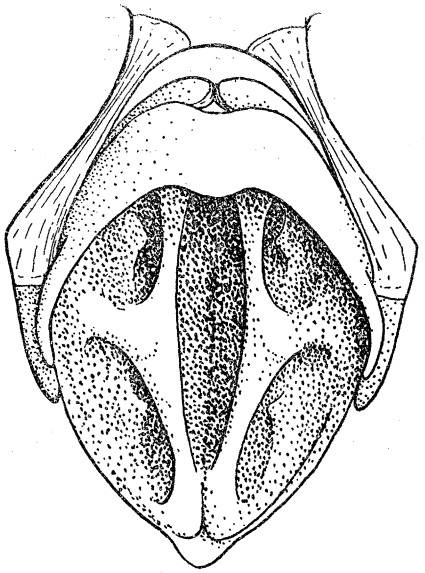

FIG. 29.—*Hyla rubra*, male. Larynx, ventral, with membranous wall removed but with vocal chords and lining of larynx in place. × 9.

M. dilitator laryngis attached at one end along the outer edge of the long cartilaginous epiphysis of the postero-medial process, at the other end to the arytænoid. *M. constrictor externus* typical, much shorter than the arytænoid, confluent in front with *m. constrictor anterior;* inter-cricoid ligament present, not continuous with hyocricoid ligaments. *M. constrictor posterior* with a short belly on the pharyngeal side only, its cardiac half being tendinous.

The vocal chord has a broad recurved lower (posterior) lip, and a tough fibrous frenulum; its supporting cartilages have been described above. In the pulmonary chamber of the larynx two fibrous prominences arise from each lateral wall, each connected with the frenulum by membrane. They are less freely movable than the single pair of bulbous prominences in the Australian Hylas (*vide infra*, p. 442), but they probablyi nfluence the nature of the call.

Hyla annectens (Jerdon).

Range: Upper Burma.

Male, 39 mm. from snout to vent, from Tongking. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Hyoid plate very short; hyoglossal sinus deep, bounded by narrow manubria, with the alary processes arising from them by narrow stems. Hyale slender, with a short anterior process. Postero-lateral process long, slender. Postero-medial process long, with the inner corner of its cartilaginous epiphysis produced, supporting the cricoid.

Arytænoid very large, 5½ mm. long, *i.e.*, 14% of the body length, with gently rounded pharyngeal border; pulvinaria vocalia small; an elongate *cartilago basalis* present. *Cricoid* broad laterally, at its syndesmotic union with the postero-medial process; without processes on the pharyngeal side; cardiac processes developed; bronchial processes short, slender, simple.

Muscles.—*M. internandibularis posterior* strong, typical. *M. interhyoideus* thin, pouched, surrounding the median, gular, vocal sac.

M. sternohyoideus with main insertion linear, near the edge of the hyoid, from the alary process backwards on to the thyroid membrane. *Sternohyoideus dorsalis* inserted on the middle third of the postero-medial process.

M. omohyoideus inserted at the origin of the postero-lateral process.

M. geniohyoideus typical; its inner portion aponeurotic over the paired part of m. hyoglossus.

M. hyoglossus attached to the ventral surface of the postero-medial process, in front of its posterior end.

M. petrohyoideus anterior attached to the lateral edge of the hyoid plate and the ventral surface of the alary process. Three *posterior petrohyoidei*, the first two attached to the edge of the posterior half of the postero-medial process, the third to its cartilaginous end.

M. dilatator laryngis a broad short band of muscle, attached to the long cartilaginous end of the postero-medial process, and to the arytænoid. *M. constrictor laryngis externus* exceptionally large, attached to the dorsal side of the bony postero-medial process. *M. constrictor anterior* as long as the arytænoids, with an antero-posterior direction; in front, divided into an inner part ending on the hyo-arytænoid membrane, and a lateral part attached to the inner edge of the bony postero-medial process. *M. constrictor posterior* uninterrupted, with tendinous antero-ventral half.

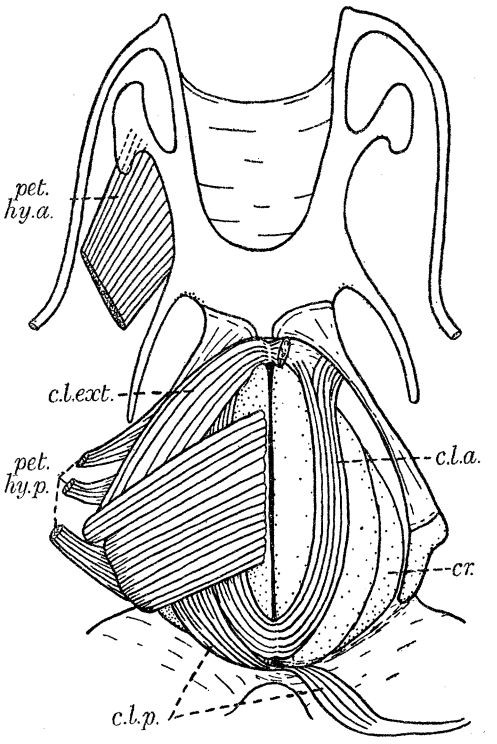

FIG. 30.—*Hyla annectens*, male. Hyoid and larynx, dorsal; × 7½. On the right mm. dilatator and constrictor externus are removed, and m. contrictor posterior is turned back.

In the *interior of the larynx* there are no enlarged prominences; the frenulum of the vocal chord is very short and, on the pulmonary side of it, the somewhat kidney-shaped outline of the *cartilago basalis* can be seen through the transparent lining of the larynx.

Hyla versicolor, Le Conte.

Range: Eastern North America.

Female, 53 mm. from snout to vent. [ZOOL. SOC.]

Hyoid and Laryngeal Skeleton.—Width of hyoid plate about three times its length in the middle line; hyoglossal sinus wide and deep, bounded on each side by a slender manubrium, from the base of which arises the alary process, consisting of a narrow,

anteriorly directed stalk terminating in a small lobe. Hyale long, slender, without anterior process. Postero-lateral process slender, simple; postero-medial process long and slender with a small cartilaginous end.

WILDER (1896, fig. 48) has figured the larynx of the male; it is very large and fills the wide space between the postero-lateral processes. In contrast to this the larynx of the female is small and leaves a considerable space between it and the posterior end of the hyoid plate. The arytænoids are small, without accessory cartilages. The cricoid has a short, blunt œsophageal process and a pair of slender, tapering bronchial processes; it is otherwise a simple ring, firmly connected by fibrous tissue to the ends of the postero-medial processes. WILDER described a pair of sesamoid cartilages in the male, but none are present in this female.

Muscles.—Mm. intermandibularis posterior and *interhyoideus* simple and typically developed.

M. sternohyoideus inserted on the manubrium and along the lateral part of the hyoid to the postero-medial process, near the anterior-end of which the dorsal portion of the muscle has its insertion.

M. omohyoideus with typical insertion at the angle between postero-lateral and postero-medial processes.

M. geniohyoideus with typical internal insertion with the hyoglossus, the contribution of *m. lateralis* to this insertion being distinguishable over the paired part of the hyoglossus as a very thin layer, with the thicker, narrower *m. medialis* lying on its ventral surface, and attached only to the epiphysis of the postero-medial process. External insertion typical, on the postero-lateral process.

M. hyoglossus typical.

M. petrohyoideus anterior attached to the edge of the hyoid, from the end of the alary process to the base of the postero-lateral.

Three *petrohyoidei posteriores*, the first and second attached to the bony postero-medial process, the third to its cartilaginous tip and to the cricoid.

Mm. dilatator laryngis and *constrictor lar. externus* stout, with typical attachments. *M. constrictor anterior* with its anterior end in part fused with the *constrictor externus*, in part inserted on the hyo-arytænoid membrane. Inter-cricoid ligament continuous on either side with the hyocricoid ligament. *M. constrictor posterior* with a short belly and with its cardiac third tendinous.

The interior of the larynx has no macroscopical peculiarities, as is to be expected in a female.

Hyla aurea, Lesson.

Range: Whole of Australia, Tasmania (introduced into New Zealand and New Caledonia).

Male and female, 65 mm. from snout to vent, from North Island, New Zealand. [Mrs. CORBET.]

Hyoid and Laryngeal Skeleton.—Width of hyoid plate little more than its length. Hyale without anterior process or extra-hyal. Alary process, a lobe on a slender stem,

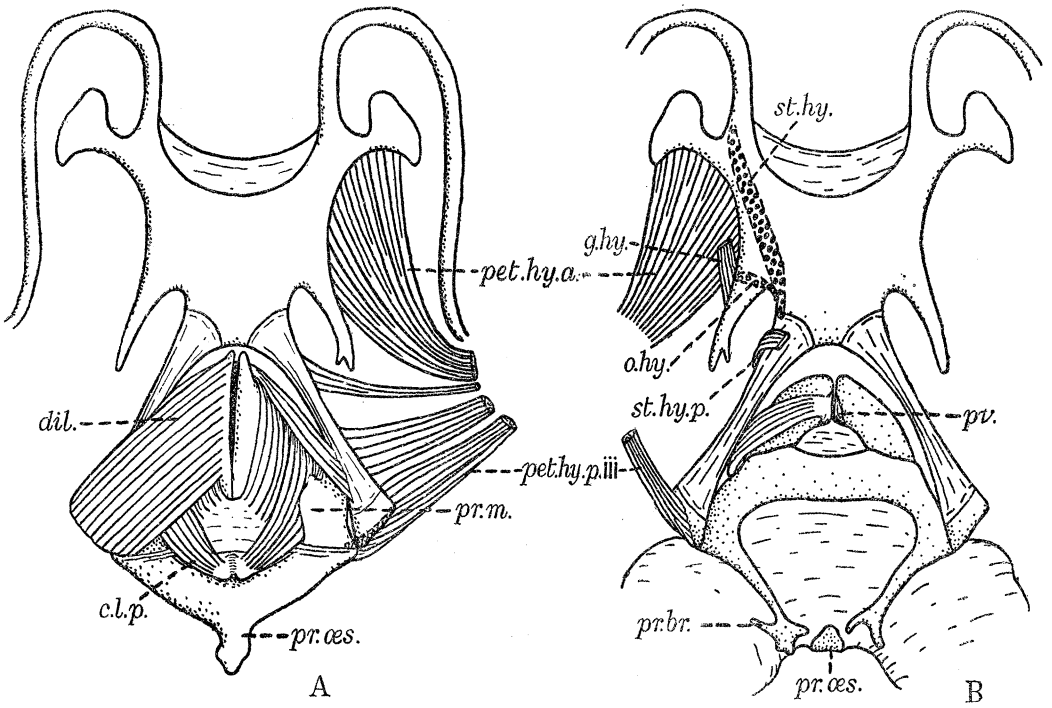

FIG. 31.—*Hyla aurea*, male. Hyoid and larynx, with some of the muscles. A. Dorsal; B. Ventral. × 4.

borne on the narrow manubrium; postero-lateral process rather long, slender and simple; postero-medial process with a cartilaginous end of moderate size.

Arytœnoid with an acute apex projecting into the pharynx; its inner concavity traversed by a ridge for the attachment of the frenulum; *cartilago basalis* absent or too small to be detected by dissection; pulvinaria vocalia moderate. *Cricoid* a complete ring, strong, broad; œsophageal process broad, trilobed, bent round posterior end of larynx so as to appear in a ventral view; articular process low; lateral process low, united by syndesmosis with the end of the postero-medial process; muscular process broad, lying on the *outer* side of m. constrictor posterior; cardiac processes blunt; bronchial processes blunt with more or less expanded ends bearing short branches.

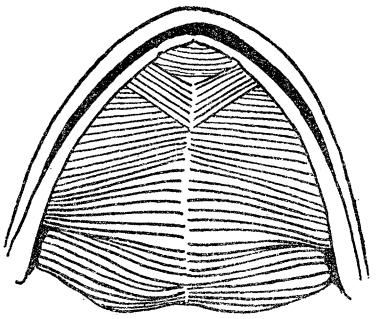

FIG. 32.—*Hyla aurea*, male. Ventral muscles of throat.

Muscles.—M. intermandibularis posterior differentiated in front into a superficial part, with fibres sloping backwards towards the middle line, and a deep part, with fibres approximately transverse; behind, composed in the male of coarse fasciculi, which function with *m. interhyoideus* in contracting the median, gular, vocal sac.

M. sternohyoideus inserted on the lateral part of the hyoid plate, from the alary process to the base of the postero-medial process; insertion of *pars dorsalis* continuous with this on the edge of the anterior part of the postero-medial process.

Mm. omohyoideus and *geniohyoideus* typical.

M. petrohyoideus anterior inserted on the lateral edge of the hyoid from the posterior edge of the alary process to half way along the postero-lateral process. Three *posterior petrohyoids*, of which the first two are inserted on the lateral edge of the bony shaft and the last on the ventral and posterior sides of the cartilaginous end of the postero-medial process.

M. hyoglossus not reaching the end of the postero-medial process, but with a rather narrow insertion near the distal end of its bony part.

M. dilatator laryngis broad, attached laterally to the distal edge of the postero-medial process and to the lateral process of the cricoid. *M. constrictor externus* typical. *M. constrictor anterior* confluent with it in front; inter-cricoid ligament continuous at each side with a band of fibres crossing, and closely connected with the lateral process of

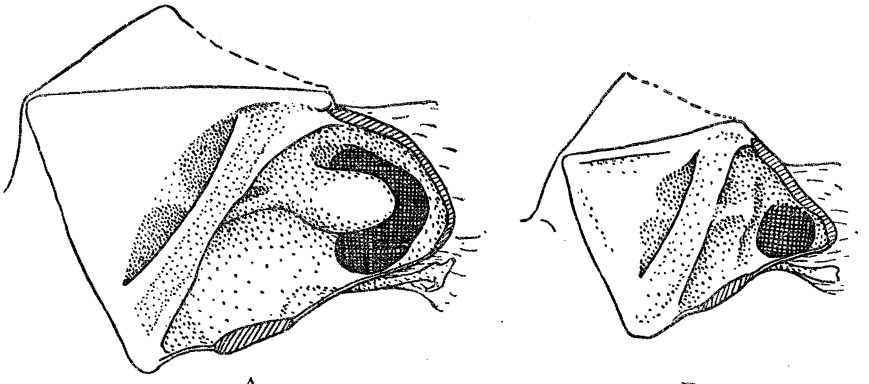

FIG. 33.—*Hyla aurea.*—Interior of right half of larynx in a male (A) and a female (B) of the same size, drawn to the same scale. × 6.

the cricoid, and ending on the postero-medial process, thus corresponding to the hyo-cricoid ligament. *M. constrictor posterior* muscular throughout, its superficial fibres attached to the edges of the muscular process of the cricoid, but its deep fibres passing beneath it without being interrupted.

Sexual Differences.

The larynx and postero-medial processes are much larger in the male than in the female of the same size, as the following measurements testify:—

Length of postero-medial process, male 8 mm., female, $6\frac{3}{4}$ mm.

Length of arytænoid, from pharyngeal apex to posterior pulvinar, male, $7\frac{3}{4}$ mm.; female, $4\frac{1}{2}$ mm.

Length of larynx, from apex of arytænoids to end of œsophageal process of cricoid, male, $9\frac{3}{4}$ mm., female, $6\frac{1}{2}$ mm.

Distance between lateral corners of postero-medial processes, male, 11 mm., female, 8½ mm.

Inside the larynx of the male at the point where the frenulum of the vocal chord is attached to the wall on each side, a large fibrous swelling, with a narrow base, projects into the cavity of the larynx across the laryngo-pulmonary opening, so that air passing out from the lungs must cause it to vibrate. This swelling is not present in the female.

Apart from these remarkable sexual differences the structure of the larynx is the same in both specimens.

Hyla ewingii, Duméril and Bibron.

Range; Eastern and southern Australia, Tasmania. (Variety introduced into New Zealand.)

Male, 30 mm. from snout to vent, from Upper Manning River, New South Wales. [Professor J. P. HILL.]

Hyoid and Laryngeal Skeleton.—The hyoid was described and figured by W. K. PARKER (1881, p. 170, Plate 31, fig. 3). Hyoid plate rather short; hyoglossal sinus

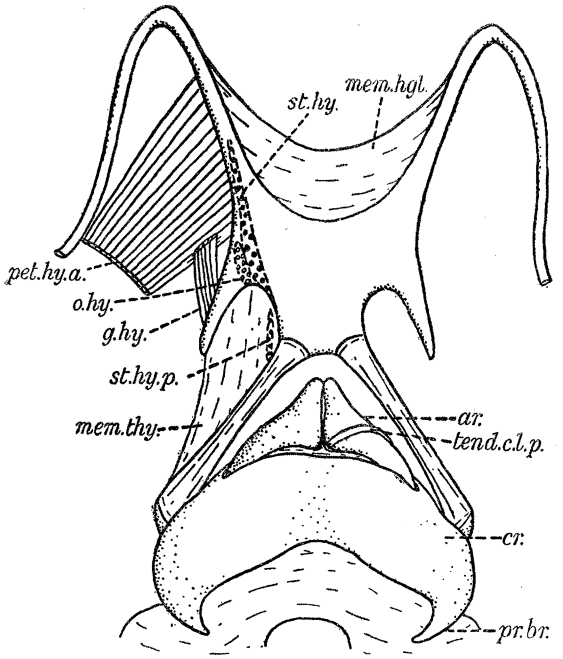

FIG. 34.—*Hyla ewingii*, male. Hyoid and larynx, ventral. × 9.

wide and deep. Hyalia slender, without anterior processes; alary process absent; postero-lateral process slender, simple; postero-medial process with small cartilaginous end, firmly attached to the cricoid.

Arytænoids large, about one-seventh of the body length; upper part of each presenting a large flat surface to the other; a process of the arytænoid supporting each end of the vocal chord, and a buttress-like ridge of its inner surface supporting the frenulum;

at the triangular base of this buttress, a flat triangular *ossicle*, in place of a basal cartilage. Pulvinaria minute. *Cricoid* very broad and strong; œsophageal process blunt; muscular process broad, plate-like, overlying the aponeurotic portion of the posterior constrictor. Cardiac side of cricoid still broader, swollen on each side of the middle line to support the walls of the large chamber between the vocal chord and the pulmonary opening, which is partially supported by the short bronchial process. The length of the larynx, from the anterior point of the arytænoids to the end of the œsophageal process, is 5½ mm., *i.e.*, is contained five and a half times in the body length.

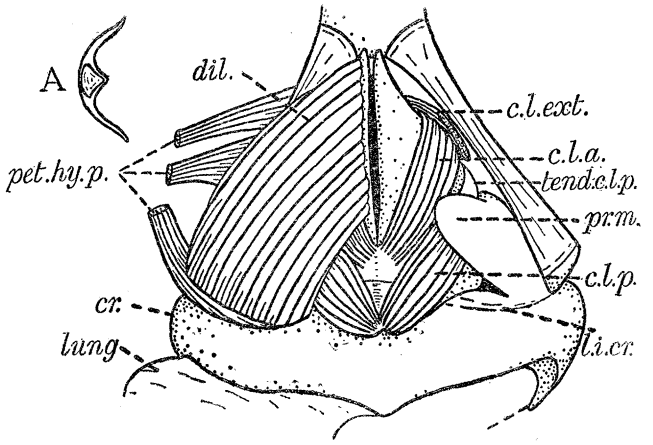

FIG. 35.—*Hyla ewingii*, male. Larynx, dorsal. × 9. A. Diagram of ventral edge of arytænoid, with basal ossicle in place (not to same scale).

Muscles.—M. intermandibularis posterior with a superficial layer differentiated anteriorly, with fibres running backwards and medialwards; behind this, and dorsal to it, fibres transverse or running slightly forwards to the middle line, where there is a *linea alba.*

M. interhyoideus pouched and very thin, with fine fasciculi, surrounding the large median gular sac.

M. sternohyoideus with a narrow insertion near the edge of the hyoid; insertion of *pars dorsalis* continuous with this, on the thyroid membrane.

M. omohyoideus typical, well developed.

M. geniohyoideus typical; internal portion aponeurotic posteriorly.

M. hyoglossus attached along the whole length of the ventral surface of the postero-medial process.

M. petrohyoideus anterior with typical insertion along edge of hyoid plate.

Three *petrohyoidei posteriores*, the first and second inserted on the lateral edge of the bony postero-medial process, the third in part on its posterior edge, but mainly on the cricoid.

M. dilatator laryngis a large, stout muscle, with broad area of attachment to the flat surface of the pharyngeal part of the arytænoid; at its other end, attached to the dorsal

surface of the posterior part of the postero-medial process, and to the cricoid, along the line strengthened by the inter-cricoid ligament. *M. constrictor anterior* confluent in front with *m. constrictor externus ; m. constrictor posterior* with a short belly between its attachment at the posterior, pharyngeal corner of the arytænoid and the muscular process of the cricoid, beneath which it is aponeurotic, continuing so to its attachment to the cardiac pulvinar vocale. Although the pharyngeal pulvinar is minute the muscle narrows abruptly to be attached to it and not directly to the surface of the arytænoid.

The interior of the larynx is remarkable for the large size of the chamber on the pulmonary side of the vocal chords. From each lateral wall of this chamber projects a large, movable spherical protuberance, continuous with the frenulum, and lying across the pulmonary orifice ; it is produced laterally into a small papilla, is narrowly attached to the wall, and must vibrate as air passes from lung to larynx or *vice versa.*

Hyla cærulea (J. White).

Range : South-eastern New Guinea, Eastern, Northern and Western Australia.

Two males, 86 and 68 mm. from snout to vent. [Zool. Soc.]

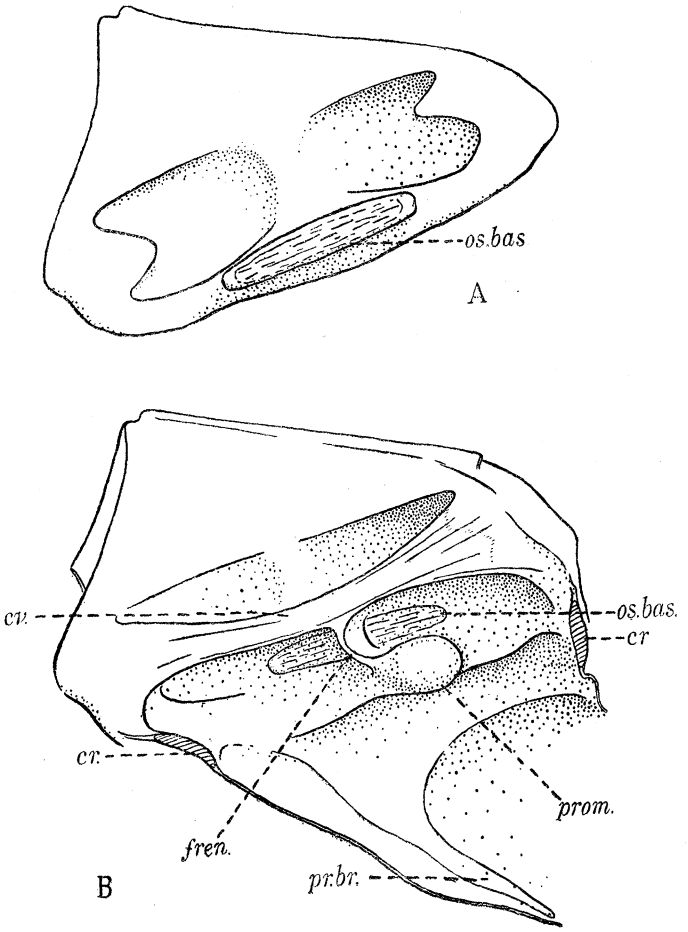

Fig. 36.—*Hyla cærulea*, male. A. Right arytænoid, from within. B. Right half of larynx, from within. *prom.* = " prominentia laryngo-trachealis."

Hyoid and Laryngeal Skeleton.—Hyoid plate very short in the middle line, its width being double its length. Hyale slender, without anterior process. Alary process reduced to a small nodule at the side of the narrow manubrium ; postero-lateral process long, tapering ; postero-medial process long, expanded at the ends, with cartilaginous epiphysis of moderate size.

Arytœnoid large, with indented apex projecting forwards into pharynx ; its apical region presenting a large flat surface to its fellow ; its concave part crossed by a supporting ridge for the frenulum of the vocal chord, and bounded at each end by a process for attachment of the vocal chord. *Cartilago basalis* represented by a flat, elongate *ossicle. Cricoid* narrow on the pharyngeal side ; œsophageal process absent or minute ; muscular process broad, as in *H. aurea* and *H. ewingii* ; cardiac process low ; bronchial process slender and simple.

Muscles.—M. intermandibularis posterior without a differentiated superficial layer. *M. interhyoideus* thin, pouched over the median gular vocal sac.

The muscles attached to the hyoid are not well enough preserved to admit of accurate description.

M. dilatator laryngis attached at one end entirely to the postero-medial process, at the other to the arytænoid.

M. constrictor externus slender, with typical attachment to the inner border of the postero-medial process.

M. constrictor anterior united to *M. constrictor externus* in front ; inter-cricoid ligament without the usual connection with the end of the postero-medial process, which ends at some distance in front of it. *M. constrictor posterior* interrupted superficially by the muscular process of the cricoid, but with its deeper layers continuous under the cartilage ; inserted on the cardiac corner of the arytænoid by a short flat tendon.

The *interior of the larynx* resembles that of the males of *Hyla aurea* and *H. ewingii* in having a bulbous prominence projecting across the mouth of the lung. No females were dissected, but the prominence is probably confined to the male as in *H. aurea.*

W. K. Parker (1881, p. 193, Plate 15, fig. 8) described the hyoid of this species and showed reduced alary processes, not completely fused with the hyoid ; he also showed an ossification in the hyoid plate which is absent in my specimens.

Phyllomedusa dacnicolor, Cope.

Range : Mexico.

Female, 65 mm. from snout to vent. [Zool. Soc.]

Hyoid and Laryngeal Skeleton.—Length of hyoid plate about one and a quarter times its width. Hyale slender, without anterior process. Alary process absent ; postero-lateral process long and slender ; postero-medial process about as long as hyoid plate, ending in a simple cartilaginous cap.

Larynx much smaller than laryngeal sinus, indicating a considerable sexual difference in size of larynx. *Arytœnoid* not deeply concave, without basal or apical cartilages ;

pulvinaria vocalia of moderate size. *Cricoid* with short œsophageal process, moderate pharyngeal articular process and very slight cardiac ; muscular process well developed, situated outside m. constrictor posterior ; bronchial processes simple, slender, not very long.

Muscles.—Mm. intermandibularis and *interhyoideus* not well enough preserved for description.

M. sternohoideus with a continuous insertion on lateral part of hyoid plate, extending on to inner edge of postero-lateral process.

M. geniohyoideus with internal division aponeurotic over paired part of m. hyoglossus.

M. omohyoideus present.

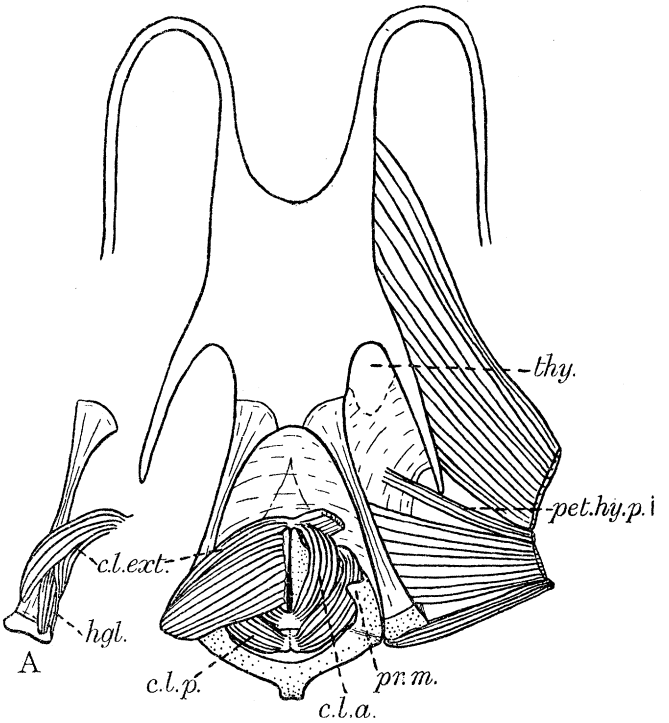

FIG. 37.—*Phyllomedusa dacnicolor*, female. Hyoid and Larynx, dorsal. A. A postero-medial process showing the hyoglossus dividing the constrictor externus.

M. hyoglossus well developed, behind wrapping round inner edge of posterior part of postero-medial process ; attached partly to its ventral and partly to its dorsal surface, the dorsal slip splitting m. constrictor laryngis externus into two.

M. petrohyoideus anterior with a long insertion on the edge of the hyoid plate and its postero-lateral process, not pierced by the lingual artery and nerve (*cf. Megalophrys*).

Three *petrohyoidei posteriores* ; the first slender, ending on the thyroid membrane ; the second broader, attached to the bony postero-medial process ; the third slender, inserted on the posterior edge of the cartilaginous end of this process.

M. dilatator laryngis well developed, simple. *M. constrictor externus* with its hyoid attachment divided into two by m. hyoglossus, the inner part the more slender, attached

by a minute tendon. *M. constrictor anterior* in front confluent with the medial end of the constrictor externus, behind attached to a well-marked inter-cricoid ligament.

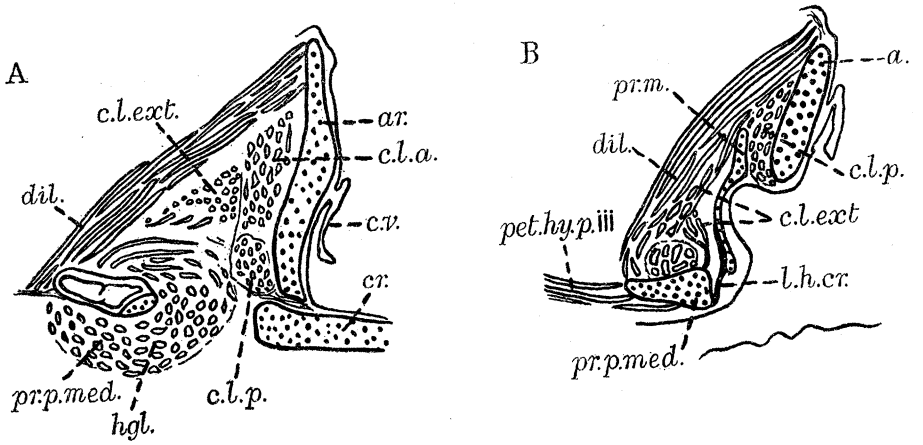

FIG. 38.—Transverse sections of half-larynx of *Phyllomedusa dacnicolor*, showing the attachment of m. hyoglossus to both surfaces of the postero-medial process. A is more anterior than B.

M. constrictor posterior passing without interruption between the arytænoid and the muscular process of the cricoid, attached at each end to a pulvinar, at the cardiac end by a short tendon.

Previous Work on Hylidæ.

HENLE described the hyoid and larynx of three species of *Hyla*, *H. punctata*, *H. venulosa* and "*H. sceleton.*" Of the last he said very little, but his figure of the hyoid of *H. venulosa* shows a very short hyoid plate, and in *H. punctata* he described a cartilage supporting the vocal chord.

W. K. PARKER (1881) figured the hyoids of seven species of *Hyla* and of *Phyllomedusa bicolor* and *Nototrema marsupiatum*. These all have a relatively short hyoid plate; the anterior processes are absent except in *Hyla rubra* (but they are absent in my specimen of this species); alary processes are absent in *H. ewingii* and *H. phyllochroa*, and much reduced in *H. arborea*, *H. albomarginata* and *H. cærulea* (= *Pelodryas cæruleus*). In the last-named and in his *H. rubra* the figures show an ossification in the hyoid plate which is absent in my specimens.

WILDER (1896) described the larynx of *Hyla versicolor*, *Acris gryllus* and *Chorophilus feriarum*. He referred to *Hyla* (*Hylodes*) *pickeringii*, but without describing it in detail. The three species have the hyoid plate very short and, in the male, a very large larynx. He described the basal cartilages of the arytænoids of the males and also "sesamoid cartilages" in the median raphe of the constrictor externus. In *Acris* and *Chorophilus* the *constrictor anterior* is continuous anteriorly with the *constrictor externus*, and this prevented WILDER from recognizing it as the homologue of the *constrictor anterior* of *Rana* and of *Hyla versicolor*. The *constrictor posterior* is absent in *Chorophilus*, half tendinous in *Acris* and *Hyla versicolor*.

BLUME (1930) described the laryngeal cartilages in seven Hylid species, namely, *Hyla arborea*, *H. faber*, *H. cinerea-evittata*, *H. pickeringii*, *Chorophilus feriarum*, *Acris gryllus* and *Phyllomedusa moschata*. Males of five species, *H. arborea*, *H. faber*, *H. pickeringii*, *C. feriarum* and *P. moschata* were described. In these the *arytænoid* is very large, with a flat triangular surface opposed to its fellow near the aditus, this region being separated from the thickened basal region by a spindle-shaped groove which in *P. moschata* is bisected by a ridge. A cartilago basalis is described in four (in *H. faber*, which was not sectioned, its presence or absence was not ascertained); it is spindle-shaped in *H. arborea*, *H. pickeringii* and *Chorophilus*. In *P. moschata** it is stated to be large and spherical and to be composed of "Jungknorpel." Sesamoid cartilaginous nodules are present; in *H. arborea* these are an anterior pair united by a commissure, and probably situated in the median raphe of *m. constrictor externus* (although BLUME does not describe the muscles), and a posterior pair, which from their position may lie in the fascia of attachment of *m. constrictor anterior;* in *H. pickeringii* there is no anterior pair, and the posterior pair are procartilaginous; in *C. feriarum* an anterior pair alone is present, probably in the *constrictor externus*. *Phyllomedusa* has no sesamoids, but a longitudinal rod of cartilage is present in the vocal chord. Pulvinaria vocalia are present in *H. arborea*, in *H. pickeringii* and *Phyllomedusa*, but they are not mentioned in the description of *Chorophilus*, and are probably absent. The *cricoid* of the male *H. arborea* is narrow on the pharyngeal side, broader laterally and ventrally, with well-developed cardiac processes, slender, simple bronchial processes, and with the œsophageal process represented by a blunt nodule. The male of *H. faber* (which BLUME examined only macroscopically) resembles *H. arborea* in the shape of the cricoid; *Chorophilus* has no important cardiac and articular processes, but in *H. pickeringii* these are as well-developed as in *Rana esculenta*. *Phyllomedusa moschata* is the only Hylid described by BLUME in which there are muscular processes of the cricoid.

Females of *H. arborea*, *H. cinerea-evittata* and *Acris gryllus* are described. In them the inner surface of the arytænoid is concave, not moulded as in the males. The cricoid of the female *H. arborea* is a ring of uniform width, with slender bronchial processes. In *Acris gryllus* the cricoid is incomplete on the cardiac side, although it is complete in the male according to WILDER.

BUFO.

Bufo arenarum, Hensel.

Range: S. America.

Male, 107 mm. from snout to vent, from Monte Video. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Width of hyoid plate three-fifths of its length in the middle line. Hyale without anterior process, somewhat expanded at the level of the angle of the jaw. Alary process elongated in an antero-posterior direction, with a bifurcated posterior lobe; postero-lateral process expanded distally; postero-medial

* But see p. 513.

process with an hour-glass shaped bony shaft, somewhat twisted and bent sharply dorsalwards in its middle, narrow region; with a large, triangular cartilaginous end, abutting proximally upon the lateral process of the cricoid.

Arytœnoid with relatively short base, and with high, acute apex projecting forwards into the pharynx; no apical cartilage or pulvinaria vocalia; dorsal and ventral corners overlapping the cricoid.

Cricoid a stout, complete ring, narrower between the cardiac processes; œsophageal process short, blunt, and slightly notched; lateral process strong, presenting a flat facet to a short ingrowth of the cartilaginous end of the postero-medial process of the hyoid,

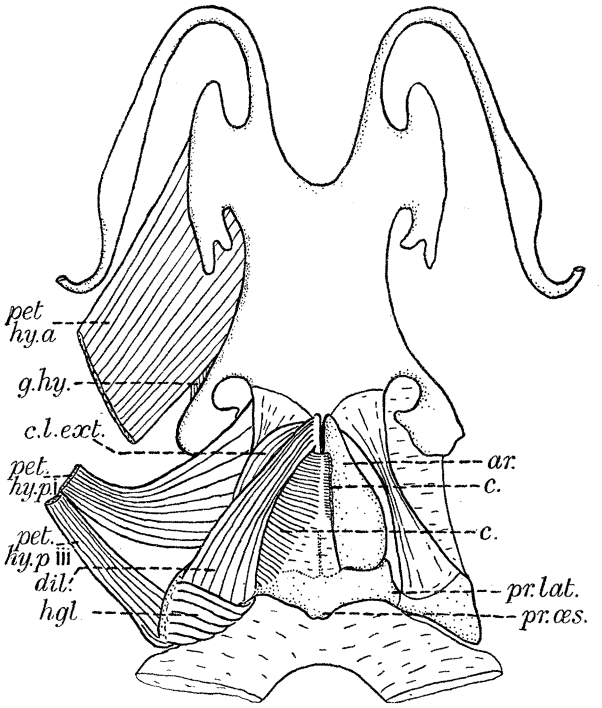

FIG. 39.—*Bufo arenarum*, male. Hyoid and larynx, dorsal. × 3. Muscles not shown on the right. Lungs diagrammatic.

from which it is separated by a thin fibrous layer; bronchial processes long and straight, with slightly expanded ends.

Muscles.—Mm. intermandibularis and *interhyoideus* typical.

M. sternohyoideus inserted on the ventral side of hyoid plate, in a narrow area, which crosses the base of the alary process, and slopes inwards to the middle line, so that on the posterior half of the hyoid plate it is adjacent to the muscle of the other side. *M. sternohyoideus dorsalis* with insertion continuous with this, extending along the whole length of the outer edge of the bony shaft of the postero-medial process.

Omohyoid muscle slender, inserted at the proximal end of the postero-medial process.

M. geniohyoideus lateralis with external insertion on the edge of the proximal part of the postero-lateral process; its internal part aponeurotic over the paired part of m. hyo-

glossus, the aponeurosis having the usual insertion round the eges of the laryngeal sinus and extending also to the dorsal side of the postero-medial process with the hyoglossus, *M. geniohyoideus medialis* superficial to *M. lateralis* on the median part of the hyoglossus. and inserted directly at the front of the laryngeal sinus.

M. hyoglossus strongly developed; posteriorly each half curving round the inner edge of the cartilaginous end of the postero-medial process to be inserted upon the dorsal face of that cartilage. Since the bony process is bent sharply dorsalwards the muscle is also bent.

M. petrohyoideus anterior inserted near the edge of the hyoid plate on its ventral side and across the base of the alary process, so that this overlies it dorsally.

Two *petrohyoidei posteriores*, the first with a long insertion on the lateral edge of the bony postero-medial process, the other, representing the third of most Anura, on the edge of its cartilaginous extremity.

M. dilatator laryngis attached at one end on the dorsal side of the proximal part of the cartilaginous end of the postero-medial process, the area of attachment extending on to the lateral process of the cricoid; at the other end inserted directly on the apical region of the arytænoid. *M. constrictor externus* typical. The rest of the constrictor consists of a sheet of muscle crossing the arytænoids dorsally and attached laterally to nearly the whole length of the inner edges of the bony postero-medial processes. The muscle sheet is interrupted in the middle line by a raphe which expands over the posterior parts of the arytænoids into a thin membrane continuous with the perichondrium of the cricoid, and so represents the intercricoid ligament. The posterior fibres of the muscle thus arise from the cricoid. This muscle has the relations of the *constrictor laryngis anterior* of most Anura; there is no *constrictor posterior*.

Bufo vulgaris, Laurenti.

Range: Europe, Asia, N.W. Africa.

Male, 49 mm., and juvenile, 17 mm. from snout to vent; from England.

Hyoid and Laryngeal Skeleton.—The hyoid is well known. It differs from *B. arenarum* in having the hyoid plate relatively longer and narrower—the least width is one-third of the length in the 49 mm. specimen; in having the ends of the postero-medial processes more widely diverging, so that the hyoglossal muscle curves round a transverse edge instead of an oblique; in having the posterior lobe of the alary process simple and the end of the postero-lateral process unexpanded.

The laryngeal skeleton is like that of *B. arenarum*. In the young specimen the lateral process of the cricoid and the cartilaginous end of the postero-medial process of the hyoid are fused, with continuous cartilage; the high power lenses of the binocular dissecting microscope reveal no line of junction by transmitted light. In the adult, however, the cartilage is interrupted by a thin fibrous layer at the plane of junction, and in a third, sectioned specimen, the microscope showed the cartilages to be nowhere continuous. HENLE may have been mistaken, as BLUME (1930, p. 352) supposes,

in describing a cartilaginous fusion in *B. cinereus* and WILDER in *B. lentiginosus*, and BLUME finds the union syndesmotic in his specimens of *B. vulgaris*; but the fibrous partition is so thin that the possibility of cartilaginous fusion as an individual variation or a specific character need not be excluded.

The *muscles* of the hyoid apparatus have been described by BIGALKE (1927) and are very similar to those of *B. arenarum*.

The *omohyoid* is always rather slender, and BIGALKE (1927) found it lacking in one female. In two females he found a *petrohyoideus posterior secundus* present on one side. In the adult here described, the insertion of *m. petrohyoideus posterior I.* encroaches on the dorsal surface of the postero-medial process, instead of keeping to the edge as in *B. arenarum*. In the larynx the origin of the *dilatator* is confined to the postero-medial process of the hyoid. In the juvenile specimen none of the fibres of the *constrictor anterior* have their inner attachment on the cricoid, but a few, originating on the posterior corner of the arytænoid end *distally* on the lateral process of the cricoid.

Bufo himalayanus, Günther.

Range: India.

(*a*) Two females, 50 and 71 mm. from snout to vent; from India. [ZOOL. SOC.]

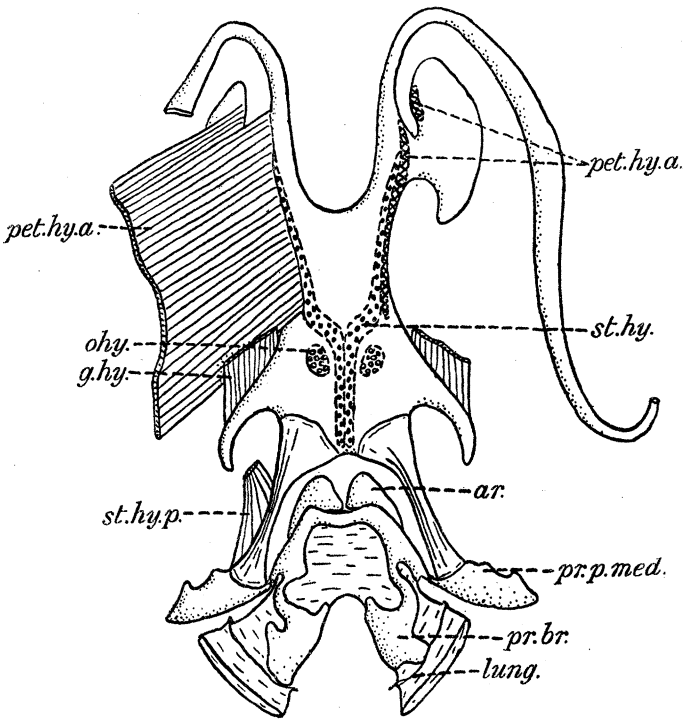

FIG. 40.—*Bufo himalayanus*, female. Hyoid and larynx, ventral. × *ca.* 3½.

Hyoid and Laryngeal Skeleton.—The hyoid is similar to that of *B. vulgaris*, but is relatively shorter, its width being about two-fifths of its length. The cartilaginous ends

of the postero-medial processes are very large, and are directed laterally. Two or three transverse fibrous bands are present in the hyoid plate and add to its flexibility.

The hyocricoid union is less intimate than in the species already described, at least as far as cartilage is concerned, but the fibrous union is very firm. The bronchial processes consist of curved stalks which expand into broad curved plates supporting the ventro-medial walls of the bronchi; the dorsal walls of the latter are vascularized.

The muscles are essentially like those of *B. vulgaris*. The *constrictor laryngis anterior*

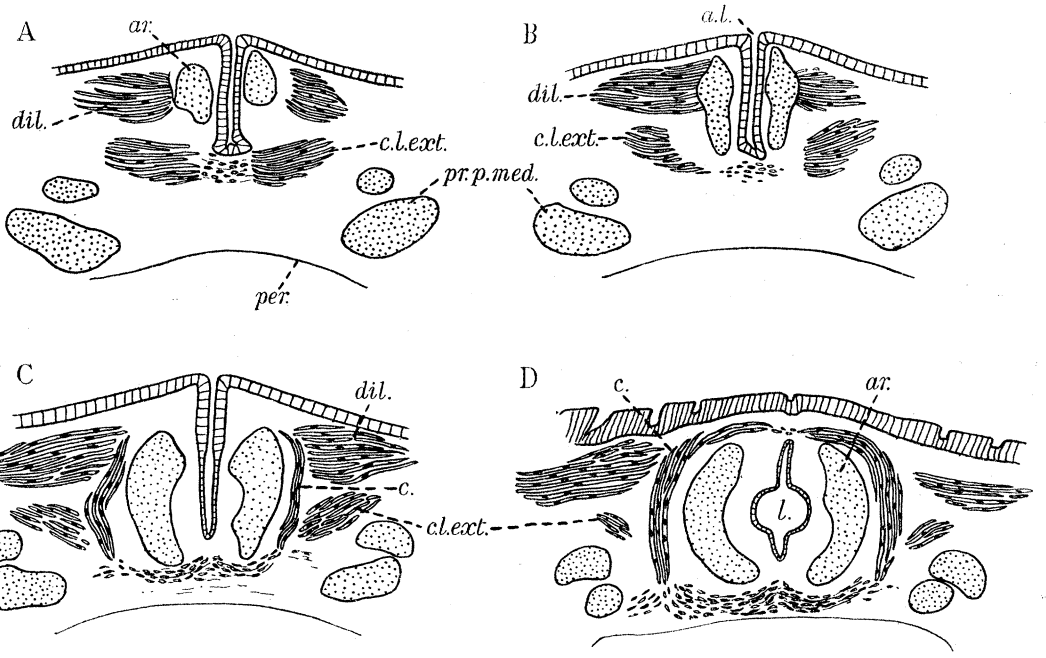

FIG. 41.—*Bufo himalayanus*.—Metamorphosing toadlet. Four sections of the larynx. A. The most anterior; D, the most posterior. *l.* = cavity of larynx. *c.* = constrictor, excluding constrictor externus.

arises from the arytænoid alone, and its insertion extends on to the dorsal side of the postero-medial process, where it is adjacent to *m. petrohyoideus posterior primus*.

(*b*) Newly metamorphosed toadlet, retaining stump of tail.*

The metamorphosis of the hyobranchial apparatus is not completed. A double bar of cartilage extends backwards from the hypobranchial plate on each side of the larynx, and represents the postero-medial process.

Cartilaginous *arytænoids* are present. The *cricoid* is a complete ring, but its mid-ventral region is procartilaginous, and its mid-dorsal region is composed of a narrow bar of thin cartilage. Bronchial processes are well developed and extend on to the roots of the lungs.

* Sections of this specimen were kindly lent to me by Mr. T. L. GREEN, then lecturer in Zoology at Imperial College of Science. They were labelled *B. melanostictus*, but, since the specimen came from India, they are more probably *B. himalayanus*.

M. dilatator laryngis is inserted on the arytænoid ; distally it ends in a condensation of tissue near the forerunner of the postero-medial process. *M. constrictor externus* extends outwards on each side from a narrow median raphe below the anterior ends of the arytænoids, and ends near the distal end of the dilatator. The remainder of the constrictor is sphincteric in character, but only its dorsal and lateral portions are muscular, the ring being completed ventrally by a broad band of tissue like that of the raphe of the constrictor externus, and continuous with it. At the junction of the muscular and aponeurotic portions, a strand of tissue extends outwards towards the postero-medial process.

Bufo carens, A. Smith.

Range : South Africa.

One male, 76 mm. from snout to vent, from Transvaal. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—The hyoid is very similar to that of *B. vulgaris*, with the exception of the postero-medial processes, which in addition to their dorsal curvature, are bowed outwards in the middle to lodge the large larynx.

The basal axis of the *arytœnoid* is nearly vertical and the cartilages are strongly convex from end to end, together forming an approximately hemispherical chamber, with short, cranially projecting apex.

The dorsal half of the cricoid is a broad band without an œsophageal process. In the region of the short lateral process it is very narrow but expands again on the ventral side. The bronchial processes have distal expansions of moderate size, as in *B. vulgaris*. The lateral process meets an outgrowth of the cartilage of the postero-medial process, but the union is syndesmotic.

The *geniohyoid* muscle has a short transverse external insertion in front of the origin of the postero-lateral process. The proximal attachment of *m. constrictor laryngis anterior* is entirely on the arytænoid, and in other respects the musculature is like that of *B. vulgaris*. The *omohyoid* muscle is very slender.

Bufo crucifer, Wied.

Range : South America.

One female, 86 mm. from snout to vent, from Brazil. [Sladen.]

Hyoid and Laryngeal Skeleton.—The length of the hyoid plate in the middle line is about three times its least width, and the whole apparatus is very similar to that of *B. vulgaris* and *B. himalayanus*, except that the alary process arises from a broader base, as in *B. arenarum*. A transverse band of fibres lies in the cartilage of the hyoid plate immediately in front of the origins of the postero-medial processes. These are curved dorsalwards and outwards, enclosing a narrow laryngeal sinus.

The *arytœnoid* is only very slightly convex from end to end ; its basal axis is nearly vertical ; the apex is high, pointed and directed cranially. The *cricoid* is like that of *B. arenarum*.

The *Muscles* are also like those of *B. arenarum*, except that the laryngeal muscles are weaker, as might be expected in a female. The last posterior petrohyoid is very slender and is attached to the extreme tip of the postero-medial process.

Bufo marinus (Linnê).

Range: South and Central America, West Indies.

One female, 130 mm. from snout to vent, from South America. [Zool. Soc.]

*Hyoid and Laryngeal Skeleton.**—Length of hyoid plate two and two-fifth times its least width; a transverse fibrous band in the cartilage in front of the origins of the postero-medial processes. Alary process with produced posterior lobe, on the right almost meeting and on the left fusing with an outgrowth of the postero-lateral process; postero-medial processes large, bent dorsalwards midway in their length; their triangular cartilaginous ends with well-marked proximal outgrowths meeting the lateral processes of the cricoid.

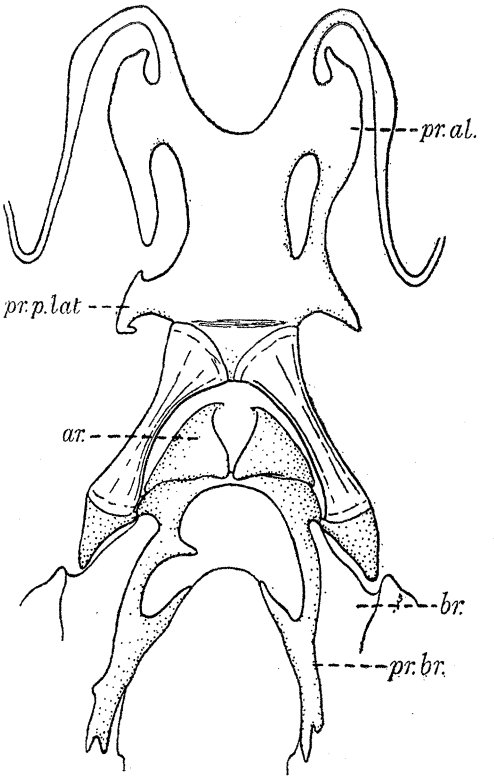

Fig. 42.—*Bufo marinus*, female. Hyoid and larynx, ventral. × 2½.

Arytœnoid concavo-convex, with base nearly vertical, and with apex pointed, directed anteriorly.

Cricoid with a short lateral process, which meets the postero-medial process in a syndesmotic union; œsophageal process short; bronchial processes long, with expanded and branched distal ends supporting the inner walls of the bronchi.

Muscles.—Anterior petrohyoid approaching the hyoid on the ventral side of the produced posterior lobe of the alary process, dividing at the edge of the hyoid plate into two layers, one with the same attachment as the whole muscle in *B. arenarum*, the other attached on the dorsal side of the hyoid plate to near the middle line.

Petrohyoideus posterior secundus present, small, inserted near the first.

Other hyoid muscles typical of the genus.

M. dilatator laryngis relatively narrow; its origin confined to the postero-medial process and not extensive enough even to hide the origin of *m. constrictor externus*. *M. constrictor laryngis anterior* like that of *B. arenarum*.

* W. K. Parker (1881, p. 204, pl. 36, fig. 5) described a specimen of *B. marinus* (= *B. agua* Latr.) in which the hyalia have lost their proximal and distal portions. This is probably abnormal, and may be an effect of old age.

Previous Work on Bufo.

DUGÈS (1835) dissected *Bufo vulgaris* and *B. calamita*, but did not see a *constrictor externus* (" hyo-pré-glottique "), and the fact that he described only one other constrictor muscle (" hyo-post-glottique ") loses its value since he missed the *constrictor posterior* even in *Rana esculenta*. He knew that only two posterior petrohyoids are present in *Bufo*.

HENLE (1839) gave a good description of the hyoid and larynx of *B. palmarum*, and referred also to *B. cinereus*. In *B. palmarum* he stated that one of the branches of the bronchial process meets its fellow in the middle line, and that the bronchus is also supported dorsally by a paired process from the dorsal part of the cricoid.

W. K. PARKER (1881) figured the hyoids of several species of *Bufo*, which, with the long rather narrow hyoid plate, the absence of anterior processes of the hyalia, the bent postero-medial processes with large terminal cartilages, conform to the pattern shown by the species here described. A specimen of *B. calamita* is described as having a band of endostosis crossing the hyoid plate behind the alary processes (*t. cit.*, p. 215, Plate 40, fig. 4).

WALTER (1887) included *Bufo cinereus* in his comparative account of the visceral skeleton and its musculature, but was inaccurate in details.

WILDER (1896) described the larynx of *B. lentiginosus*, which is typical of the genus, except that the very diagrammatic figure shows a very weak musculature.

BIGALKE (1927) described the hyoid musculature of *Bufo vulgaris*. He gave the first accurate description of the distribution of the fibres of *mm. geniohyoideus lateralis* and *medialis* in a typical Anuran. His discovery of the exceptional absence of the omohyoid in one specimen and of the occasional presence of a second posterior petrohyoid has been referred to under the heading of *Bufo vulgaris*.

Finally, BLUME (1930) has described the skeleton of the larynx in *B. vulgaris*, *B. mauretanica*, *B. calamita*, and *B. variabilis*. He noted the acute (in *B. calamita* mushroom-shaped) pharyngeal angle of the arytænoids, the absence of pulvinaria, the strong lateral processes (*tubercula hyoidea*) of the cricoid, the close, but syndesmotic, union of these with the hyoid, and the large, distally expanded bronchial processes. In *B. variabilis* the distal ends of these processes are united with a median *processus obturatorius* as in *Rana esculenta*. His method also enabled him to describe, in some species, processes from arytænoid or cricoid supporting the vocal chord.

BRACHYCEPHALIDÆ.

Dendrophryniscus stelzneri (Weyenbergh).

Range: Eastern South America.

Male, 28 mm., and female, 29 mm. from snout to vent; from Maciero, Alto Itatiaya, Brazil. [SLADEN.]

Hyoid and Laryngeal Skeleton.—Length of hyoid plate nearly three times its least width. Hyale, although broader anteriorly, without anterior process. No postero-

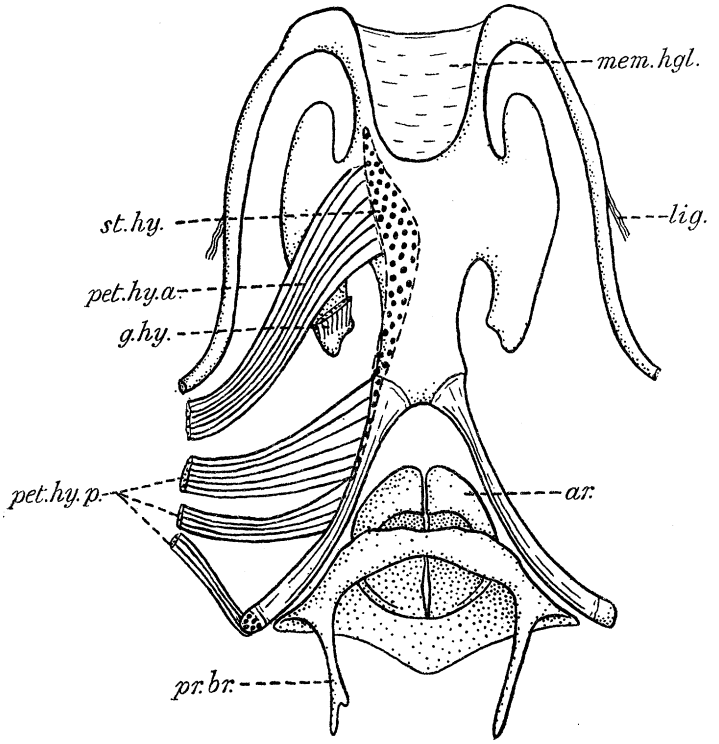

FIG. 43.—*Dendrophryniscus stelzneri*, male. Hyoid and laryngeal skeleton, with some hyoid muscles; ventral. × 13⅓.

lateral process, but posterior lobe of alary process produced, serving for the external attachment of the geniohyoid muscle; postero-medial process slender, bent dorsalwards and outwards, with small cartilaginous end.

Arytœnoid deeply concave, without apical cartilage or pulvinaria. *Cricoid* relatively, stout; with œsophageal process short, obtuse; with well-marked lateral, and straight slender bronchial processes, one of which has a minute branch.

Muscles.—M. intermandibularis posterior simple and typical. *M. interhyoideus* larger in the male than in the female, in connection with the large vocal sac.

M. sternohyoideus meeting its fellow of the opposite side on the hyoid plate; dorsal portion inserted on the outer edge of the proximal half of the postero-medial process of the hyoid, this area of insertion being continuous with that of the bulk of the muscle.

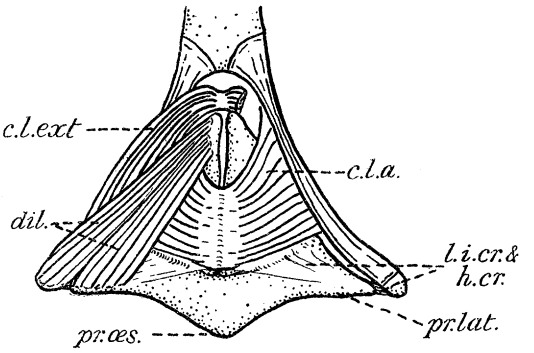

FIG. 44.—*Dendrophryniscus stelzneri*, male. Larynx, dorsal, with dilatator and constrictor externus removed on the right. × 13⅓.

M. omohyoideus absent.

M. geniohyoideus with its external insertion on the long posterior lobe of the alary process; internal portion aponeurotic over the paired part of *M. hyoglossus*.

Mm. petrohyoidei.—Anterior petrohyoid crossing the alary process and attached to the ventral surface of the hyoid. Three posterior petrohyoids, with typical attachments.

M. hyoglossus attached to the ventral surface of the epiphysis of the postero-medial process of the hyoid.

Laryngeal muscles chiefly remarkable for the attachment of part of the dilatator laryngis to the lateral process of the cricoid, the absence of a *constrictor laryngis posterior* and the great breadth of the *constrictor laryngis anterior*, the whole of which is attached on each side to the postero-medial process.

The interior of the larynx of the male differs from that of the female in the presence on each side of an enlarged *prominentia laryngo-trachealis* and a well-marked *frenulum chordæ vocalis*.

Oreophrynella quelchii, Boulenger.

Range: British Guiana.

Male, 20 mm. from snout to vent. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Hyoid with no postero-lateral processes; alary processes not enlarged; postero-medial processes in a dorsally inclined plane making an angle with the hyoid plate.

Arytænoid half-dome shaped, without apical cartilage or pulvinaria vocalia.

Cricoid forming a flat ring, incomplete ventrally, under, but smaller than the rim of the dome formed by the two arytænoids. Œsophageal process fairly long; lateral processes strongly developed, fused with the cartilaginous epiphyses of the postero-medial processes of the hyoid, the fusion taking place in the region in which the two structures meet in *Bufo*. Bronchial processes absent.

Muscles.—M. intermandibularis posterior in two separate portions, an anterior, whose fibres slope backwards and medialwards, and a posterior, whose fibres slope forwards and medialwards.

M. interhyoideus typical.

M. sternohyoideus with hyoid insertion almost meeting that of its fellow of the opposite side; dorsal portion with insertion on the outer edge of the proximal half of the postero-medial process of the hyoid, continuous with that of the bulk of the muscle.

M. omohyoideus absent.

M. geniohyoideus externus inserted on that part of the hyoid plate where the postero-lateral process usually arises. *M. geniohyoideus internus* aponeurotic over the paired portion of the hyoglossus.

M. petrohyoideus anterior with a short insertion near the edge of the hyoid plate. Two *petrohyoidei posteriores*, in the positions of the first and third of most Anura.

Paired posterior part of *M. hyoglossus* wrapped round the posterior edge of the lateral process of the cricoid, attached on the dorsal surface of the epiphysis of the postero-medial process of the hyoid.

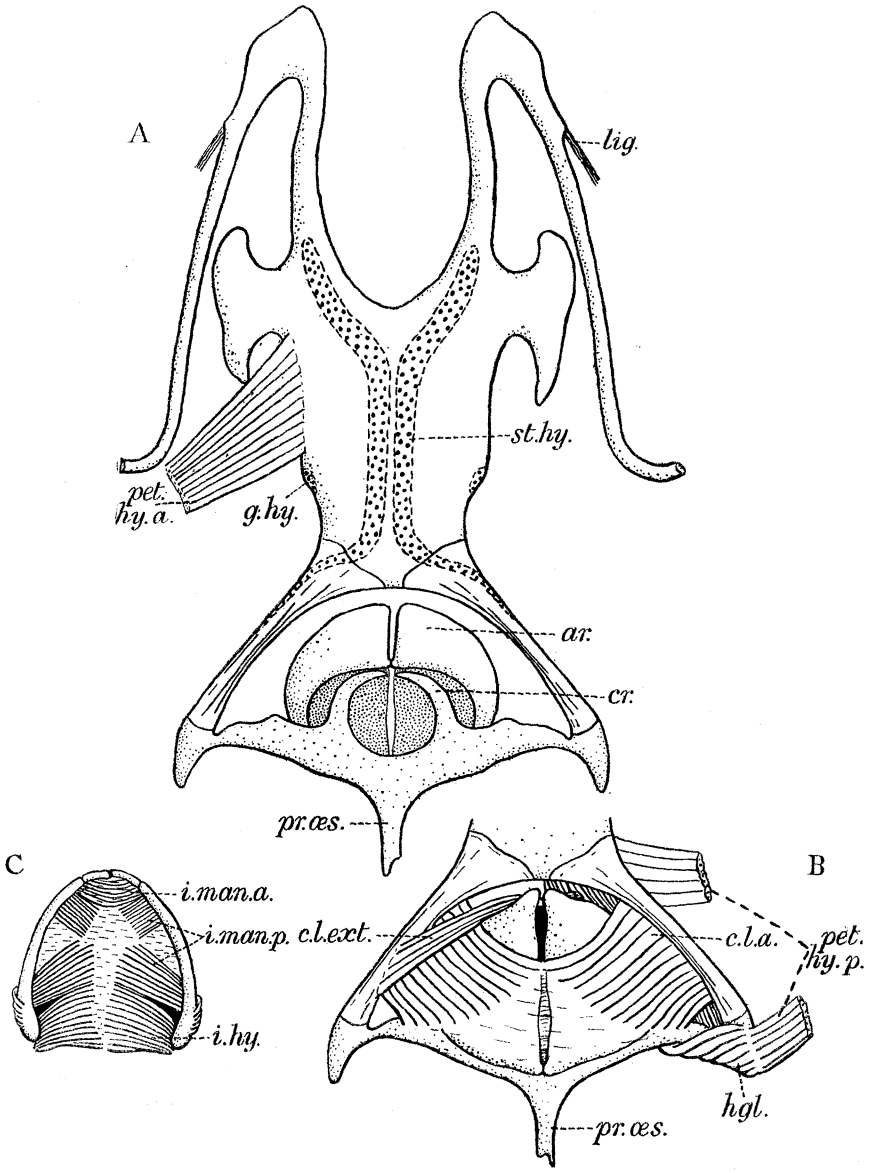

FIG. 45.—*Oreophrynella quelchii*, male. A. Hyoid and laryngeal skeleton, with insertions of hyoid muscles; ventral. B. Larynx, dorsal; dilatator not shown; constrictor externus removed on the right. C. Muscles of the throat. A and B × 18.

M. dilatator laryngis and *M. constrictor laryngis externus* typical. *M. constrictor posterior* absent. *M. constrictor* anterior broad, its proximal attachment extending on to the lateral process of the cricoid; attached laterally to the postero-medial process.

The vocal chord has a posterior lip only, and its frenulum is on the pharyngeal side, the reverse of the usual position.

Atelopus ignescens (Cornalia).

Female, 45 mm. from snout to vent; from West Ecuador. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Hyoid with the typical processes, except the postero-lateral processes, which are absent. In this specimen, but not in the one figured by W. K. Parker (1881), the anterior process of one side is united at both ends to the hyale, a variation which is common in *Rana temporaria* and *R. esculenta*. Postero-medial processes bent sharply dorsalwards and outwards, midway in their length.

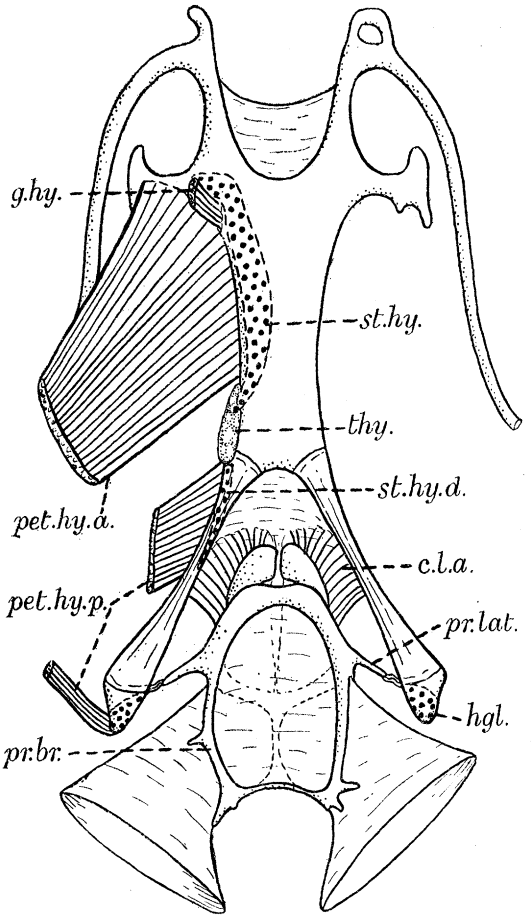

Fig. 46.—*Atelopus ignescens*, female. Hyoid and larynx, ventral, with muscle insertions, and with roots of lungs shown diagrammatically. × 9.

Arytœnoids simple, shaped as in *Bufo*, with an acute pharyngeal angle.

Cricoid with slender lateral processes joined by ligament to the antero-internal point of the cartilaginous epiphysis of the postero-medial process; no muscular process; œsophageal and bronchial processes long, and slender, and unique in being all three continuous at the angle between the lungs.

Muscles.—M. intermandibularis posterior differentiated as in *Oreophrynella quelchii* (see fig. 45).

M. sternohyoideus with right and left insertions almost meeting on the hyoid plate; dorsal portion inserted on the ventral surface of the postero-medial process.

M. omohyoideus absent.

M. geniohyoideus with typical internal attachment, aponeurotic posteriorly; external insertion far forwards, just behind the root of the alary process, an unusual position related to the absence of postero-lateral processes of the hyoid.

More than half of *m. hyoglossus* attached to the ventral surface of the cartilaginous epiphysis of the postero-medial process, the rest curved round it, and attached to its dorsal surface.

Two *mm. petrohyoidei posteriores*, representing the first and third of most Anura.

M. dilatator laryngis with a slip having its origin on the lateral process of the cricoid, as in *D. stelzneri*. *M. constrictor laryngis externus* with hyoid attachment extending on to the hyocricoid ligament. *M. constrictor laryngis posterior* absent. *M. constrictor*

anterior arising from a broad aponeurosis dorsal to the arytænoids and inserted mainly on the postero-medial process of the hyoid, but in part also on the hyo-arytænoid membrane.

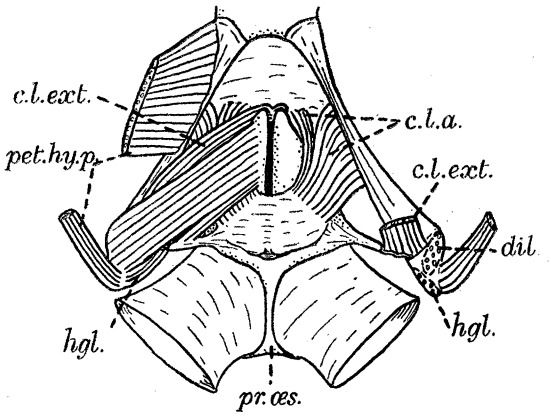

FIG. 47.—*Atelopus ignescens*, female. Larynx, dorsal. On the right the dilatator is removed and the constrictor externus cut short at each end.

W. K. PARKER (1881, pl. 40, fig. 9; pl. 41 figs. 4 and 9) described and figured the hyoid in *Atelopus ignescens* (= *Phryniscus lævis*, Gthr.), *A. cruciger* (= *P. cruciger*, Martins and Gthr.) and *A. varius* (= *P. varius* Stan.). In all the hyoid plate is long and narrow with widely diverging processes, and in *A. cruciger* and *A. varius* there are no anterior processes of the hyalia.

Brachycephalus ephippium, Spix.

Male, 17mm. from snout to vent, from Forest Jardin, Rio. [SLADEN.]

Hyoid and Laryngeal Skeleton.—Length of hyoid plate double its least width. Anterior processes long and straight; alary and postero-lateral processes much reduced; postero-medial processes diverging widely, to embrace the broad larynx.

Arytænoids, as a result of this unusual breadth, forming a rather flat dome; their postero-dorsal ends widely separate, but the gap bridged behind by large pulvinaria; ventral pulvinaria small and internal; no apical cartilages.

Cricoid with a short œsophageal process, well-marked articular and cardiac processes, and narrow, spatulate muscular processes; laterally contiguous with the postero-medial process, the lateral process of the cricoid fitting over the end of the postero-medial process like the bowl of a spoon. Bronchial processes represented by a minute vestige on one side.

Muscles.—*M. intermandibularis posterior* with a lateral superficial strip of fibres taking a longitudinal direction (fig. 48) as in the Brevicipitidæ.

In the absence of a sternum the bulk of *M. sternohyoideus* is a continuation of *m. rectus abdominis*, but two small slips arise on each side from the posterior end of the fused epicoracoid cartilages. One of these slips is the dorsal portion of the muscle and

is inserted on the postero-medial process of the hyoid. Its insertion, however, is continuous with that of the rest of the muscle, which extends to the middle line on the hyoid plate.

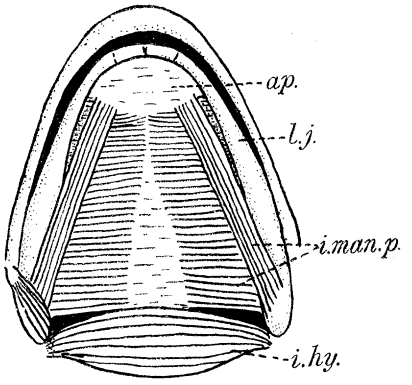

FIG. 48.—*Brachycephalus ephippium*, male. Muscles of throat. *ap.* = aponeurosis of intermandibularis posterior, hiding intermandibularis anterior.

M. omohyoideus absent.

M. geniohyoideus externus inserted on the reduced postero-lateral process; *m. geniohyoideus internus* sharing the peculiar attachment of *m. hyoglossus* (see below).

M. petrohyoideus anterior attached in the usual way to the edge of the hyoid plate. Two *mm. petrohyoidei posteriores*. The last of these, with *m. hyoglossus*, has, except for a few fibres, become detatched from its normal insertion, the epiphysis of the postero-medial process of the hyoid. This may be an abnormality in this specimen, but is the same on both sides.

M. dilatator laryngis with a narrow insertion on the anterior part of the arytænoid, overlapped here by the *constrictor externus*, which becomes narrow posteriorly, and is attached to the tip of the epiphysis of the postero-medial process, wedged between this and the spoon-shaped lateral process of the cricoid. *M. constrictor laryngis anterior* with the usual relationships, but appearing complicated owing to the fact that some of its fibres cross each other, while others are continuous from right to left sides. *M. constrictor laryngis posterior* well developed, interrupted by the muscular process of the cricoid.

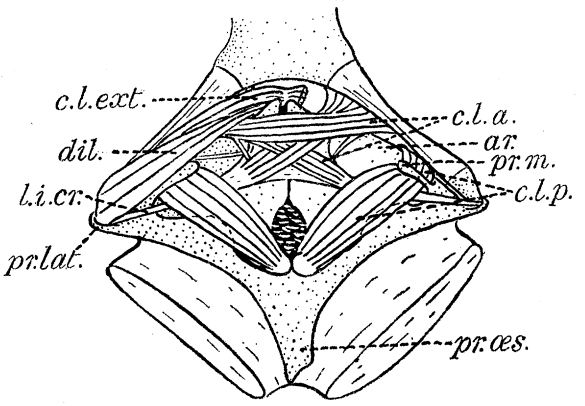

FIG. 49.—*Brachycephalus ephippium*, male. Larynx, dorsal. × 15.

Interior of Larynx.—The frenula of the vocal chords and the prominentiæ laryngo-tracheales are present, but weakly developed in comparison with those in the male of *Dendrophryniscus stelzneri.*

Dendrobates tinctorius (Schneider).

Range: South America.

Female, 32·5 mm. from snout to vent. [ZOOL. SOC.]

Hyoid and Laryngeal Skeleton.—Hyoid plate long and narrow, with a relatively shallow hyoglossal sinus, whose sides are bordered almost entirely by the long anterior processes of the hyalia. Manubrium very short; alary processes arising well behind the

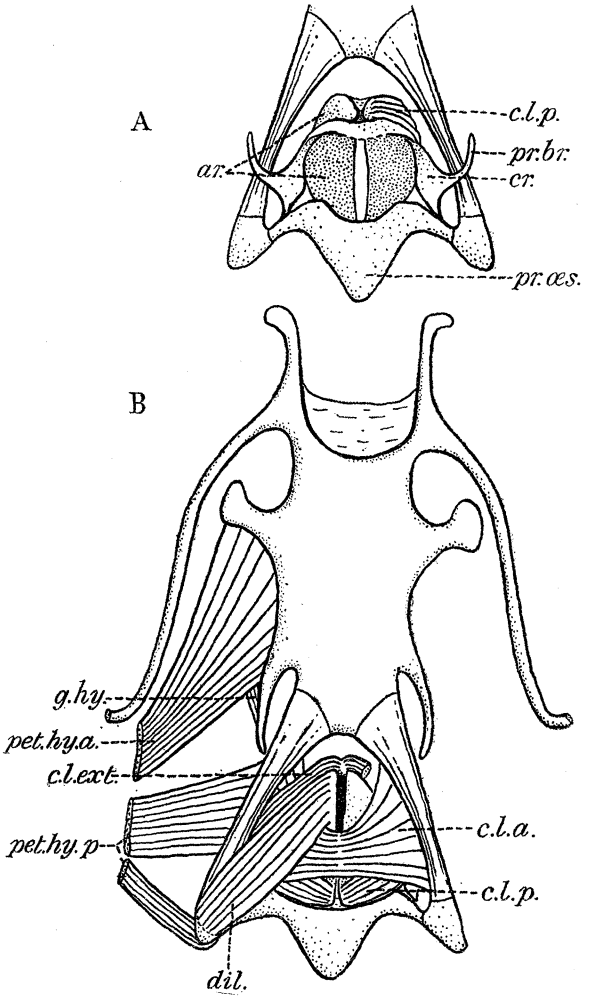

FIG. 50.—*Dendrobates tinctorius*, female. A. Laryngeal skeleton, ventral; m. constrictor posterior shown on one side. B. Hyoid and larynx, dorsal; dilatator and constrictor externus removed on the right. × 10⅔.

hyoglossal sinus; postero-lateral processes fairly long, slender and simple; postero-medial processes bent dorsalwards at an angle of about 45°.

Arytænoid triangular with pharyngeal angle a little less than a right angle; small pulvinaria present. Dorsal and ventral halves of the cricoid meeting at each side at a point between the lateral and bronchial processes, where the cartilage appears to be discontinuous. [BLUME (1930, p. 343, fig. 44) finds the two halves separated by

connective tissue in sections of three individuals.] Dorsal half with a broad triangular œsophagcal process, an articular process and a strong lateral process, which meets and fuses with a process of the cartilaginous end of the postero-medial process of the hyoid, the line of fusion being marked by a thin layer of fibrous tissue. The ease with which the two cartilages could be separated along this plane shows that this is not merely a superficial ring round a core of continuous cartilage. BLUME (loc. cit., p. 344, fig. 46) has demonstrated cartilaginous continuity between hyoid and cricoid in his specimens, whose size he does not give. The union of the two processes perhaps becomes closer with age and may also be subject to individual variation.

Bronchial processes short and slender, supporting the lateral walls of the laryngo-pulmonary openings.

Ventral part of cricoid a narrow strip of thin cartilage articulating with the arytænoid by low cardiac processes.

Muscles.—M. intermandibularis posterior simple.

Right and left *sternohyoidei* with widely separate hyoid insertions; insertion of *sternohyoideus dorsalis* continuous with that of the main part of the muscle, extending nearly to the posterior end of the bony postero-medial process of the hyoid.

M. omohyoideus absent.

M. geniohyoideus typical.

M. hyoglossus inserted on the ventral surface and the edge of the cartilaginous end of the postero-medial process.

An *anterior* and two *posterior petrohyoidei* present, with typical insertions.

Mm. dilatator laryngis and *constrictor laryngis externus* typical. *M. constrictor anterior* forming with its fellow of the opposite side a band of muscle attached broadly at each side to the bony postero-medial process. *M. constrictor posterior* present, uninterrupted, attached at each end to a small, fibrous pulvinar vocale.

BLUME'S account (1930, p. 418) of the laryngeal skeleton of *D. tinctorius* has already been referred to. He describes large pulvinaria vocalia, and their small size in my specimen is probably due to the rather shrunken condition of the specimen.

W. K. PARKER (1881, p. 250, Plate 44, fig. 4) described the hyoid; the reversed direction of his anterior processes is probably abnormal.

RANIDÆ.

Rana kuhlii (Schlegel).

Range: Oriental region.

Male, 80 mm. from snout to vent. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Width of hyoid plate behind alary processes one and a half to one and three-quarter times the length. Hyale with a short anterior process. Alary process a large lobe with a broad base; hyoid plate narrowing rapidly to root of postero-lateral process, which is slender and tapering; postero-medial processes

slender, lying in approximately the same plane as the hyoid plate; each expanding posteriorly to end in a triangular cartilage; laryngeal sinus wide.

Arytœnoid approximately equilateral, with a discrete apical cartilage between two prominentiæ; apical cartilage conical in shape, with base applied to aditus and apex projecting laterally into the dilatator. Large dorsal and ventral pulvinaria vocalia present. *Cricoid* in a plane at about 45° to the horizontal; œsophageal process of moderate length, slender and tapering; articular process represented by a slight expansion; no lateral process; muscular process a broad expansion; cardiac processes large, united by fibrous tissue with the arytænoid; bronchial processes slender bars extending across the ventral surface of the entrance to the lung, almost to the middle line.

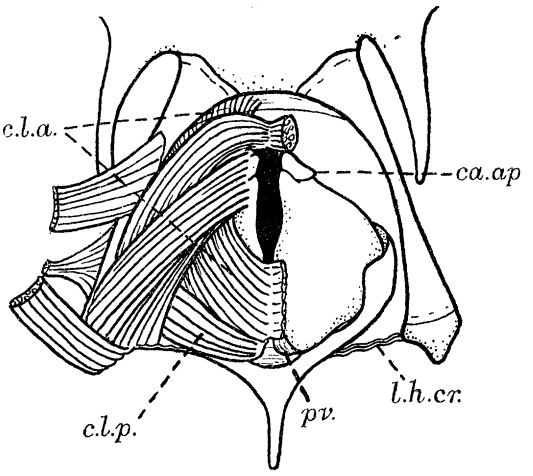

FIG. 51.—*Rana kuhlii*, male. Larynx, dorsal. × 4. Muscles removed on the right.

Muscles.—M. intermandibularis posterior simple; *M. interhyoideus* typical.

M. sternohyoideus with a broad area of insertion on the ventral surface of the hyoid plate, from the manubrium and the bases of the alary, postero-lateral and postero-medial processes inwards, meeting its fellow in the middle line in the posterior half of the hyoid plate; *sternohyoideus dorsalis* inserted separately on the thyroid membrane, adjacent to the middle third of the postero-medial process.

M. omohyoideus attached to the root of the postero-lateral process.

M. geniohyoideus with its external insertion behind the omohyoid on the postero-lateral process and on the thyroid membrane.

M. hyoglossus attached to the ventral surface of the posterior end of the postero-medial process.

M. petrohyoideus anterior inserted on the ventral surface of the posterior part of the alary process and on the edge of the hyoid plate behind this.

Three *petrohyoidei posteriores*, the first two attached to the bony shaft of the postero-medial process, the last to its cartilaginous end.

M. dilatator laryngis attached at one end to the prominentiæ and apical cartilage of the arytænoid, and at the other to the cartilaginous end of the postero-medial process and to the hyocricoid ligament; *m. constrictor externus* well developed, with typical attachment; *m. constrictor anterior* attached to the inner edge of the anterior half of the postero-medial process and nearly meeting its fellow ventral to the small hyo-arytænoid membrane; *m. constrictor posterior* attached at each end to the pulvinaria vocalia, completely interrupted midway by the muscular process of the cricoid.

Rana limnocharis, Wiegmann.

Range: India and Ceylon, China and Japan, Malay Peninsula and Archipelago.

Male, 37 mm. from snout to vent, and female, 40 mm. from snout to vent, from Tonking. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Width of the hyoid plate behind the alary processes equal to or a little greater than its length. Hyalia with short anterior processes. Bases of the alary processes varying in width, but never as broad as in *R. kuhlii;* postero-lateral processes simple, tapering; postero-medial processes in approximately the same

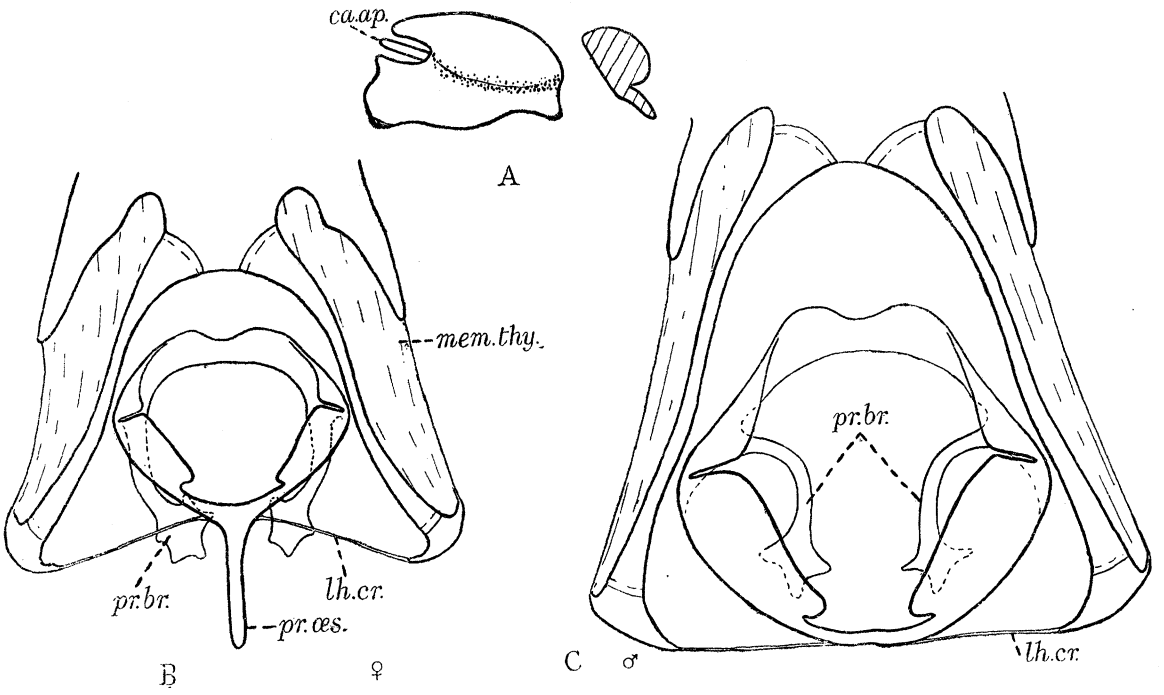

FIG. 52.—*Rana limnocharis*. A. Left arytænoid of a male specimen, seen from the outside, and in vertical section. B. Cricoid and posterior end of hyoid, of female; dorsal view. C. The same of a male. B and C × 12. A drawn to a smaller scale.

plane as the hyoid plate, curved, very slender, with the cartilaginous end of each produced medialwards to form a pointed support for the hyocricoid ligament, and laterally to support similarly the edge of the thyroid membrane (fig. 52); about one and a half times as long in the male as in the female.

Arytænoid with a deep *incisura apicalis*, and a slim *cartilago apicalis*, which appears in dissection to have a fibrous union with the arytænoid at its base; inner surface of arytænoid not ridged. Frenulum of vocal chord small, without a basal cartilage, as far as dissection reveals. Pulvinaria vocalia fitting cap-like over the corners of the arytænoid. The arytænoid of the male specimen has on its pharyngeal edge a large fibrous swelling, which may be pathological; in addition, the length of the arytænoid is one and two-thirds that of the female, although the hyoid plate is the same length

in the two specimens. *Cricoid* a complete ring, consisting of a pair of broad dorso-lateral plates and a broad ventral region, united by a narrow dorsal bar and very narrow lateral bridges of cartilage; cardiac processes united by a bar of moderate width; each bronchial process expanded into a stellate plate on the ventral wall of the entrance to the lung; a long, cylindrical œsophageal process present in the female but not in the male. The antero-posterior measurement of the cricoid in the female, including the median pharyngeal process, is about equal to that of the male, and its width is much less.

Muscles.—M. intermandibularis typical. *M. interhyoideus* pouched in the male to accommodate the sub-gular vocal sac.

M. sternohyoideus with a fairly broad hyoid insertion, but not reaching the middle line; insertion of *M. sternohyoideus dorsalis* continuous with that of the rest of the muscle, on the thyroid membrane outside the thyroid gland.

M. geniohyoideus with its external insertion on the hyoid plate at and immediately in front of the root of the postero-lateral process; internal insertion typical.

M. omohyoideus adjacent to *M. geniohyoideus.*

M. hyoglossus attached to ventral surface of posterior end of postero-medial process.

M. petrohyoideus anterior inserted on the edge of the hyoid plate between the alary and postero-lateral processes.

Mm. petrohyoidei posteriores I and II attached to lateral edge of bony postero-medial process; the third inserted on the posterior edge of the cartilaginous end of this process and on the hyo-cricoid ligament.

M. dilatator laryngis relatively small in both sexes; whole muscle extending without interruption from its origin on the postero-medial process to its insertion on the apical prominences and apical cartilage of the arytænoid; *m. constrictor laryngis externus* larger than the dilatator; *m. constrictor anterior* attached in front to the inner edge of the shaft of the postero-medial process, well behind the front end of the laryngeal sinus; *m. constrictor posterior* attached at each end to large fibrous pulvinaria vocalia, interrupted midway, its dorsal half being attached to the dorsal edge, its ventral half to the ventral edge of the lateral cleft of the cricoid, but the two parts apparently united by an aponeurosis crossing the cleft, and connected with the base of the vocal chord.

Rana grayi, Smith.

Range: South Africa.

Male, 37 mm. from snout to vent. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Length of hyoid plate a little greater than its width. Anterior process represented by a small triangular expansion of the hyale. Alary process as in *R. esculenta*, arising by a narrow stem behind the level of the hyoglossal sinus; postero-medial processes a little longer than the hyoid plate, inclined dorsally to it at an angle of about 45°, expanded distally, with short cartilaginous ends.

Arytœnoid approximately equilateral with two prominentiæ apicales, between which is an apical cartilage; inner surface without a ridge. The condition of the specimen does not justify any statement about pulvinaria vocalia. *Cricoid* a slender ring, expanded laterally, with low pharyngeal and cardiac articular processes; a narrow, dorsally directed muscular process; bronchial process stout, recurved over the ventral surface of the root of the lung, where it gives off two or three short blunt branches; œsophageal process long, slender; no definite lateral process but cricoid connected laterally with the end of the postero-medial process by a triangular fibrous membrane, the edges of which form tough ligaments, attached to the root of the bronchial process and to the pharyngeal portion of the cricoid.

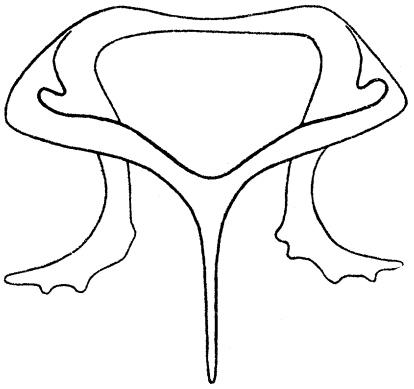

FIG. 53.—*Rana greyi*, male. Cricoid, dorsal.

Muscles.—*M. intermandibularis posterior* typical.

M. interhyoideus pouched over the median vocal sac.

M. sternohyoideus with a narrow insertion on the ventral surface of the hyoid plate, widely separated from its fellow by the belly of the hyoglossal muscle, continuous behind with insertion of *M. sternohyoideus dorsalis*, on the bony postero-medial process.

M. omohyoideus attached to the root of the postero-lateral process.

M. geniohyoideus with its external insertion along the whole length of the postero-lateral process; internal insertion typical.

M. hyoglossus attached to the ventral surface of the posterior end of the postero-medial process.

M. petrohyoideus anterior with typical insertion on the lateral edge of the hyoid.

Mm. petrohyoidei posteriores I and II inserted on the bony shaft of the postero-medial process, the third on its cartilaginous end and on the hyo-cricoid ligament.

M. dilatator laryngis originating on the dorsal surface of the posterior end of the postero-medial process and on the hyo-cricoid ligament, inserted on the prominentiæ apicales and cartilago apicalis of the arytænoid; *m. constrictor laryngis externus* well-developed, typical; *m. constrictor anterior* attached to the inner edge of the bony postero-medial process. *M. constrictor posterior* only partially interrupted by the muscular process of the cricoid.

Rana fuscigula, Duméril and Bibron.

Range: South Africa.

Female, 80 mm. from snout to vent. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Width of hyoid plate considerably greater than its length. Hyoglossal sinus broad, bounded by stout manubria and distally by short broad anterior processes, whose edges of thin cartilage suggest that the processes have been increasing in extent and changing in shape during the adult life of the frog. Alary

process large, with relatively narrow base, and with somewhat irregular anterior edge of thin cartilage; postero-lateral process long, curved inwards distally and forked; the lateral arm of the fork giving attachment to the fine fibrous edge of the thyroid membrane, which at the other end is attached to the postero-medial process; the inner arm of the fork supporting a strong fibrous tract of the same membrane which extends forwards to the

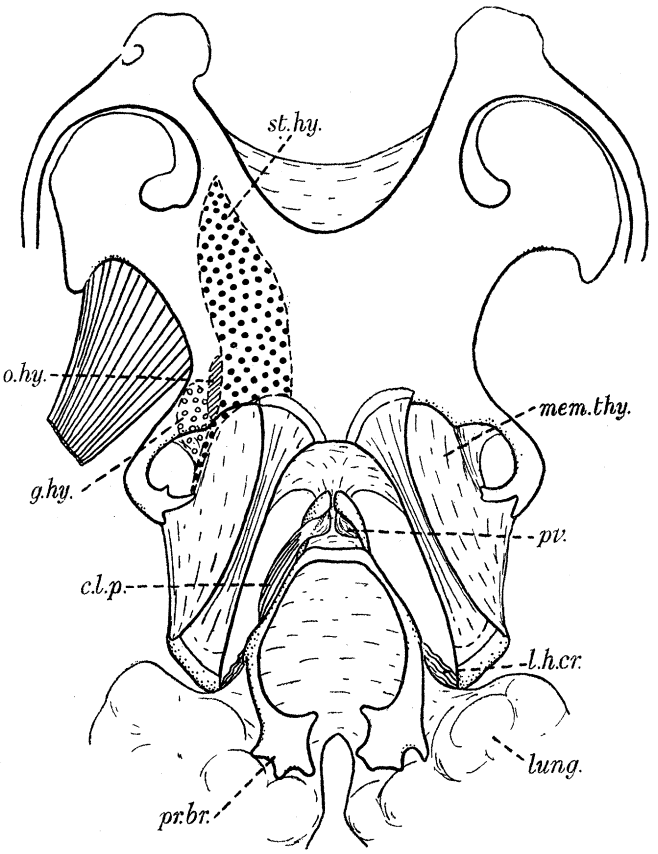

FIG. 54.—*Rana fuscigula*, female. Hyoid and larynx, with roots of lungs; ventral. × 5. Muscle insertions shown on one side.

hyoid plate at the root of the process and affords attachment to *m. sternohyoideus dorsalis* and to the thyroid gland; postero-medial processes only slightly inclined to the plane of the hyoid plate, expanded distally into broad cartilaginous ends, of which the outer corners are produced for attachment of the edge of the thyroid membrane, and the inner corners for attachment of the hyocricoid ligament.

Arytœnoid a long narrow and almost flat cartilage, with typical Ranid apical cartilage and prominentiæ, and with large pulvinaria vocalia; no ridge on its inner surface. Cricoid broad in the region of the articular and muscular processes, but narrower near the middle line; œsophageal process long, slender; cardiac processes insignificant; each bronchial process stout, expanded at the root of the lung into a stellate plate.

Muscles.—Mm. intermandibularis posterior and *interhyoideus* typical.

M. sternohyoideus with its hyoid insertion well separated from that of its fellow; *m. sternohyoideus dorsalis* with insertion extending from that of the main part of the muscle backwards on the fibrous tract of the thyroid membrane to the end of the postero-lateral process.

M. omohyoideus well developed, typical.

M. geniohyoideus with its external insertion on the base of the postero-lateral process, and behind this on the thyroid membrane adjacent to the *M. sternohyoideus dorsalis*; internal insertion typical.

M. hyoglossus attached to the ventral surface of the cartilaginous end of the postero-medial process.

M. petrohyoideus anterior inserted on the lateral edge of the hyoid plate. First *petrohyoideus posterior* inserted on the lateral edge of the postero-medial process and on

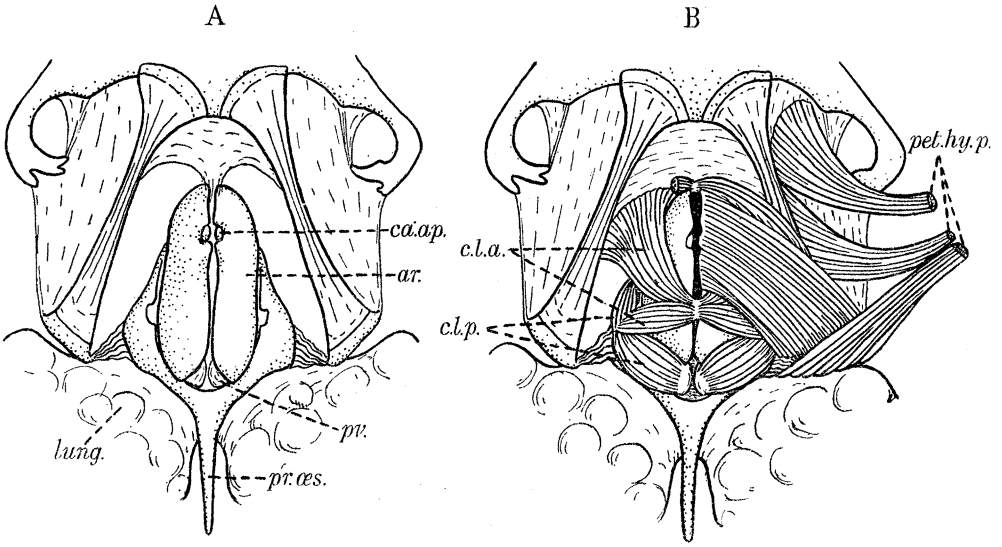

FIG. 55.—*Rana fuscigula*, female. A. Laryngeal skeleton, with posterior part of hyoid; dorsal. B. The same, with muscles, the dilatator and constrictor externus removed on the left. × 5.

the thyroid membrane, the second just behind it on the edge of the same bone, and the third on the inner corner of the cartilaginous end of the process and on the hyocricoid ligament.

M. dilatator laryngis inserted at one end at the apex of the arytænoid and its apical cartilage, at the other on the dorsal surface of the postero-medial process and on the hyocricoid ligament; without a deep slip interrupted by the cricoid. *M. constrictor externus* typical; *m. constrictor anterior* attached behind to the inter-cricoid ligament; a considerable part of it extending from here to the midway tendon of the constrictor posterior, which is attached to the muscular process of the cricoid, the rest ending in an arc including the edge of the hyo-arytænoid membrane and a short part of the inner edge of the postero-medial process. *M. constrictor posterior* attached at each end to a

pulvinar, interrupted midway by an aponeurosis attached to the cricoid in the broad region including the muscular process.

The relatively large space in front of the larynx, occupied by the hyo-arytænoid membrane, is no doubt a character of the female sex, and in the male would be filled by a larger larynx.

Rana labrosa (Cope).

Range: Madagascar.

Female, 54 mm. from snout to vent, from South-west Madagascar. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Width of hyoid plate slightly greater than its length. Hyoglossal sinus fairly deep, manubria slender. Anterior process of hyale a triangular

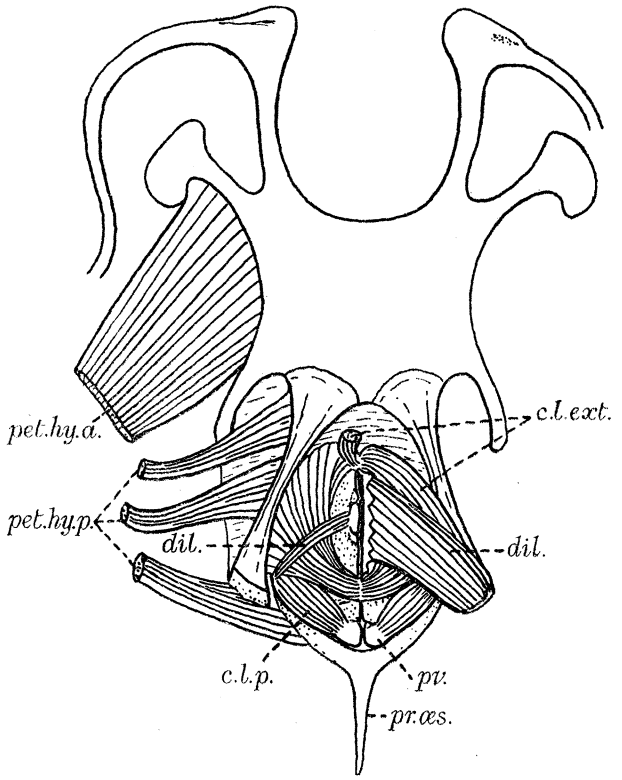

FIG. 56.—*Rana labrosa*, female. Hyoid and larynx, dorsal. × 6. Constrictor externus and main part of dilatator removed on the left.

expansion with a thin central area. Alary process with rather long, narrow base, arising immediately behind level of hyoglossal sinus.

Arytænoid of Ranid type, with prominentiæ, as well as cartilago apicalis, segmented off from the arytænoid.* Corners of arytænoid truncate, with large pulvinaria. *Cricoid*

* The perichondrium appears to be continuous over prominentiæ and main part of arytænoid; whether the cartilaginous discontinuity is complete cannot be discovered by dissection.

a complete ring, with well-marked cardiac and moderate articular processes ; muscular process low ; œsophageal process long, simple ; lateral process inconspicuous ; bronchial process slender, directed postero-medially, forked distally.

Muscles.—Mm. intermandibularis and *interhyoideus* typical.

M. sternohyoideus with hyoid insertion on lateral region of hyoid plate, not near middle line.

M. omohyoideus well-developed, typical.

Mm. geniohyoideus and *hyoglossus* typical.

M. petrohyoideus anterior inserted on lateral edge of hyoid plate.

Three *petrohyoidei posteriores*, the first and second attached to the lateral edge of the postero-medial process, the third to its cartilaginous end, and to the edge of the cricoid.

Main bulk of *m. dilatator laryngis* attached to the postero-medial process at one end, to the prominentiæ and cartilago apicales at the other ; a slender, deep arytæno-cricoid slip attached to the muscular process of the cricoid. *M. constrictor anterior* attached to the inter-cricoid ligament behind, and in front to a wide arc including part of the inner edge of the postero-medial process, the hyo-arytænoid membrane, and the raphe of *m. constrictor externus ;* a few fibres attached to the muscular process. *M. constrictor posterior* only partially interrupted by the muscular process, attached at each end by a short tendon to the pulvinar.

Rana halecina, Kalm.

Range : North America.

Male, 60 mm. from snout to vent. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Length and breadth of hyoid plate approximately equal. Hyale with a short narrow anterior process curved outwards distally. Alary process a small lobe with narrow base, arising immediately behind the level of the shallow hyoglossal sinus ; postero-lateral process long, about three-quarters length of postero-medial process, incurved distally ; between it and the postero-medial process a notch in which the thyroid body is firmly lodged ; postero-medial processes bent beyond their origin, so as to make an angle of about 30° with the plane of the hyoid plate, with distal ends widely expanded, ending in cartilage.

Arytænoid rather deep from apex to middle of base ; inner surface flat near the *aditus*, concave in the region of the vocal chord, without a ridge for the frenulum ; apex with the typical Ranid incisura, prominentiæ and apical cartilage ; pulvinaria vocalia large. *Cricoid* expanded laterally to form a large triangular muscular process ; blunt articular and broad cardiac processes ; œsophageal process long ; bronchial processes long, slender, simple, directed posteriorly on the floor of the larynx.

The laryngeal skeleton fills the laryngeal sinus completely in a way which suggests that it will be found to be relatively smaller in the female.

Muscles.—M. intermandibularis posterior typical. *M. interhyoideus* relatively small. Vocal sacs small, covered by the posterior part of *M. intermandibularis* and by *M. interhyoideus.*

M. sternohyoideus inserted on the lateral part of the ventral surface of the hyoid, widely separated from its fellow; *m. sternohyoideus dorsalis* attached to a strong fibrous tract (of the thyroid membrane) which runs from the lateral edge of the thyroid body to the end of the postero-lateral process.

M. omohyoideus well developed, inserted in the usual way to the postero-lateral corner of the hyoid plate, on the inner side of the external geniohyoid insertion.

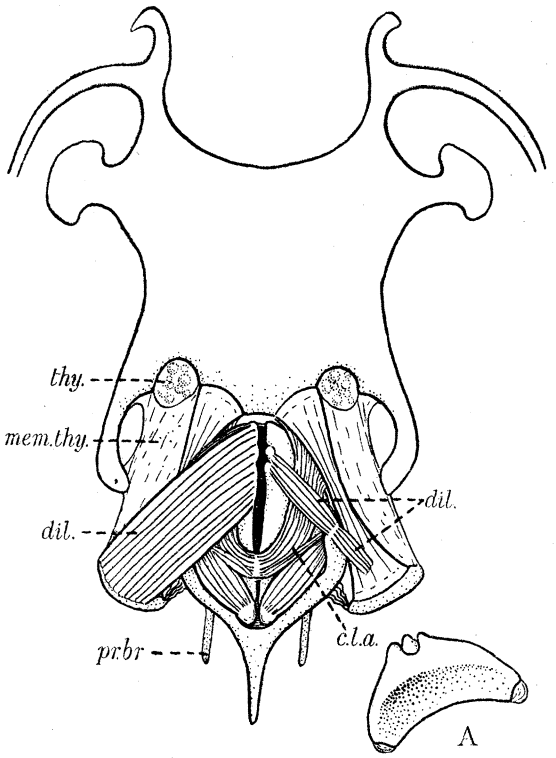

FIG. 57.—*Rana halecina*, male. Hyoid and larynx, dorsal. × 5. Constrictor externus and superficial portion of dilatator removed on the right. A. Right arytænoid, from within.

M. geniohyoideus with its external insertion at the root of the postero-lateral process.

M. hyoglossus rather slender, its main part arising from the posterior end of the ventral surface of the postero-medial process; a thin layer adjacent to the hyoid plate arising from the anterior end of the bone.

M. petrohyoideus anterior attached to the lateral edge of the hyoid plate. *Mm. petrohyoidei posteriores primus* and *secundus* inserted on the lateral edge of the postero-medial process, *m. tertius* to the posterior edge of its cartilaginous end.

M. dilatator laryngis with a deep portion divided into arytæno-cricoid and hyo-cricoid parts by the muscular process of the cricoid. *M. constrictor externus* well developed and typical. *M. constrictor anterior* weakly developed; except a few fibres inserted on the muscular process of the cricoid, attached in front to the inner edge of the postero-medial process. An intercricoid ligament present. *M. constrictor laryngis posterior* attached to the large pulvinaria vocalia and, midway, to inner surface of muscular process of cricoid.

Rana erythræa (Schlegel).

Range: Farther India, East Indies.

Male, 22 mm. from snout to vent. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Length of hyoid plate greater than its width. Hyale with narrow anterior processes, longer than in *R. halecina.* Alary, postero-lateral and postero-medial processes like those of *R. esculenta* and *temporaria.*

Arytœnoid well rounded, approximately equilateral, with apex turned forwards, and lodging an *apical cartilage* in a typical Ranid *incisura apicalis. Cricoid* a slender ring, with long, narrow œsophageal process, and prominent articular and muscular processes; bronchial processes slender, united at their ends by a simple transverse bar of cartilage which supports the angle between the two lungs. In this last feature *R. erythræa* resembles *R. esculenta* and its sub-species *R. ridibunda,* but in these the bronchial processes are produced a short distance beyond the origin of the transverse cartilage which has in addition a median anterior process.

Muscles.—Hyoid muscles like those of *R. halecina.*

M. dilatator laryngis with a deep layer, divided at the muscular process of the cricoid into hyo-cricoid and crico-arytænoid slips. *M. constrictor anterior* with a small slip to the same process; its main portion attached in part to inner edge of postero-medial process, in part to edge of hyo-arytænoid membrane. *M. constrictor posterior* interrupted at the muscular process of the cricoid.

Previous Work on the Ranidæ.

Several more or less complete accounts exist of the hyoid and larynx in *Rana temporaria* and *R. esculenta.* Dugès (1835) described both hyoid and larynx with their muscles, but missed the constrictor laryngis posterior. Henle (1839) gave good figures of the laryngeal cartilages, which show well certain contrasting features of the two species, notably the unique anastomosis of the bronchial processes in *R. esculenta.* He first gave the name "cartilago santoriniana" to the apical cartilage of the arytænoid, and noted that it had been described by St. Ange in *R. temporaria.*

He saw all the laryngeal muscles, but described incorrectly the attachments of the constrictor posterior, and he saw the hyo-cricoid slip of the dilatator, but not the arytæno-cricoid. Goeppert (1895 and 1898) gave the first correct account of the laryngeal muscles of *R. temporaria,* and his terminology was adopted by Gaupp in his description of the larynx of *R. esculenta.* Gaupp also described the hyoid and its musculature and the histological structure of the interior of the larynx. This last was again described in 1920 by Krause. Wilder (1896) and Blume (1930) included both *Rana temporaria* and *R. esculenta* in their studies of the larynx. These are the chief, but not the only published accounts of the hyolaryngeal apparatus of these two species.* In addition,

* Ridewood (1897, *a*) described and figured the laryngeal skeleton of *Rana esculenta* for comparison with *Xenopus.* He showed a fine cartilaginous network extending over the proximal end of the lung from the bronchial processes, but this has been seen by no other author and an examination of several specimens convinces me that he was mistaking blood vessels for cartilage.

WILDER has described the skeletal parts in *Rana virescens*, *R. clamitans*, and *R. sylvatica*; FRAZIER (1924) described the skeleton in four oriental species, *R. limnocharis*, *R. nigromaculatus*, *R. plancyi* and *R. rugulosa*; BLUME (1930) has accounts of the laryngeal skeleton also in *R. arvalis*, *R. catesbyana*, *R. halecina*, *R. sylvatica* and *R. mascareniensis*.

The development of the laryngeal cartilages is described by MÄRTENS (1897) in *R. temporaria*, and, in 1920, EDGEWORTH described the development of the muscles.

RHACOPHORIDÆ.

Megalixalus madagascariensis, Duméril and Bibron.

Range: Madagascar.

Young male, 19 mm. from snout to vent.

Young female, 20 mm. from snout to vent. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Hyoglossal sinus narrow, of moderate depth; hyoid plate long, expanded on each side to form a broad lobe bearing the alary process. Hyale slender, forked proximally, the posterior limb continuous with the manubrium and bearing the anterior process, the anterior limb almost meeting the distal end of the anterior process. No postero-lateral process; proximal part of the postero-medial process unossified.

Arytœnoid short, with an apical cartilage between well-marked prominentiæ and with relatively large pulvinaria vocalia.

Cricoid a complete ring, with a narrow, tapering œsophageal process, a well-developed lateral process and a muscular process which interrupts the posterior constrictor, and anastomoses with the cardiac process, forming with it an arch, under which, in the male, the cricoid gives off a short extra process opposite the origin of the bronchial process. Bronchial process slender and simple, except on the right in the male, where it bears a short branch.

Muscles. *M. intermandibularis posterior* with a broad median aponeurosis; superficially with a narrow band of fibres parallel to lower jaw and ending in an aponeurosis on the ventral side of *M. intermandibularis anterior*. *M. interhyoideus* typical.

M. sternohyoideus inserted in a straight line on the ventral surface of the hyoid, across the base of the lateral lobe, and behind this on the edge of the hyoid to the proximal end of the postero-medial process; insertion of dorsal portion continuous with that of the main part.

M. omohyoideus inserted on the lateral edge of the hyoid, between the base of the postero-medial process and the lateral lobe.

M. geniohyoideus medialis, joined by a very small slip of *M. gen. hy. lateralis*, continued as an aponeurosis over the paired part of the hyoglossus. Rest of the m. lateralis passing to the external insertion on the edge of the hyoid at the posterior end of the base of the lateral lobe. In the female m. lateralis does not contribute to the internal

insertion, which is restricted to the posterior edge of the hyoid plate, and does not extend over the paired part of the hyoglossus.

M. hyoglossus attached to the ventral surface of the bony part of the postero-medial process and its cartilaginous tip.

M. petrohyoideus anterior inserted along posterior edge of lateral lobe of hyoid and stem of alary process. Insertion of first posterior petrohyoid continuing this line

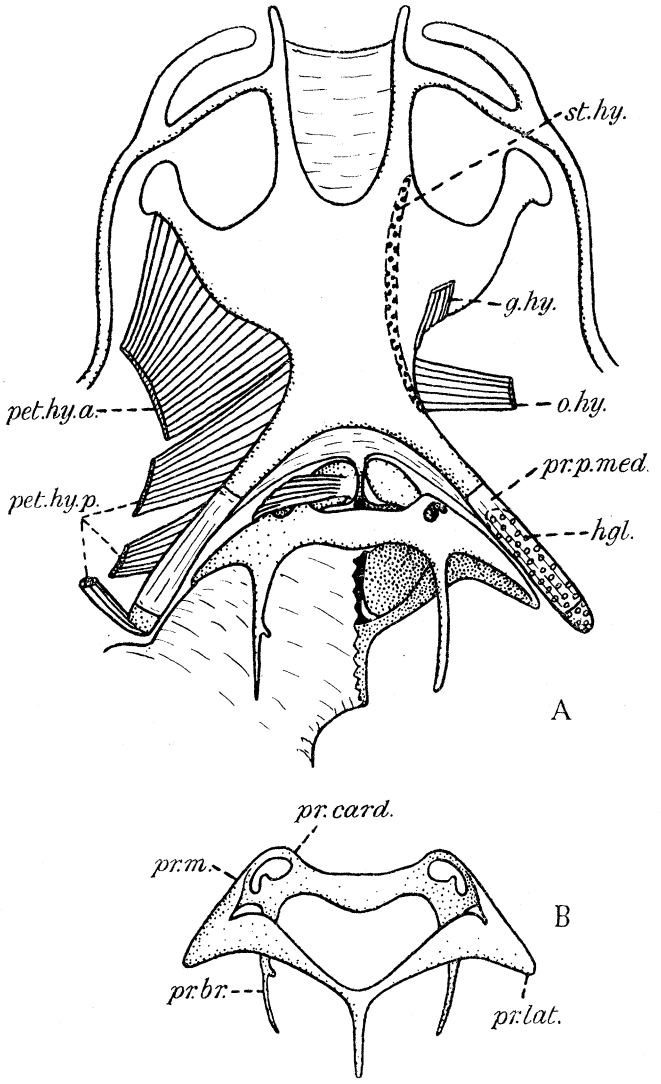

FIG. 58.—*Megalixalus madagascariensis*. A. Hyoid and larynx, ventral. Insertions of petrohyoids and constrictor posterior shown on the left of the figure, those of other hyoid muscles on the right. B. Dorsal view of cricoid. × 20.

backwards to the bony part of the postero-medial process, to which the second posterior petrohyoid is attached. Third with the usual insertion on the cartilaginous tip of the process.

M. dilatator laryngis simple and typical. *M. constrictor laryngis externus* typical. *M. constrictor anterior* attached to inner edge of the postero-medial process; in the female, a few fibres ending on edge of hyo-arytænoid membrane. *M. constrictor posterior* attached at the ends to the pulvinaria, and midway to the muscular process of the cricoid.

Some features of this apparatus may be due to the immaturity of the specimens, *e.g.*, the weak ossification of the postero-medial processes, and the anterior extension of the origin of m. hyoglossus.

Rhacophorus maculatus (Gray).

Range: India and Ceylon.

Female, 60 mm. from snout to vent, from Ceylon. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Length of hyoid plate nearly 1½ times its width. Hyale long and slender, without anterior processes, extending to the otic region of the

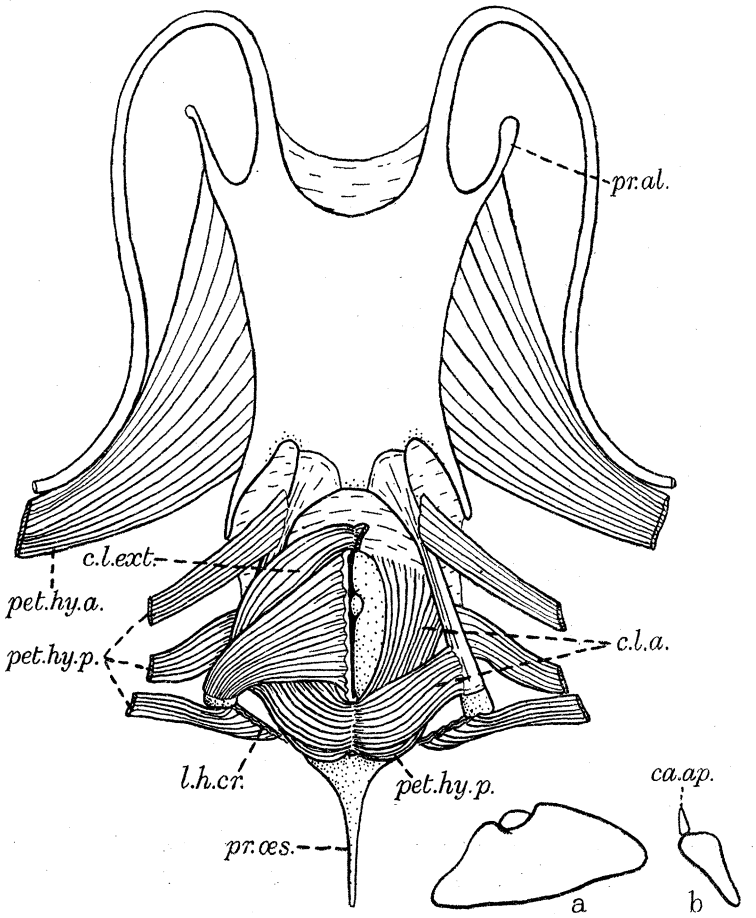

FIG. 59.—*Rhacophorus maculatus*, female. Hyoid and larynx, dorsal. × 6⅔. Dilatator and constrictor externus removed on the right. *a*. Left arytænoid, from without. *b*. Transverse section of the same.

skull in the typical manner. Alary process a narrow, anteriorly directed bar of about the same size as the postero-lateral process, which is typical. Postero-medial processes slender, bones lying almost in the plane of the hyoid plate.

Arytænoid about twice as long as deep, with pharyngeal edge evenly rounded, including a compressed, triangular apical cartilage lying in a rather shallow incisura apicalis; inner surface neither excavated nor ridged; pulvinaria small and inconspicuous. *Cricoid* a complete ring with well-marked articular and cardiac processes, but without a muscular process; œsophageal process long, slender; bronchial processes simple and short.

Muscles.—Mm. intermandibularis posterior and *interhyoideus* typical.

M. sternohyoideus inserted near lateral edge of hyoid plate, from manubrium to base of postero-lateral process; *m. sternohyoideus dorsalis* with a long insertion on lateral edge of postero-medial process.

M. omohyoideus with an unusual insertion adjacent to main part of sternohyoid, from the postero-lateral process forward almost to the alary process.

M. geniohyoideus also with a long external insertion, adjacent to omohyoid.

M. hyoglossus typical.

M. petrohyoideus anterior attached to the edge of the hyoid plate from the proximal part of the alary process to the origin of the postero-lateral process.

Mm. petrohyoidei posteriores primus and *secundus* attached in a typical way to the middle part of the postero-medial process, and *M. tertius* to its cartilaginous end and to the hyo-cricoid ligament.

M. dilatator laryngis simple and typical. *M. constrictor externus* well developed; *M. constrictor anterior* attached to the intercricoid ligament behind, and at the other end, in part to the hyo-arytænoid membrane, in part to the inner edge of the bony postero-medial process, its superficial portion forming a stout bundle attached to the bone unusually far back, immediately in front of its cartilaginous end. *M. constrictor posterior* muscular throughout and uninterrupted.

Rhacophorus leucomystax, Kuhl.

Range: India, Farther India, China.

Male, 42 mm. from snout to vent, from Thai-Nien, Tongking. [B.M.N.H.]

The hyoid apparatus and larynx of this frog resemble closely those of *Rh. maculatus*. The chief differences are associated with the relatively larger larynx in *Rh. leucomystax* and are sexual, not specific. The antero-posterior length of the arytænoids in this male is 6 mm., exactly one and a half times the corresponding measurement in the female *Rh. maculatus*, although the body lengths of the two specimens are in the inverse ratio. It is, no doubt, as a direct result of this that the œsophageal process of the cricoid is reduced to a mere stump in *Rh. leucomystax* (*cf.* male and female of *Rana limnocharis*, fig. 52 and of *Crinia signifera*, fig. 26).

The only difference in the musculature is in the more complete division of *M. constrictor laryngis anterior* into two parts; the superficial portion, as in *Rh. maculatus*, is attached to the posterior end of the bony part of the postero-medial process, but the whole of the deeper portion is attached to the hyo-arytænoid membrane near the median raphe of *M. constrictor externus*.

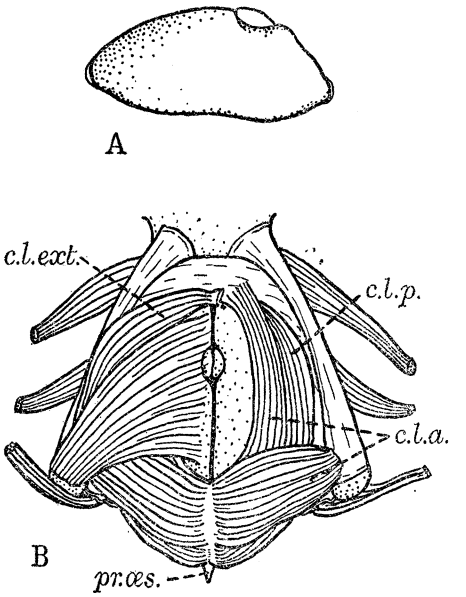

FIG. 60.—*Rhacophorus leucomystax*, male. A. Right arytænoid, from without. B. Larynx, dorsal. × 6. Dilatator and constrictor externus removed on the right.

Rhacophorus goudoti, Tschudi.

Range, Madagascar.

Female, 75 mm. in total length, from Madagascar. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Hyoid plate a rectangular cartilage 8 mm. long and 6 mm. wide, without alary processes. Manubria continued into slender hyalia with simple tapering anterior processes; postero-lateral processes short, simple; postero-medial processes relatively short (nearly 6 mm.) with expanded cartilaginous ends.

Arytænoid with its base but little longer than its other sides and making a steep angle with the horizontal, so that the apex is turned forwards. A rather flat triangular apical cartilage between well-marked prominentiæ; pulvinaria vocalia narrow fibrous caps. *Cricoid* a narrow ring, rather broader laterally, where it gives attachment to the hyo-cricoid ligament and *m. constrictor laryngis posterior;* no lateral or muscular processes; œsophageal process broad, flat, over 3 mm. long, with scalloped edges; bronchial processes short, straight, not nearly reaching the paired part of the air passage; cardiac processes low.

Muscles.—M. intermandibularis posterior with a wide median aponeurosis. *M. interhyoideus* typical.

M. sternohyoideus with a continuous insertion from proximal part of manubrium backwards extending on to the thyroid membrane, widely separated from its fellow on the hyoid.

M. omohyoideus with insertion adjacent to the most anterior part of *M. sternohyoideus*, on the manubrium, a most unusual position.

M. geniohyoideus with external insertion on the edge of the hyoid plate, in front of and including the postero-lateral process, and between this and the postero-medial process on the thyroid membrane; internal portion completely aponeurotic over paired part of *m. hyoglossus*.

M. hyoglossus typical.

M. petrohyoideus anterior attached to the lateral edge of the hyoid plate as far forwards as the point where the glossopharyngeal nerve and lingual artery pass from its ventral

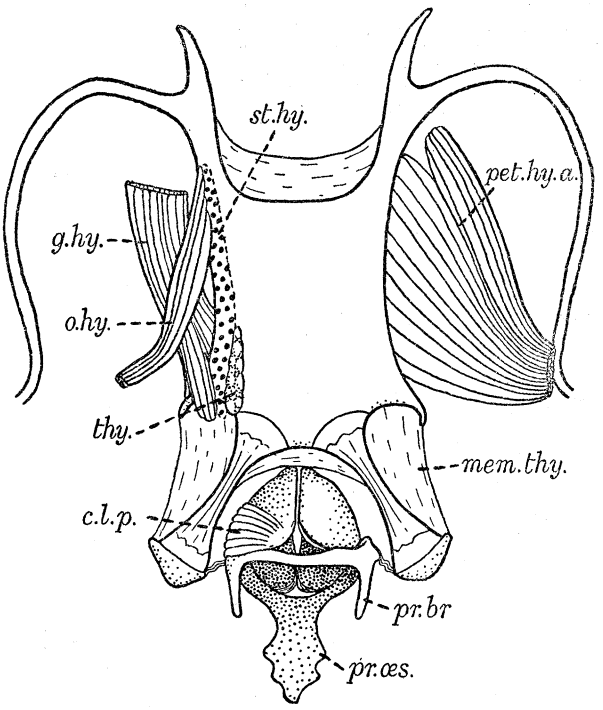

FIG. 61.—*Rhacophorus goudoti*, female. Hyoid and larynx, ventral. × 3⅘. Muscle insertions shown on either the left or the right.

side to the dorsal side of the manubrium (this usually occurs immediately in front of the alary process), and, in front of this, ending on the membrane between the manubrium and the hyale.

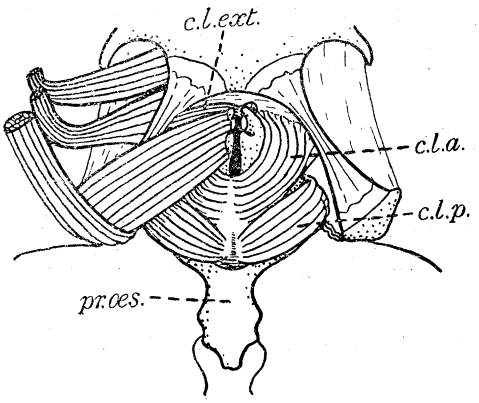

FIG. 62.—*Rhacophorus goudoti*. Larynx, dorsal. × 4½.

M. petrohyoideus posterior ending on the lateral edge of the anterior end of the postero-medial process, and of the thyroid sinus in front of it; *m. secundus* with typical insertion on the lateral edge of the bone, and *m. tertius* on its cartilaginous end.

M. dilatator laryngis simple and typical; lateral attachment of *M. constrictor laryngis externus* extending nearly to anterior end of postero-medial process, so that its anterior fibres are almost transverse, a condition probably related to the shape and tilt of the arytænoids; *M. constrictor anterior* spreading fanwise to be inserted on an arc from the median raphe of the *constrictor externus* to the middle of the inner edge of the postero-medial process; *M. constrictor posterior* stout, attached to the pulvinaria

vocalia by short aponeuroses, and partially interrupted midway by an attachment to the cricoid.

Rhacophorus rhodoscelis, Boulenger.

Range, Madagascar.

Female, 38½ mm. from snout to vent, from Madagascar. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Hyoid plate square; its processes like those of *Rh. goudoti*, but postero-lateral processes even shorter, and postero-medial processes as long as the hyoid plate and slender.

Larynx small in comparison with the laryngeal sinus. Cartilago apicalis small, between prominentiæ which do not break the rounded outline of the *arytænoid. Cricoid* slender, with narrow œsophageal and short bronchial processes; laterally with its width increased by the addition of thin cartilage; with thin cartilage also filling the angle of the V at the base of the œsophageal process.

Muscles.—M. omohyoideus was unfortunately not observed. *M. petrohyoideus anterior* attached uninterruptedly to edge of hyoid plate. Other hyoid and laryngeal muscles as in *Rh. goudoti.*

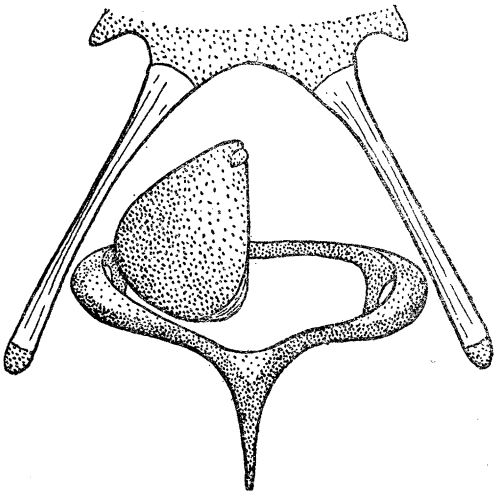

FIG. 63. — *Rhacophorus rhodoscelis*, female. Posterior part of hyoid, with cricoid and left arytænoid. × 15.

Previous Work on Rhacophoridæ.

FRAZIER (1924) described the hyoid and laryngeal skeleton in *Rhacophorus* (= *Polypedates*) *dennysi*. This is very peculiar in having the hyale reduced to a mere short process of the antero-lateral corner of the hyoid plate, and in having the cricoid ring incomplete mid-dorsally. As in *R. leucomystax*, the apical region of the arytænoid is evenly curved and the apical cartilage is lodged in an incisura not bounded by prominentiæ. This was all that was known of the larynx of the Rhacophoridæ up to the present. The hyoid has been figured by W. K. PARKER (1881) in some species of *Rhacophorus*.

CACOSTERNUM.

Cacosternum capense, Hewitt.

Range: Cape Peninsula.

Male, 29 mm. from snout to vent; from Cape Peninsula. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Hyoid plate a little longer than wide, without ridges or thickened region. Anterior process represented by a broad flange on the anterior convexity of the hyale, a little thinner than the hyale, but not sharply marked off from

it. Alary processes narrow-based lobes; postero-lateral processes simple; postero-medial process with its cartilaginous epiphysis long, about two-thirds of the length of the bony shaft, its distal end incurved.

Arytænoid very long, five and a third times in the body length, with a compressed cartilago apicalis in a deep incisura, between prominentiæ which are not very high. Anterior and posterior pulvinaria vocalia well developed, the posterior on the ventral side of the ends of the arytænoids. Cricoid ring complete; on the cardiac side with a posterior median expansion; laterally broad and strong, with a slender bronchial process, directed inwards on the ventral wall of the larynx, bearing a minute branch

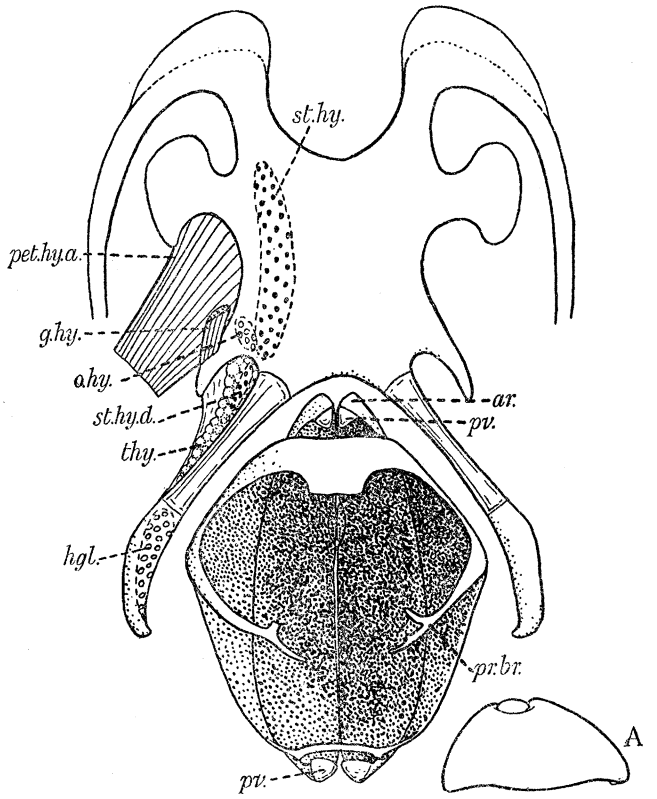

FIG. 64.—*Cacosternum capense*, male. Hyoid and laryngeal skeleton, with insertions of hyoid muscles; ventral. × 10½. A. Left arytænoid. × 5.

and one or two tubercles; "pharyngeal" region very narrow, overlapped dorsally by the arytænoids, so that it is in fact invisible in a dorsal, or pharyngeal, view; articular processes minute, intimately united by syndesmosis to the arytænoids; no lateral or muscular processes.

Muscles.—M. intermandibularis posterior with the superficial layer undifferentiated, although anteriorly the deep layer consists of fibres with a postero-medial direction, almost at right angles to those of the superficial layer.*

* *Cf. Hyla aurea* and *Rhinoderma darwinii*, in which, however, it is the superficial layer which is thus differentiated.

M. interhyoideus expanded to form a very thin layer over the median gular vocal sac.

M. sternohyoideus inserted on the lateral part of the hyoid plate, its dorsal portion on the anterior part of the thyroid gland, which in this species has a narrow extension backwards to the cartilaginous epiphysis of the postero-medial process.

M. geniohyoideus typical.

M. omohyoideus typical and well developed.

M. hyoglossus attached to the ventral surface and inner edge of the cartilaginous epiphysis of the postero-medial process ; entering the tongue in its entirety.

M. petrohyoideus anterior attached to the lateral edge of the hyoid plate, and the posterior edge of the alary process.

Two *mm. petrohyoidei posteriores*, the first rather slender, attached to the hyo-arytænoid membrane in the middle line, immediately behind the hyoid plate, the other, representing

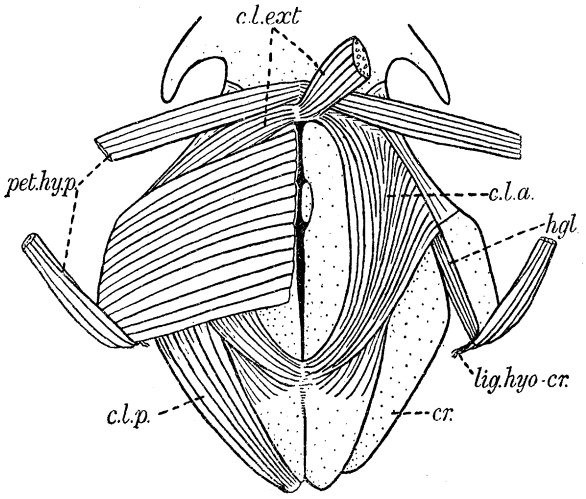

FIG. 65.—*Cacosternum capense*, male. Larynx, dorsal. × 10½. On the right *M. constrictor externus* is cut off short and turned back, and *mm. dilatator* and *constrictor posterior* are removed.

the third of *Rana*, etc., inserted on the posterior edge of the postero-medial process and on the hyo-laryngeal ligament, which here ends on the lung, without reaching the cricoid.

M. dilatator laryngis simple, attached to the arytænoid in the region of the prominentiæ and cartilago apicales. *M. constrictor externus* typical. *M. constrictor anterior* attached behind to the arytænoid, without an inter-cricoid ligament, in front partly continuous with *m. constrictor externus*, but in the main spreading fanwise to an insertion on the hyo-arytænoid membrane and the postero-medial process. *M. constrictor posterior* attached by a short aponeurosis at each end to the large pulvinaria vocalia, not interrupted midway.

No accessory cartilages in the interior of the larynx are visible in dissection. The vocal chords are typical in shape, not densely fibrous, with a short, rather weak frenulum.

Brevicipitidæ.

Hemisus marmoratum (Peters).

Range: tropical Africa.

Female, 35 mm. from snout to vent; from Portuguese East Africa. [B.M.N.H.]

The hyoid and larynx were first dissected, then stained to determine special points.

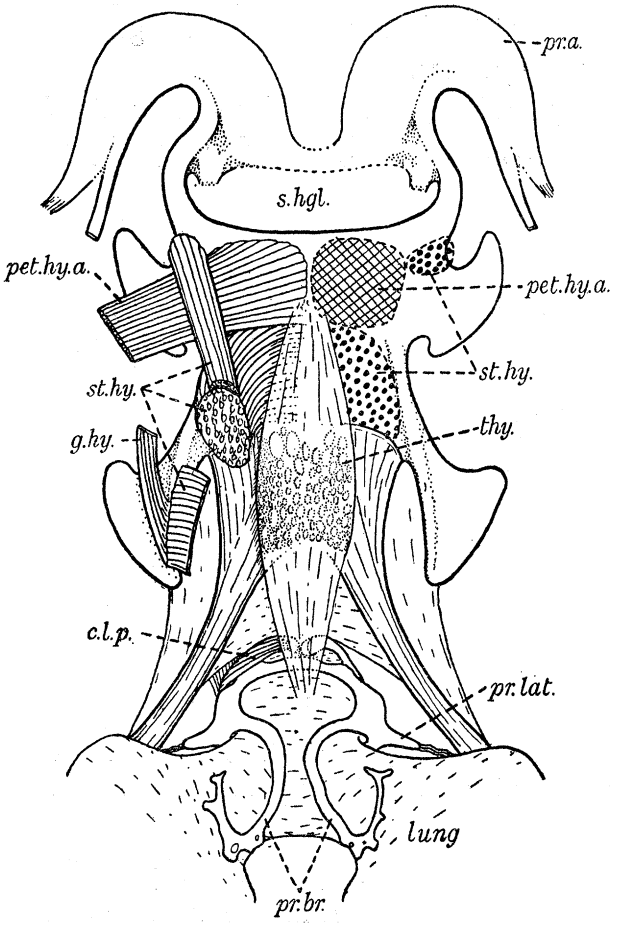

Fig. 66.—*Hemisus marmoratum*, female. Hyoid and larynx, with roots of lungs; ventral. × 10.

Hyoid and Laryngeal Skeleton.—Length of cartilaginous hyoid plate equal to its least width, but length of median part of hyoid increased behind this by the anterior ends of the postero-medial processes, which are expanded and massive and are united to each other for a considerable distance by a very narrow strip of cartilage. Hyale with an anterior process or "extra-hyal," in the form of a broad flange of cartilage, which is different in texture from the rest of the hyoid, and which extends across the hyoglossal sinus, approaching its fellow of the opposite side, to which it is united by a narrow bridge of thin cartilage; the flange is very thin in places, and its edge, especially in the angles between it and the hyale may pass insensibly into membrane.

Alary process arising behind hyoglossal sinus from a rather broad base. Postero-lateral process expanded distally; a ridge of thicker cartilage on its inner border, continued anteriorly along the edge of the hyoid plate. Postero-medial processes bent dorsalwards, distally fairly slender, with small cartilaginous ends.

Arytænoid with a distinct apical cartilage between two well-marked prominentiæ; dorsal and ventral corners of arytænoid narrow, each bounded laterallyby an incisura and mesially by a pulvinar vocale (fig. 68, p. 490). *Cricoid* with an articular process corresponding to dorsal incisura of arytænoid, and with the cardiac process more lateral than the ventral incisura; œsophageal process present, but turned forwards above larynx so as to hide the dorsal pulvinaria from view, and serving for the attachment of muscles; lateral process prominent, joined by ligament to postero-medial process of hyoid; bronchial process long, slender, recurved over ventral surface of lung, slightly expanded and fenestrated at its posterior turning point, and with short branches distally.

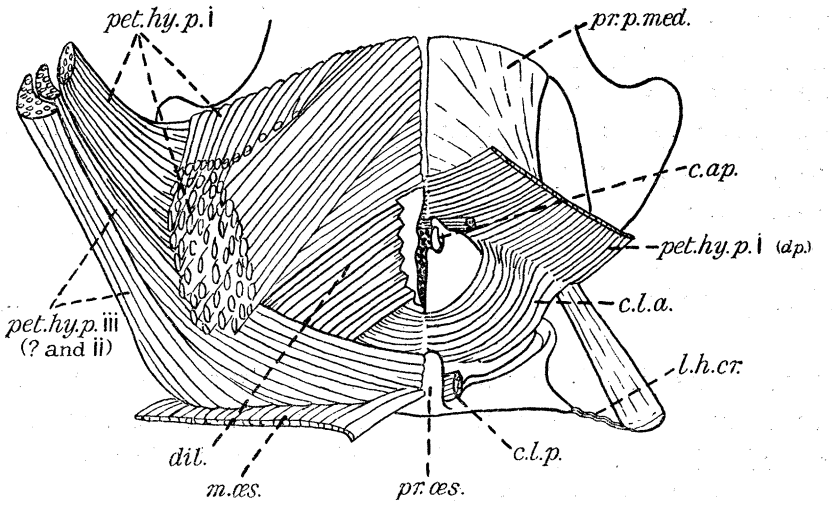

FIG. 67.—*Hemisus marmoratum*, female. Larynx, dorsal. × 13⅓. On the right the dilatator and the constrictor externus are removed, and the deepest portion only of *m. petrohyoideus posterior I* is left.

Muscles. *M. intermandibularis posterior* with a narrow lateral slip, running parallel to lower jaw, and attached in front to an expansion of the mento-meckelian bone. *M. interhyoideus* typical.

M. sterno-hyoideus inserted in three parts:—(i) a ventral strip attached to hyoid plate at an angle between alary process and manubrium, (ii) the main part of the muscle on the hyoid plate in an oval area adjacent to its fellow, not extending on to the postero-medial process, and (iii) *m. sternohyoideus dorsalis*, inserted on the ridge of the postero-lateral process.

M. omohyoideus absent.

M. geniohyoideus with external insertion on ridge of postero-lateral process, adjacent to *sternohyoideus dorsalis*. Internal insertion typical.

M. hyoglossus arising from ventral surface of end of postero-medial process and passing dorsad to bridging cartilage of anterior processes of hyalia, to enter the tongue in its entirety.

M. petrohyoideus anterior inserted on a roughly circular area between the first two insertions of the sternohyoid, meeting its fellow in the middle line.

M. petrohyoideus posterior I massive, inserted on the medial part of the dorsal side of the root of the postero-medial process, and, behind this, on the hyo-arytænoid membrane in the middle line and on its posterior edge; fibres attached to hyo-arytænoid membrane forming a deep layer, which curves round the rest of the muscle anteriorly to join some of the superficial fibres, ending in the floor of the pharynx; rest of muscle with the usual attachment on the skull.

M. petrohyoideus posterior II absent, unless it is to be considered as contributing to *I* or *III*.

M. petrohyoideus III stout, imperfectly divided into two layers, attached to the end of the postero-medial process, to the hyocricoid ligament, to the lateral process of the cricoid and to the edge of the up-turned œsophageal process. Part of the "œsophageal muscle" is inserted with this.

M. dilatator laryngis attached to apical cartilages and prominentiæ of arytænoid.

M. constrictor externus typical.

M. constrictor anterior attached to a membrane posteriorly, ending anteriorly on the hyo-arytænoid membrane, adjacent to the deep layer of m. petrohyoideus posterior I.

M. constrictor posterior attached to the small pulvinaria vocalia, and, midway, to the cricoid.

Thyroid Gland.—The thyroid is a single median body and is seen, on removing the hyoglossus, to lie ventral to the broad proximal ends of the postero-medial processes, attached by bands of fibrous tissue to the middle of the hyoid plate in front, and to the ventral surface of the larynx behind.

The only other Anuran in which, to my knowledge, the thyroid is median is *Breviceps adspersus* (see below).

Previous Work on Hemisus.

De Villiers (1931 *a*, p. 326) described the hyoid of *Hemisus marmoratum*. In his specimen "there are two backwardly directed cartilaginous bars running parallel to the manubria and confluent with the anterior processes in front." The presence or absence of a cartilaginous bridge connecting these two bars may be a matter of individual variation in this species, or, more probably, may depend on age. In other respects De Villiers' description appliesalso to the specimen described above, except that the alary process is evidently not delimited behind by so deep a notch.

Beddard (1908 *c*, p. 907, figs. 176, 178, 179, 180) described the hyoid and its musculature in *H. guttatum*. The anterior processes of the hyale are united to form a "hood" ventral to the hyoglossal muscle. Alary and postero-lateral processes are

not described. A plate of bone is said to exist dorsal to the hyoid plate, close under the pharynx; it is probably the fused anterior ends of the postero-medial processes, The hyoid plate is thickened posteriorly in a way that is reminiscent of the cartilaginous pad* in *Pseudohemisus* and the rest of the Brevicipitidæ, excluding *Breviceps*. The anterior petrohyoid separates the two anterior insertions of the sternohyoid as in *H. marmoratum*. The position as figured (fig. 179) of the first posterior petrohyoid is consistent with an insertion like that of *H. marmoratum*, and supports the suggestion that Beddard's "dorsal plate of bone" is part of the postero-medial processes. The last petrohyoid, however, is stated not to extend on to the larynx. The omohyoid is absent.

Breviceps adspersus, Peters.

Range, S. Africa.

Female, 52 mm. from snout to vent, from Klein Letaba, Transvaal. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Length of Hyoid plate greater than its width. Hyale stout except in region of anterior process, where it is abruptly narrower; anterior process attached to hyale at one end, recurved, with distal end approaching but not fused with hyale, almost enclosing a triangular fenestra; its antero-medial portion broad, with two or three small fenestræ and with a process lying ventral to the hyoglossal muscle, united to its fellow of the other side by a short, thin band of fibres. Alary process small, imperfectly formed, of very thin cartilage. Postero-lateral process long and stout. Postero-medial process broad at each end, narrow in the middle, where it is bent dorsalwards; attached with its fellow to a triangular posterior segment of the hyoid plate, separated by a fibrous layer from the main cartilage.

Arytænoid approximately equilateral, with a discrete apical cartilage between well-marked prominentiæ; pulvinaria vocalia small. Cricoid a complete ring, broadest on the cardiac side, very narrow laterally; no œsophageal or muscular processes; lateral processes low, united by ligament with hyoid. Bronchus very long (6 mm.), directed dorsally; bronchial process an extensive, branched and fenestrated cartilage supporting ventral, medial and lateral walls of bronchus and extending on to root of lung for about 2 mm.

Muscles.—*M. intermandibularis posterior* with a superficial strip adjacent and parallel to lower jaw.

M. interhyoideus typical.

M. sternohyoideus inserted in three parts; the ventral slip on anterior part of manubrium; the main part in a narrow area on the hyoid plate adjacent to its fellow, and along the division between main and posterior segments of the hyoid plate; *pars dorsalis* on thyroid membrane; a minute bundle of muscle fibres found attached to the end of the postero-lateral process may be part of this or of the geniohyoid.

* BEDDARD, however, describes a spongy centre to this thickening. Can he have seen the thyroid gland?

M. omohyoideus. There is no muscular connection between the scapula and the hyoid.

M. geniohyoideus with external insertion on inner edge of postero-lateral process. *M. geniohyoideus medialis* not distinguishable; internal part of muscle consisting posteriorly mainly of transverse fibres crossing the hyoglossus from a weak median

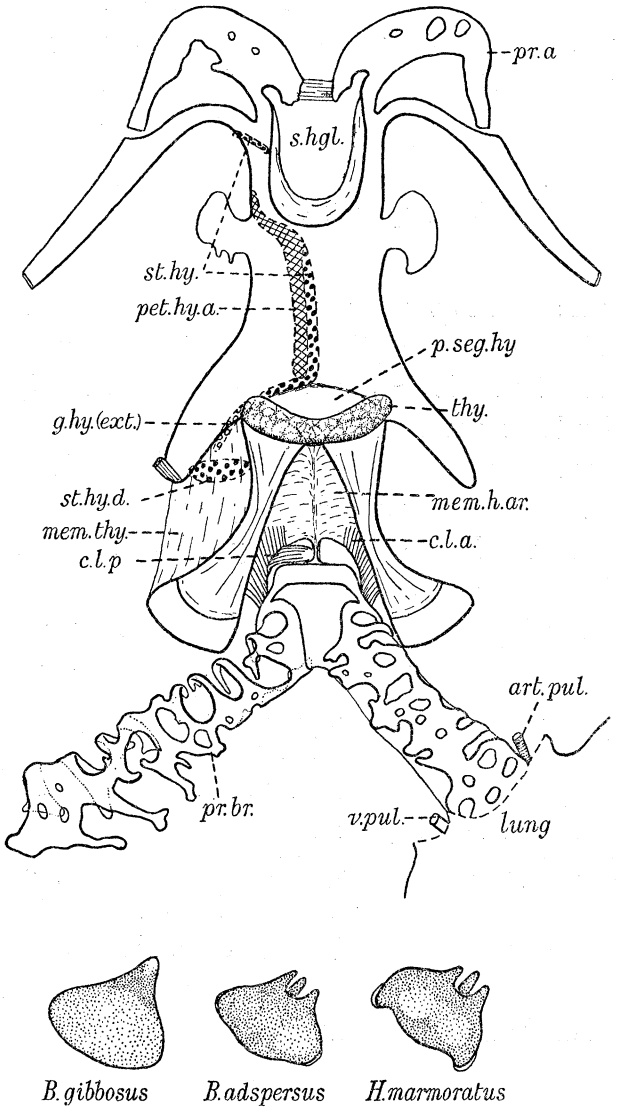

FIG. 68.—*Breviceps adspersus*, female. Skeleton of hyoid and larynx, with some muscle-insertions; ventral. × 6. Below, left arytænoid in *B. gibbosus*, *B. adspersus* and *Hemisus marmoratus*. *p. seg. hy.* = posterior segment of hyoid plate.

fascia, and mostly inserted on the outer edge of the postero-medial process, a few on its inner edge.

M. hyoglossus with an angular course, corresponding to the sharp bend in the postero-

medial processes* ; its lateral and dorsal layers with fibres parallel to the perimysium, but fasciculi of bulk of muscle twisted in a rope-like manner. I have seen a similar twisting in some other Anura ; it is probably connected with great extensibility of the tongue, as BEDDARD (1908, *a*) has suggested for *Breviceps* sp.

M. petrohyoideus anterior inserted between first and second insertions of sterno-hyoid, and, continuously, adjacent to main part of sternohyoid.

M. petrohyoideus posterior I inserted on posterior segment of hyoid and on hyo-arytænoid membrane, meeting its fellow in the middle line.

M. petrohyoideus posterior II absent. *III* imperfectly divided into two layers, the ventral attached to the cartilaginous end of the postero-medial process, the dorsal to the hyocricoid ligament, and, with its fellow, to a median fascia between dorsal end of arytænoid and pharynx. This fascia is in the position of the œsophageal process of *Hemisus* and probably replaces it in this species.

M. dilatator laryngis simple, attached to prominentiæ and apical cartilage of arytænoid. *M. constrictor externus* typical. *M. constrictor anterior* attached to bony shaft of postero-medial process behind the middle of its length ; a few fibres also ending on hyo-arytænoid membrane. *M. constrictor posterior* attached at each end to a pulvinar vocale, and partially interrupted midway by cricoid.

Thyroid Gland.—As in *Hemisus marmoratum* this is a single, median body. It is transversely elongate and is closely applied to the ventral surface of the hyoid at the bases of the postero-medial processes.

Breviceps gibbosus (Linné).

Range, S. Africa.

Female, 46 mm. from snout to vent. [ZOOL. SOC.]

The hyoid and larynx were first dissected, then stained in bulk with toluidin blue and cleared in oil of wintergreen.

Hyoid and Laryngeal Skeleton.—Hyoid similar to that of *B. adspersus*, but with no alary processes, with the hyoglossal sinus wider and deeper, with the anterior processes simple loops of cartilage fused at each end with the hyale and having no medially directed processes.

Arytænoid with an acute pharyngeal angle, without prominentiæ or apical cartilage. Cricoid as in *B. adspersus*. Bronchus much shorter than in *B. adspersus*, with ventral and lateral walls supported by a correspondingly shorter fenestrated and branched expansion of the bronchial process.

Muscles.—M. intermandibularis posterior differentiated as in *B. adspersus*.

* The transverse direction of the fibres of the geniohyoid muscle is no doubt the result of this bent course, as only so can they perform their usual function of helping to raise the floor of the mouth without causing the larynx to project. This has not happened, however, in other Brevicipitidæ, where the course of the hyoglossus is similar, if less extreme.

M. sternohyoideus with main insertion as in *B. adspersus* but with ventral slip inserted adjacent to, not in front of, m. petrohyoideus anterior; *pars dorsalis* inserted on postero-lateral process.

M. omohyoideus absent.

M. geniohyoideus with external insertion on the postero-lateral process. The muscle is not well enough preserved to be described further.

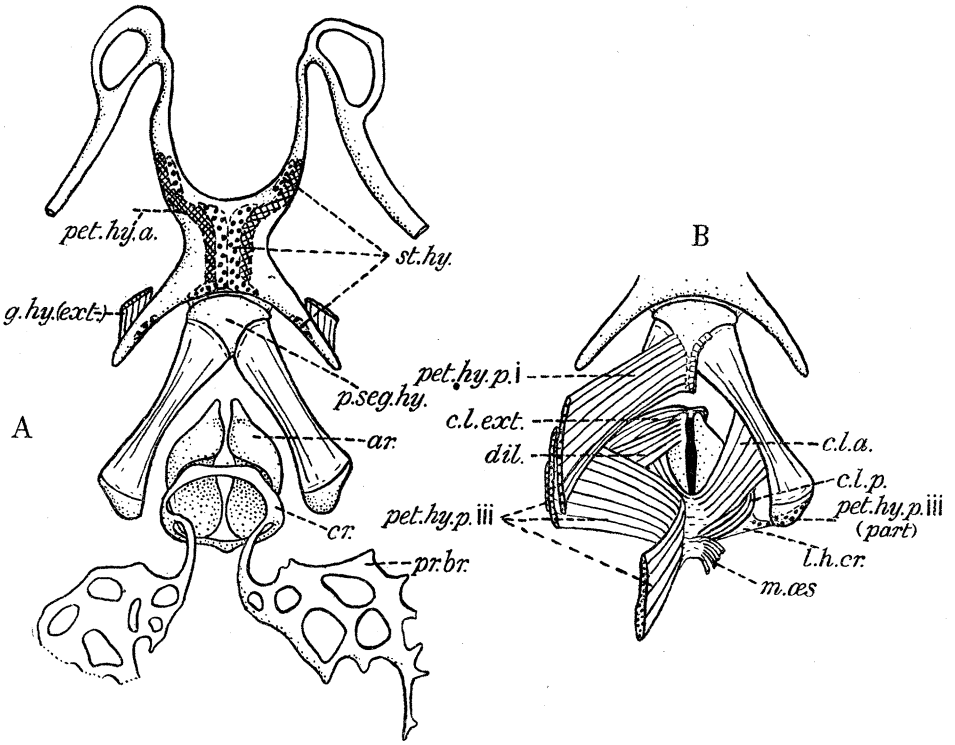

FIG. 69.—*Breviceps gibbosus*, female. A. Hyoid and laryngeal skeleton, showing insertions of hyoid muscles; ventral view. B. Larynx, dorsal. × 5⅓.

M. hyoglossus attached to ventral surface of end of postero-medial process, entering the tongue in its entirety; with twisted fasciculi.

M. petrohyoideus anterior inserted on a narrow area adjacent to the two anterior insertions of *m. sternohyoideus*. *Petrohyoidei posteriores* as in *B. adspersus*.

Laryngeal muscles as in *B. adspersus*.

The *thyroid gland* was not examined in this specimen.

Previous Work on Breviceps.

HENLE (1839, pp. 11, 13, 14, 24, figs. 31-33) described the larynx of "*Engystoma gibbosum* Cuv.," which differs so much from that described above that he probably had a different species. The pharyngeal angle of the arytænoid is indented, the bronchial processes anastomose proximally, and although they are broad distally they are not fenestrated.

BEDDARD (1908, *a*) gives some account of the hyoid and its musculature in *Breviceps* sp. The anterior processes are like those of *B. gibbosus* but extend further towards the middle line where, as in *B. adspersus*, they nearly meet. The postero-medial processes are said to be inserted on the ventral surface of the hyoid plate, in front of its posterior edge, a state of affairs difficult to imagine where the processes are dorsally inclined. The sternohyoid and geniohyoid muscles are evidently similar to those of *B. gibbosus* and *adspersus*. The third posterior petrohyoid is attached to the hyocricoid ligament but is not described as reaching the middle line. *M. intermandibularis posterior* is differentiated as described above.

In 1911 BEDDARD described another species of Breviceps probably *B. gibbosus*, but the respiratory apparatus is only briefly mentioned.

DE VILLIERS (1931, *b*, pp. 172-3, fig. 7) described the hyoid apparatus of *B. fuscus*. In it the alary process is vestigial in young, absent in older animals. In *Probreviceps* (de Villiers, 1933, p. 273) his description of the hyoid shows it to be similar to that of *Breviceps gibbosus*.

Kaloula pulchra (J. E. Gray).

Range, India, Farther India, South China, Malay Archipelago.

Female, 71 mm. from snout to vent. [ZOOL. SOC.]

Hyoid and Laryngeal Skeleton.—The hyoid was described by W. K. PARKER (1881, p. 245 pl. 44, fig. 11). Width of hyoid plate one and a third times its median length hyoglossal sinus deep, very narrow posteriorly; a cartilaginous thickening between the origins of the postero-medial processes. Anterior process represented by a strip of thinner cartilage bordering the convex edge of the hyale, and called " extra-hyal " by W. K. PARKER in *Microhyla ornata* and others, but not described by him in *Kaloula*. Alary process very long antero-posteriorly; postero-lateral process small, simple; postero-medial process stout, inclined dorsally, its width increased posteriorly by a wider lateral and a narrower medial bony flange; cartilaginous epiphysis very narrow.

Larynx much smaller than laryngeal sinus. *Arytœnoid* with a concave edge at the *aditus laryngis*, bounded by low prominentiæ, between which is fibrous tissue but no *cartilago apicalis;* pulvinaria vocalia narrow. Pharyngeal half of *cricoid* without processes; cardiac processes prominent; bronchial processes curved towards middle line, then diverging, each expanded distally into a branched and fenestrated plate supporting a bronchus of considerable length, but much shorter than in *Breviceps adspersus*. On the dorsal side the lung encroaches on the bronchus, particularly on the right in this specimen, and a considerable part of the dorsal bronchial wall is vascularized.

Muscles.—M. intermandibularis posterior not sharply divided into two parts, but with anterior superficial fibres more oblique than deep layer. *M. interhyoideus* typical.

M. sternohyoideus with ventral and main portions inserted on a narrow area at edge of hyoglossal sinus and adjacent to middle line on hyoid plate, diverging behind at

the cartilaginous thickening. *Sternohyoideus dorsalis* attached to lateral edge of postero-medial process.

M. omohyoideus absent.

M. geniohyoideus with external insertion on edge of postero-medial process, with *sternohyoideus dorsalis*.

M. hyoglossus attached to ventral surfaces of cartilaginous ends of postero-medial processes, entering the tongue in its entirety.

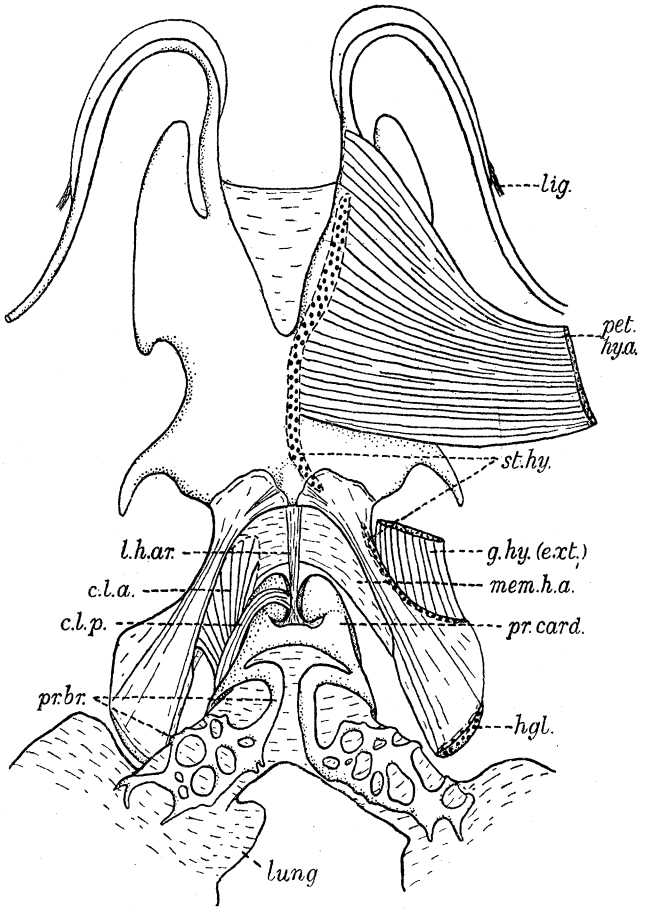

FIG. 70.—*Kaloula pulchra*, female. Hyoid and larynx, with roots of lungs; ventral. × 5. Insertions of hyoid muscles shown on the right of the figure, of laryngeal on the left.

M. petrohyoideus anterior overlapping hyoid ventrally, with long insertion adjacant to that of *m. sternohyoideus*.

M. petrohyoideus posterior I crossing dorsal side of postero-medial process, inserted in middle line of posterior end of hyoid plate and hyo-arytænoid membrane. No *petrohyoideus posterior II*. *M. III* large, attached to end of postero-medial process, to hyocricoid ligament, and with its fellow, to a median raphe dorsal to larynx behind the *aditus*.

Mm. dilatator laryngis and *constrictor laryngis externus* typical. *M. constrictor anterior* attached in front partly with *constrictor externus*, but with main part dipping under

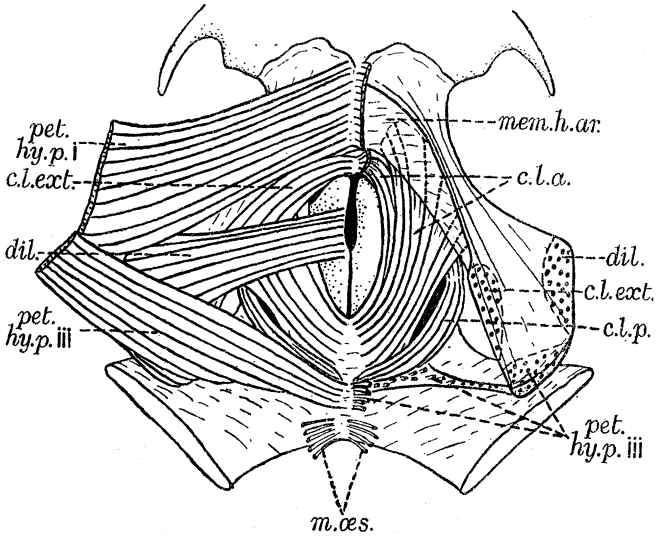

FIG. 71.—*Kaloula pulchra*. Larynx, dorsal. × 5. Superficial muscles removed on the right.

hyo-arytænoid membrane and attached to ventral side of this and to inner edge of postero-medial process.

M. constrictor posterior rather slender, attached at each end to pulvinaria vocalia, interrupted midway where it is attached to the cricoid.

Pseudohemisus longimanus, Angel.

Range, Southern and Western Madagascar.

Male, 26 mm. from snout to vent, from S.W. Madagascar. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Width of hyoid plate a little greater than its median length; a rather large ventral cartilaginous thickening between origins of postero-medial processes. Anterior process of hyale represented by a narrow extra-hyal, continued laterally as a ligament to the angle of the jaw. Alary process very long antero-posteriorly. Postero-lateral process slender, simple. Postero-medial processes widely diverging, with inner and outer flanges, as in *Kaloula pulchra* and with narrow distal cartilages.

Larynx very large; length of arytænoid contained six and a half times in body length. *Arytænoid* very gibbous, of thick cartilage, with somewhat concave edge bordering aditus, without apical or basal cartilages; *pulvinaria vocalia* narrow. Ventral edge of arytænoid, between cardiac and pharyngeal incisuræ articulares, strongly projecting so as partially to occlude the pulmonary opening. *Cricoid* slender, incomplete ventrally, where its ends are connected by fibrous tissue with the pulvinaria. No œsophageal process; lateral and muscular processes blunt; bronchial process curved over a short bronchus, divided into a short ventral and a longer dorso-lateral branch.

Muscles.—M. intermandibularis posterior with a weakly differentiated tract running parallel to the lower jaw. Vocal sac protruding between this muscle and *m. interhyoideus.*

M. sternohyoideus inserted as in *Kaloula.*

M. omohyoideus absent.

Mm. geniohyoideus and *hyoglossus* as in *Kaloula.*

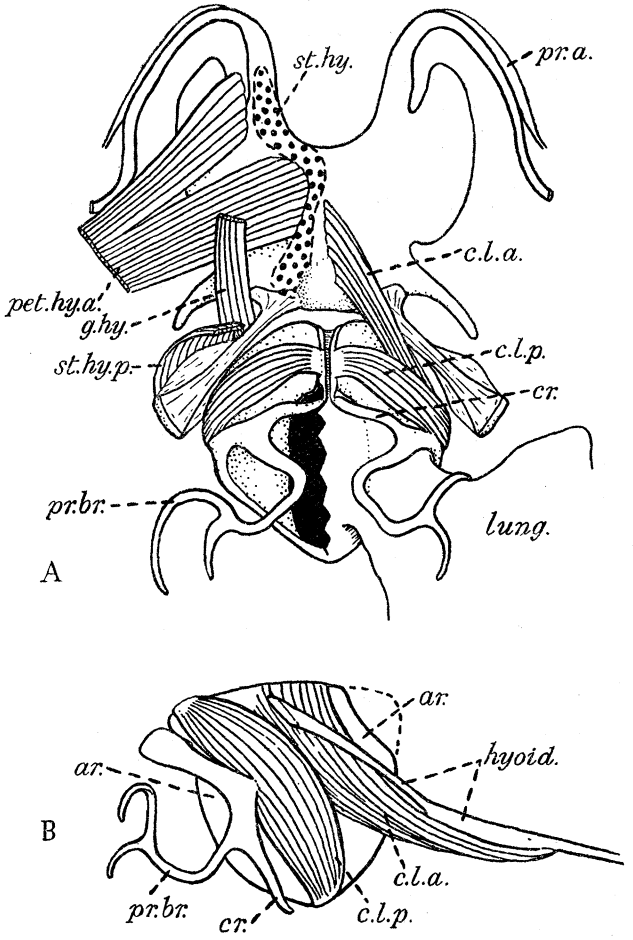

FIG. 72.—*Pseudohemisus longimanus*, male. A. Hyoid and larynx, with root of left lung; ventral. × 8⅓. The membranous wall of the right half of the larynx is removed to show the edge of the arytænoid. Most of the muscles are shown on one side only. B. Diagrammatic lateral view of larynx with mm. constrictores anterior and posterior.

M. petrohyoideus anterior inserted in two parts, one on the ventral surface of the alary process, the other on the hyoid plate adjacent to *M. sternohyoideus.*

M. petrohyoideus posterior I inserted in the middle line on the dorsal surface of the posterior end of the hyoid plate. No *M. petrohyoideus posterior II. M. III.* inserted on end of postero-medial process and on hyocricoid ligament.

M. dilatator laryngis attached to the triangular membranous lip of the aditus laryngis, above the concave border of the arytænoid. *M. constrictor externus* attached as in *Kaloula*, to the inner flange of the postero-medial process.

M. constrictor anterior with a broad attachment behind the aditus; in front, whole muscle extending forwards on ventral side of hyoid plate and attached to this and to its cushion-like thickening near the middle line, between the sternohyoids, the insertion occupying more than half the length of the hyoid plate. *M. constrictor posterior* attached at each end by a short aponeurosis to the pulvinar vocale, partly interrupted midway by muscular process of cricoid.

The larynx is remarkable for its rotundity, owing to the great development of the arytænoids. In proportion the pulmonary openings and the aditus are very small.

The vocal chords have the pars basalis almost in the sagittal plane; a rostral lip and a deep caudal lip are developed, and there is a conspicuous frenulum.

Oreophryne celebensis (Friedr. Müller).

Range, Celebes.

Female, 30 mm. from snout to vent. [B.M.N.H.]

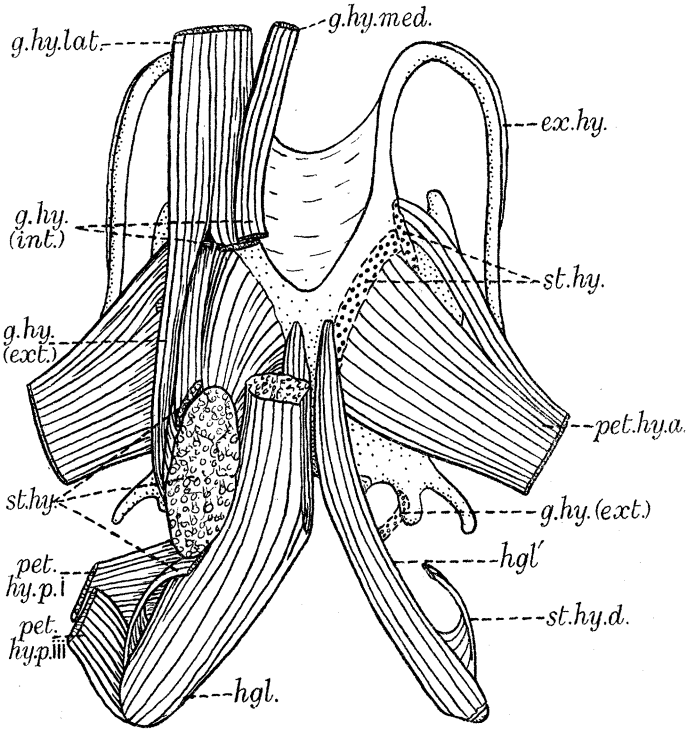

FIG. 73.—*Oreophryne celebensis*, female. Dissection of the hyoid and its muscles, from below. × 9.

Hyoid and Laryngeal Skeleton.—Length of hyoid plate equal to its width; a cartilaginous thickening between origins of postero-medial processes; hyoglossal sinus deep. Anterior process represented by a very narrow "extra-hyal." Alary process as in *Kaloula*; postero-lateral process forked, the outer limb the longer; postero-medial

process rather slender, dorsally inclined, with a thin inner bony flange, and with very narrow cartilaginous tip.

Larynx much smaller than laryngeal sinus. *Arytænoid* small, with a truncate or slightly concave edge at the aditus laryngis, without apical cartilage or prominentiæ; pulvinaria vocalia small. *Cricoid* complete, without processes on the pharyngeal side; cardiac processes small, closely applied to arytænoid; bronchial processes curved towards middle line, then diverging, each expanded as a fenestrated plate on ventral wall of root of lung.

Muscles.—M. intermandibularis posterior weakly differentiated into a deep transverse layer and a superficial layer with fibres parallel to lower jaw. *M. interhyoideus* typical.

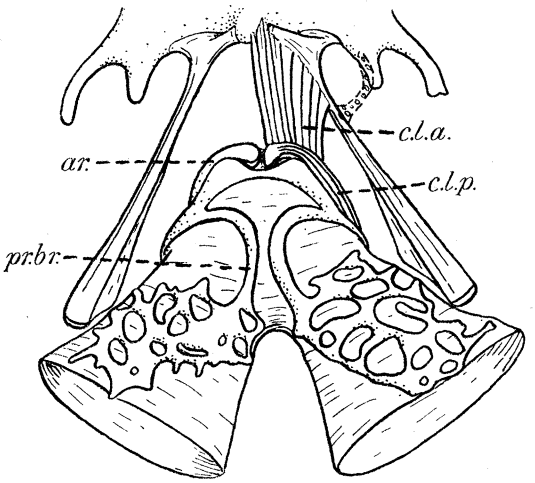

FIG. 74.—*Oreophryne celebensis*.—Larynx in position; ventral. × 10. Constrictores anterior and posterior shown on one side.

M. sternohyoideus with hyoid insertion of its ventral strip dividing insertion of anterior petrohyoid into two; main insertion as in *Kaloula; sternohyoideus dorsalis* attached near posterior end of postero-medial process.

M. omohyoideus absent.

M. geniohyoideus inserted on inner limb of postero-lateral process and on thyroid membrane between this and postero-medial process.

M. hyoglossus with origin on ventral surface of posterior part of postero-medial process; bulk of muscle entering tongue but the layer adjacent to hyoid attached to hyoid plate near middle line (fig. 73, *hgl'*), between right and left sternohyoids, as described in *Cacopus systoma* by DEVANESEN (1922).

M. petrohyoideus anterior with a small insertion in front of ventral layer of sternohyoid, and a larger insertion adjacent to main part of that muscle.

First *petrohyoideus posterior* as in *Kaloula*, etc., the other extending on to the hyocricoid ligament and cricoid, but not meeting its fellow dorsal to larynx.

M. dilatator laryngis inserted on the tough membranous lip of the aditus laryngis and on the edge of the arytænoid.

M. constrictor externus arising from inner flange of postero-medial process. *M. constrictor anterior* extending forward to the ventral side of the proximal part of the postero-medial process and to the thickened cartilage between the origins of the two bones, thus approaching the condition of the muscle in *Pseudohemisus* (and in *Calluella* and *Microhyla berdmorei*, below). *M. constrictor posterior* continuous between its attachments to the pulvinaria.

Calluella guttulata (Blyth).

Range, Farther India.

Male, 45 mm. from snout to vent. [Dr. MALCOLM SMITH.]

Hyoid and Laryngeal Skeleton.—Hyoid plate nearly as long as broad, with a ventral keel in the middle line, as well as a posterior thickening between origins of postero-

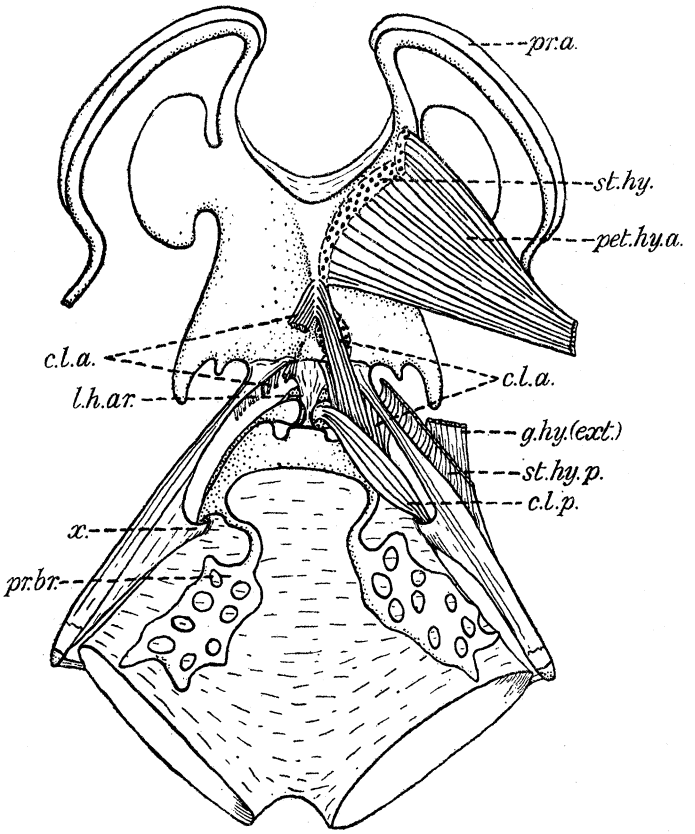

FIG. 75.—*Calluella guttulata*, male. Hyoid and larynx, with muscle insertions of one side; ventral. × 6⅔. *l.h.ar.* = hyo-arytænoid ligament (all that remains of the hyo-arytænoid membrane). *x* = laryngeal process of postero-medial process. As in other figures of Brevicipitidæ, the hyoid plate and the postero-medial processes are drawn as though in one plane; in reality the postero-medial processes are directed dorsally.

medial processes; hyoglossal sinus moderate. Hyale with a long, narrow "extrahyal." Alary process large, with fairly narrow base; postero-lateral process divided, the inner limb very short; postero-medial process slender, dorsally inclined, with very

small cartilaginous tip; width of bone increased by a triangular inner flange with its apex produced into a facet, firmly united by dense fibrous tissue to the membranous wall of the larynx, just behind the lateral part of the cricoid.

Larynx large. *Arytænoid* greatly elongate, with nearly straight edge bordering the long aditus, which is almost in the dorso-ventral line, opening forwards; a small fenestra in the cartilage; pulvinaria vocalia present. *Cricoid* without processes on pharyngeal side, broad laterally, with a low ridge representing the muscular process; cardiac processes prominent; between them a median process; bronchial processes curved, each ending in a fenestrated plate which lies on the ventral wall of this large larynx.

Muscles.—M. intermandibularis posterior with a weakly differentiated anterior superficial portion running parallel to lower jaw. *M. interhyoideus* with stout fasciculi; a large sub-gular vocal sac pouched out behind it.

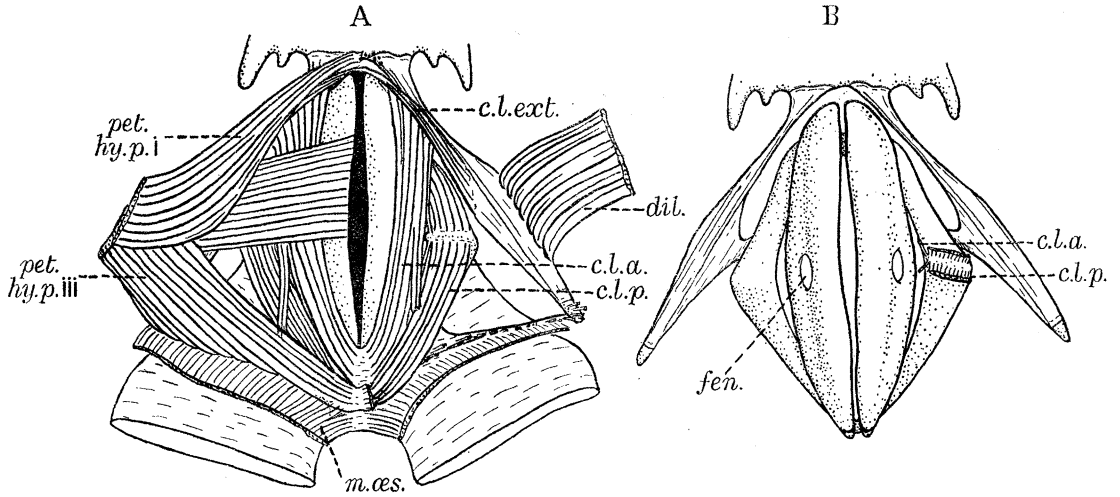

FIG. 76.—*Calluella guttulata.* A. Larynx, dorsal, with dilatator turned back and petrohyoids removed on the right. B. Laryngeal skeleton; bronchial processes not shown. *fen.* = arytænoid fenestra.

M. sternohyoideus with its anterior and main insertions distinct but adjacent; main insertion as in *Pseudohemisus; sternohyoideus dorsalis* with a long insertion on outer edge of postero-medial process.

M. omohyoideus absent.

M. geniohyoideus with external insertion adjacent to that of sternohyoideus dorsalis.

M. hyoglossus with typical origin and with typical insertion in the tongue.

M. petrohyoideus anterior with linear insertion adjacent to that of anterior and main insertions of sternohyoid.

M. petrohyoideus posterior I meeting its fellow in a narrow raphe attached to median posterior part of hyoid plate and to inner edge of proximal part of postero-medial process; no middle posterior petrohyoid; last petrohyoid attached to end of postero-medial process, to a weak hyocricoid ligament on the root of the lung (to which part

of the " œsophageal muscle " is also attached) and meeting its fellow in a narrow raphe dorsal to the larynx, behind the aditus.

M. dilatator laryngis originating from a more anterior part of the postero-medial process than is usual, inserted directly on the arytænoid. *M. constrictor externus* attached to inner flange of postero-medial process. *M. constrictor anterior* inserted in front in part on anterior margin of laryngeal sinus, in part on the ventral keel of the hyoid plate, between the sternohyoids. *M. constrictor posterior* attached to the pulvinaria vocalia, and, midway in its length, to the lateral ridge of the cricoid.

Microhyla berdmorei (Blyth).

Range, Farther India and Sumatra.

Female, 46½ mm. from snout to vent. [Dr. Malcolm Smith.]

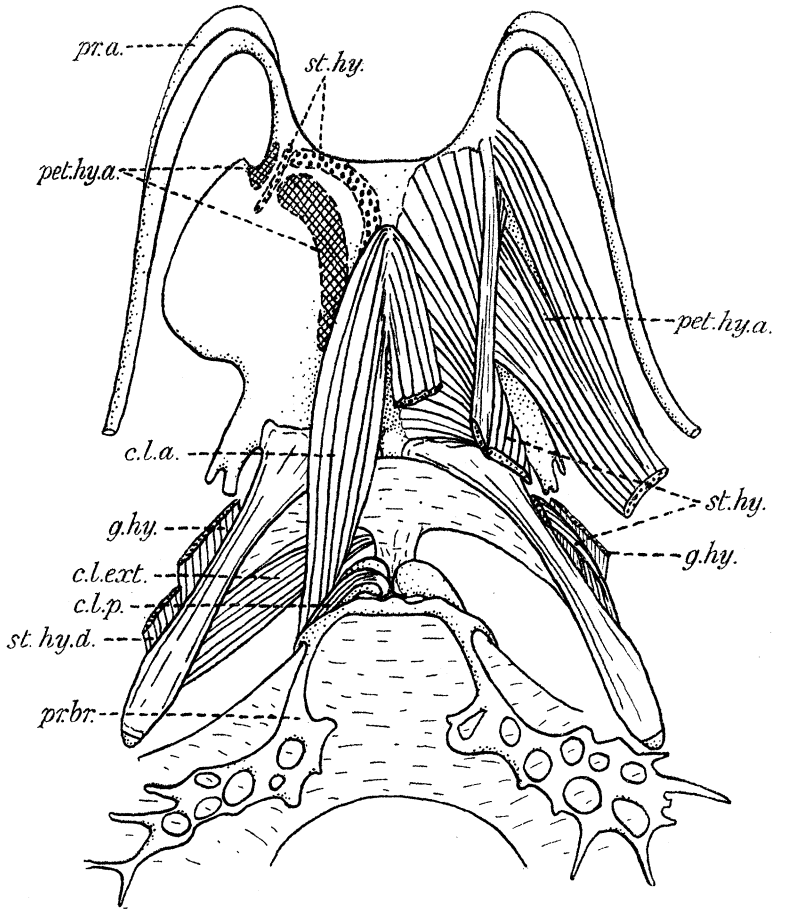

Fig. 77.—*Microhyla berdmorei*, female. Hyoid and larynx, ventral, with hyoid muscles on the righ the figure and laryngeal on the left. × 10.

Hyoid and Laryngeal Skeleton.—Length of hyoid plate equal to its width ; a ventral cartilaginous thickening between proximal ends of postero-medial processes ; hyoglossal sinus shallow. Alary process with a broad base ; postero-lateral process forked distally ;

postero-medial process fairly stout, inclined dorsally, with very small distal cartilage.

Larynx much smaller than laryngeal sinus. *Arytænoid* a little longer than high, pierced by a fenestra ; edge at aditus slightly concave, without apical cartilage. *Cricoid* without processes on pharyngeal side, with a small median process between the cardiac processes ; bronchial processes each ending in a fenestrated plate on ventral wall of root of lung.

Muscles.—M. intermandibularis with lateral superficial layer parallel to lower jaw. *M. interhyoideus* broad.

Ventral slip of *m. sternohyoideus* inserted at base of manubrium, between the two

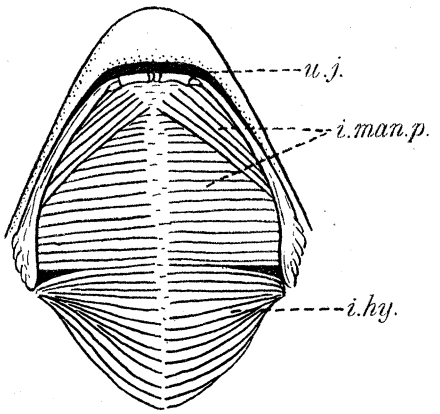

FIG. 78.—*Microhyla berdmorei*. Muscles of throat. × 4. *u.j.* upper jaw.

parts of *m. petrohyoideus anterior*. Main part of *sternohyoideus* as in *Pseudohemisus*, etc. *Sternohyoideus dorsalis* attached to outer edge of posterior half of postero-medial process.

M. omohyoideus absent.

M. geniohyoideus with external insertion on edge of postero-medial process in front of sternohyoideus dorsalis.

M. hyoglossus attached to ventral surface of postero-medial process, and entering the tongue in its entirety.

M. petrohyoideus anterior with its hyoid insertion adjacent to that of m. sterno-hyoideus, divided into two by the ventral slip of that muscle.

M. petrohyoideus posterior I inserted on a median raphe attached to hyoarytænoid membrane and posterior end of hyoid, as in the foregoing species of Brevicipitidæ ; last posterior petrohyoid attached to end of postero-medial process and to hyocricoid ligament.

Œsophageal portion of *m. obliquus internus* also attached to hyocricoid ligament and closely associated with dorsal part of larynx and floor of this part of œsophagus.

M. dilatator laryngis attached to membranous lip of aditus laryngis and to edge of arytænoid. *M. constrictor externus* typical. *M. constrictor anterior* extending forwards on ventral side of hyoid plate, to which it is attached by the median raphe in which it meets its fellow ; at its posterior end superficial fibres are associated with fibres of

the "œsophageal" muscle in a fascia attached to the floor of the œsophagus. *M. constrictor posterior* attached to dorsal and ventral pulvinaria vocalia, and interrupted

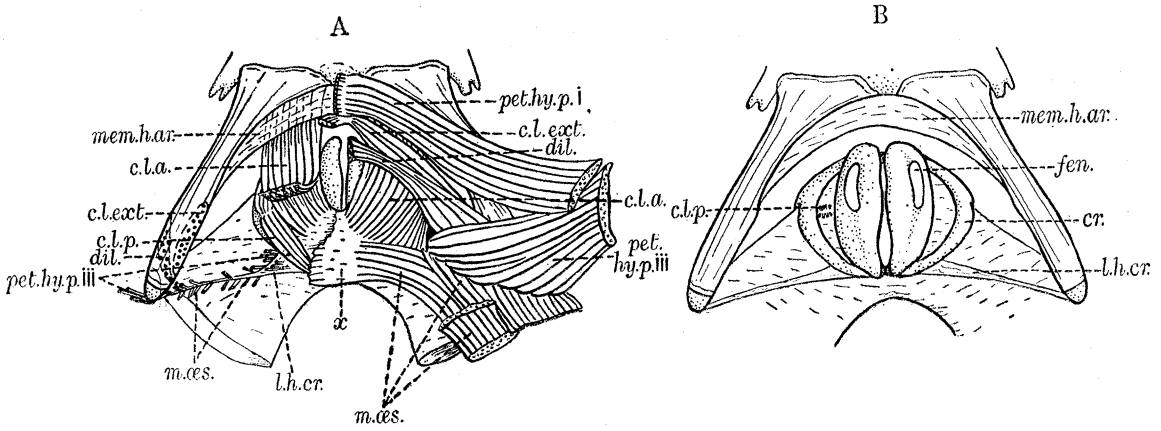

FIG. 79.—*Microhyla berdmorei*, female. A. Larynx, dorsal. On the left the petrohyoidei, dilatator and constrictor externus are removed, and the superficial layer of the constrictor anterior is cut away from the tissue (*x*) in which it and part of the œsophageal muscle end. B. The same, with muscles removed.

midway by an insertion on the membranous wall of the larynx, between arytænoid and cricoid.

Microhyla ornata (Duméril and Bibron).

Range, India, Farther India, South China.

Female, 24 mm. from snout to vent; from Kedah. [B.M.N.H.]

In structure of hyoid and larynx, this agrees essentially with *M. berdmorei*. The postero-medial process consists of a relatively slender shaft flanked by narrow lateral and broader inner flanges.

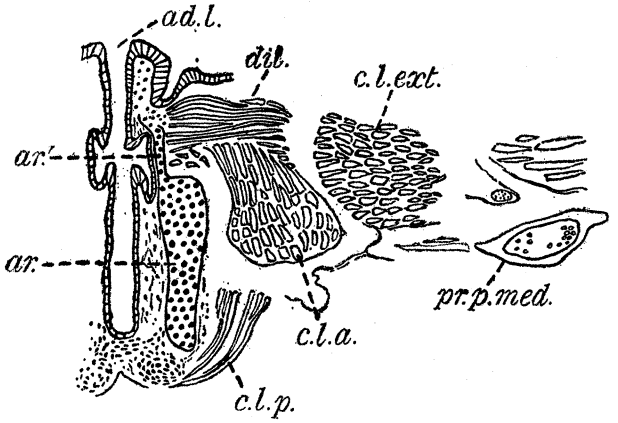

FIG. 80.—*Microhyla ornata*.—Transverse section of half larynx. *ar'* = thin pharyngeal region of arytænoid.

The bronchial plates are only weakly fenestrated. *M. constrictor laryngis* anterior extends even farther forward on the ventral surface of the hyoid than in *M. berdmorei*, almost to the hyoglossal sinus.

The hyoid and larynx of this specimen have been sectioned and the following facts are revealed :—The ventral cushion of the hyoid plate, between the postero-medial processes, consists of hyaline cartilage, with more matrix between the cells than in other parts of hyoid and larynx. The extrahyals, on the other hand, consist of cartilage with small elements and little matrix.

The arytænoids are not fenestrated. At the aditus laryngis their edges are produced into a thin layer of typical cartilage, which merges at its upper edge, without perichondrium, into the firm connective tissue of the lip of the aditus. To this thin cartilage the *dilatator* is attached. Dorsal and ventral *pulvinaria vocalia* are present and serve for the attachment of *m. constrictor laryngis posterior*.

Microhyla inornata, Boulenger.

Range : Farther India, Sumatra, Borneo.

Female, 22 mm. from snout to vent ; from Chantaboon, Siam. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Least width of hyoid plate nearly equal to its median

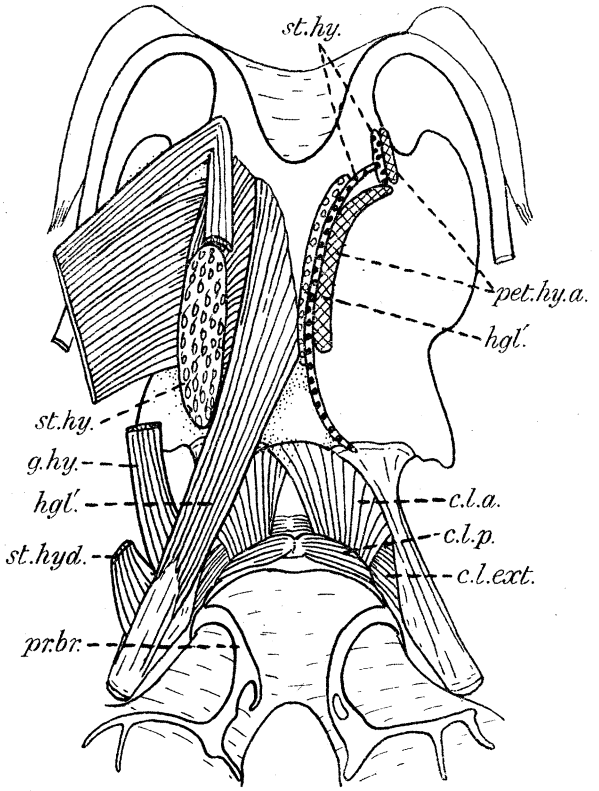

FIG. 81.—*Microhyla inornata*, female. Hyoid and larynx ; ventral. × 20. *hgl'* = hyo-hyoid portion of hyoglossus.

length ; a cartilaginous thickening between proximal ends of postero-medial processes, and a median ventral, ridge in front of this. Hyoglossal sinus shallow. Hyale with

an " extrahyal " continuous with ligament to angle of jaw. Alary process with broad base ; postero-lateral process short, feebly divided ; postero-medial process with narrow distal cartilage and with narrow lateral and broader inner flanges.

Arytænoid not fenestrated ; with edge at aditus prolonged into a thin vertical plate, as in *M. ornata ;* pulvinaria present. *Cricoid* a complete ring, rather slender, overlapped at articular regions by arytænoid, to which it is intimately united ; no processes on pharyngeal side ; bronchial process recurved and branched on ventral surface of root of lung, on the left with two short branches uniting to enclose a small fenestra.

Muscles.—M. intermandibularis posterior with a differentiated superficial portion parallel to lower jaw.

M. interhyoideus typical.

M. sternohyoideus with insertions of its ventral and main portions distinct but adjacent, the main insertion linear, approaching middle line ; *m. dorsalis* attached to posterior part of postero-medial process.

M. omohyoideus absent.

M. geniohyoideus inserted as in *M. berdmorei.*

M. hyoglossus attached behind to ventral surface of posterior half of postero-medial process ; the layer adjacent to the hyoid inserted on ventral surface of hyoid plate between right and left sternohyoids, as in *Oreophryne ;* remainder of muscle entering tongue.

M. petrohyoideus anterior inserted on ventral surface of hyoid in two parts, which are only partially separated by the anterior part of *M. sternohyoideus.*

M. petrohyoideus I. abnormally asymmetrical in this specimen, the right muscle weaker and ending in loose tissue dorsal to postero-medial process, the left attached to edge of laryngeal sinus for some distance to right of middle line. This is obviously only an individual aberration from the condition typical of Brevicipitidæ.

Remaining posterior petrohyoid inserted on edge of postero-medial process and on hyocricoid ligament nearly to middle line.

M. dilatator laryngis attached to thin edge of arytænoid at aditus, *M. constrictor externus* to inner flange of postero-medial process. Inter-cricoid ligament affording attachment to *constrictor anterior* even in its cricoid region, so that part of this muscle comes from beneath the constrictor posterior ; anterior end of constrictor anterior attached to anterior margin of laryngeal sinus to beyond middle line, slightly overlapping its fellow, not extending on to ventral surface of hyoid plate. *M. constrictor posterior* small, attached at each end to a pulvinar, and mid-way to the cricoid.

Previous Work on Microhyla.

FRAZIER (1924) described the skeleton of hyoid and larynx in *Microhyla okinavensis.* The hyoid is like those of the species described above, but no " extrahyals " are figured, and no ventral thickening of the hyoid plate is described. The arytænoids

are sharply notched at the aditus, and are pierced by a narrow fenestra. A long œsophageal process of the cricoid is figured in the ventral view, but not in the lateral. The bronchial processes end in fenestrated plates.

Gastrophryne texensis, Girard.

Range: Texas.

Male, 23 mm. from snout to vent, from Co. Duval, Texas. [B.M.N.H.]

Hyoid and Laryngeal Skeleton.—Hyoid similar to that of *Microhyla*, but with deeper hyoglossal sinus and with alary processes better defined. Postero-medial processes rather stout, without flanges.

Arytænoids very large and gibbous, occupying, if the larynx be taken as a sphere, more than a hemisphere, so that both ends appear in a cardiac view; edge at aditus

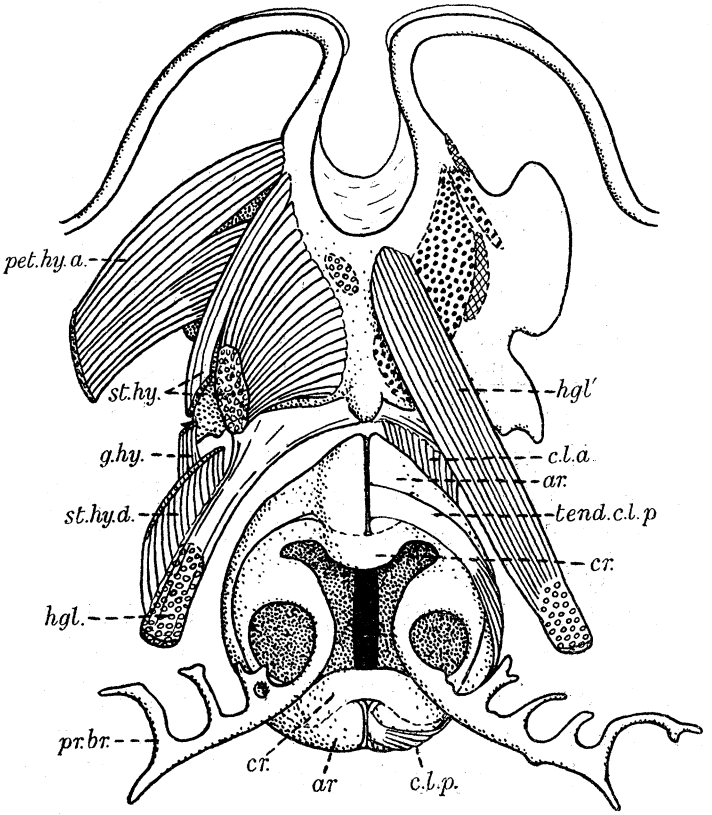

FIG. 82.—*Gastrophryne texensis*, male. Hyoid and larynx; ventral. × 15. The membranous wall of the larynx is removed, showing the vocal chords within. *hgl'* = hyo-hyoid portion of hyoglossus.

slightly concave, without apical cartilage; pulvinaria vocalia very narrow, mostly internal to larynx. *Cricoid* rather slender, fused to arytænoids anteriorly and posteriorly, free laterally where it bears, on each side, a curved, branched, bronchial process; on right side, two of the branches united, enclosing a fenestra. A hyocricoid ligament present.

Muscles.—M. intermandibularis posterior with a superficial slip running parallel to lower jaw.

M. interhyoideus typical.

M. sternohyoideus with a broad insertion on ventral surface of hyoid, nearly reaching middle line; ventral strip with a narrow insertion adjacent to this, but distinct; *pars dorsalis* attached along most of the length of the postero-medial process.

M. omohyoideus absent.

M. geniohyoideus with external insertion on postero-medial process adjacent to that of m. sternohyoideus dorsalis.

M. hyoglossus attached to ventral surface of posterior part of postero-medial process; bulk of muscle entering tongue, but strip adjacent to hyoid inserted on ventral surface of hyoid plate in two small areas, a right and a left, not far behind hyoglossal sinus.

M. petrohyoideus anterior inserted in two parts, separated by insertion of ventral slip of sternohyoid.

M. petrohyoideus posterior I with a narrow insertion on posterior edge of hyoid plate, near middle line. Last posterior petrohyoid with insertion extending from end of postero-medial process inwards on a fascia over-lying posterior part of larynx and its muscles, to middle line, where it is associated with some fibres of the "œsophageal muscle."

M. dilatator laryngis attached to edge of arytænoid and to membranous lip of aditus. *M. constrictor anterior* attached in front to anterior margin of laryngeal sinus, slightly on the ventral side, extending nearly to middle line; the membrane on which it is inserted behind the aditus is not prolonged in the usual way as the intercricoid ligament. *M. constrictor posterior* with its ventral part aponeurotic, attached to the narrow pulvinaria.

Vocal Chords.—These are unusual. Rostral and caudal lips are attached separately to the wall, instead of arising in the usual way from a common pars basalis. Each lip is supported mid-way by a transverse thickening, but no typical frenulum is present. The very small size of the pulvinaria and the semi-tendinous condition of m. constrictor posterior are no doubt related to this division of the chordæ.

Previous Work on Gastrophryne.

W. K. Parker (1881, pl. 43, fig. 10) figured the hyoid of *G. carolinensis.* It is essentially similar to that of *G. texensis.*

Discussion.

The tensor mechanism of the vocal chords.

In *Alytes* and *Discoglossus* the main part of the constrictor laryngis is sphincteric, interrupted dorsally and ventrally, where it is in part attached directly to the arytænoid, in part to a pad of dense fibrous tissue between the ends of the arytænoids and con-

tinuous with the vocal chords. Its contraction must stretch the vocal chords both indirectly (by reducing the convexity of the arytænoids) and directly.

In frogs in which distinct anterior and posterior constrictors are differentiated, the posterior usually functions directly as a "tensor chordarum." The corners of the arytænoids become modified as cushions of flexible parenchymatous cartilage or of fibrous tissue,* to which the constrictor posterior is attached on the one hand and the vocal chord on the other. These cushions are the pulvinaria vocalia. Mid-way between the pulvinaria, the muscle often becomes fixed to the cricoid, which may develop a processus muscularis to receive it; the frenulum chordæ vocalis provides a corresponding fixed point in the vocal chord.

The function of the pulvinar is to give flexibility to the corner of the arytænoid, which then acts as a pulley in the tensor chordarum mechanism.

In *Bufo*, *Dendrophryniscus*, *Atelopus* and *Oreophrynella*, where there is no constrictor posterior, there are likewise no pulvinaria. In *Chorophilus feriarum*, where, according to Wilder, the constrictor posterior has atrophied, the pulvinaria are apparently also absent; at least Blume, who describes pulvinaria in the species possessing them, does not mention them in his account of *Chorophilus*. In *Eupemphix nana*, in which the ventral half of m. constrictor posterior is lacking, the ventral pulvinaria are very small and weak, quite unlike the large, tough ventral pulvinaria in the closely related *Physalæmus cuvieri*.

Thus the view stated above of the function of the pulvinaria is confirmed by the fact that where there is no constrictor posterior there are also no pulvinaria.

Discoglossidæ and Liopelmidæ.

The Discoglossidæ and *Liopelma* have short tongues, not adapted for swift, accurate movements, and the hyoglossal muscle is comparatively weak and short, having its origin on the anterior part of the postero-medial process, whereas in other Phaneroglossa it is at the posterior end, at least in adults.

The geniohyoid muscle retains in these families the primitive condition found in Urodeles (see WALTER, 1887, for an account of these muscles in *Salamandra*). In *Liopelma*, as in *Salamandra*, the posterior attachment of the geniohyoid is immediately in front of the anterior attachment of the sternohyoid. In *Bombina*, although the geniohyoid extends far back, to the ends of the postero-lateral and postero-medial processes, this is only *outside* the sternohyoid. In *Discoglossus* the geniohyoid forks over the sternohyoid, but the inner slip is very small, and is inserted on the parahyoid bone. In other Phaneroglossa, and in *Xenopus* at least among the Aglossa, the internal portion of the geniohyoid extends backwards to the end of the postero-medial process. We can thus add the condition of the geniohyoid to the characters in which the Discoglossidæ are more primitive than the Aglossa, and we may conclude that the

* They have been described in detail by BLUME (1930, p. 441).

development and extension backwards of an inner portion of this muscle is not connected with the development of the tongue as a swiftly erectile organ.

The presence of an *os parahyoideum* in *Discoglossus*, *Alytes* and *Liopelma* emphasizes their inter-relationship. The fact that the bone has become incorporated in the hyoid plate in *Liopelma*, does not, in my opinion, argue against its homology with that found in the others. The parahyoid bone of *Liopelma* does not appear on the dorsal side of the hyoid plate, but the hyoid ossifications of *Bombina* do. Otherwise the paired ossifications in *Bombina* bear to the paired parahyoid bones of *Discoglossus* the same relation that is borne by the single bone of *Liopelma* to that of *Alytes*, and it seems legitimate to assume that the hyoid ossifications in the four genera are homologous. The microscopic ossification found by Fuchs in *Bombina variegata* (= *pachypus*) may not be significant in this connection, situated as it is *behind* the hyoid plate.

The larynx of *Bombina* is specialized on its own lines, but it is interesting to note that the *constrictor* musculature is entirely intrinsic, without a hyoid attachment. In *Liopelma*, *Discoglossus* and *Alytes* a ventral slip is atached to the postero-medial process, and foreshadows the *constrictor externus*, which, in other adult Phaneroglossa is connected to the larynx much farther forward, near the apex of the arytænoid, and is separate from the constrictor posterior. In the constrictor of *Liopelma* a *dorsal* slip also is attached to the postero-medial process; this may perhaps represent the constrictor anterior, but differs from it in having a more posterior hyoid attachment, and in lying *outside* the sphincteric portion at its arytænoid end; the absorption into it of the small sphincteric layer that remains would, however, produce a condition very similar to that of *Bufo*.

The family Liopelmidæ was established to emphasize the closer affinity of *Liopelma* and *Ascaphus* to each other than to the Discoglossidæ. The only known feature of the hyolaryngeal apparatus which supports this classification is the presence in the Discoglossidæ of large alary processes of the hyoid, and their absence in *Liopelma* and *Ascaphus*, and this is balanced by the presence of a parahyoid ossification in *Liopelma*, and its absence in *Ascaphus*. The figure of the hyoid and laryngeal skeleton of *Ascaphus truei* (Frazier, 1924) suggests resemblances to the *Pelobatidæ* in the shape of the postero-medial processes, and in the deep division of the œsophageal process, although this is single for half its length; on the other hand the very small size of the arytænoids is reminiscent of *Bombina*. A study of the laryngeal muscles of *Ascaphus* would be of interest.

Pelobatidæ.

The skeleton of the hyoid and larynx is known in seven* species of Pelobatidæ, as well as the one here described, namely, *Pelobates fuscus* (hyoid described by Dugès, 1835; W. K. Parker, 1881, pl. 20, fig. 4; Ridewood, 1897, *b*; Kothe, 1910; larynx by Henle, 1839, pl. i, figs. 28-30, and by Blume, 1930, pp. 395-7, fig. 106), *Megalophrys nasuta* (Beddard, 1907, *a*, pp. 388-442, fig. 97), *M. montana*, "*Xenophrys monticola*,"

* Six, if Beddard's "*Xenophrys monticola*" be identical with *Megalophrys montana*.

Megalophrys (= *Leptobrachium*) *hasseltii* (BEDDARD, 1907, *b*, pp. 875, 892-903, figs. 237-240), *Megalophrys fecæ* (BEDDARD, 1911) and *M. bœttgeri* (FRAZIER, 1924). The hyoid of *Pelodytes punctatus*, was figured by DUGÈS (1835), W. K. PARKER (1881) and by RIDEWOOD (1897, *b*), who also described its development and musculature. BEDDARD described the hyoid musculature in his species, but the laryngeal musculature has never been described before.

The hyoid of the Pelobatidæ is characterized by a more or less complete reduction of the hyale. This is represented in all the investigated species of *Megalophrys* by its anterior process only, and this may be united by a *processus confluens* with the alary process (*M. fecæ*, BEDDARD). In *Pelobates* a small cartilage, united with the anterior process or detached, represents the middle region of the hyale; in *Pelodytes* this cartilage is also present, always, as far as is known, detached. *Pelodytes* possesses a parahyoid bone, similar to that of *Alytes*, but this is not represented in other Pelobatidæ.

The hyoid muscles of the Pelobatidæ are essentially like those of generalized Leptodactylidæ and Ranidæ. The geniohyoid, in particular, has lost the more primitive relations characteristic of the Discoglossidæ, and has acquired the typical Anuran condition. There are usually three posterior petrohyoid muscles (two in *Pelodytes*, *see* RIDEWOOD, 1897, *b*), the last of which may be attached in part to the cricoid. If the position of the first two on the ventral side of the thyroid membrane in *Megalophrys robusta* is characteristic of the family, this provides a small point of contrast with all other Anura, except *Alytes* and *Discoglossus*.

The most characteristic feature of the larynx is the incompleteness mid-dorsally of the cricoid ring. This might have been considered a primitive feature, in view of the fact that the cricoid is known to develop from a pair of distinct cartilages (MÄRTENS, 1897), but the cricoid is incomplete dorsally in *Rhacophorus* (*Polypedates*) *dennysi*, (FRAZIER, 1924), which also, curiously enough, has the hyalia represented by anterior processes alone. This is regarded as an instance of convergence, but throws doubt on the primitiveness of the condition in the Pelobatidæ.

In *Pelobates* (*fide* HENLE and BLUME) and in *Megalophrys* (*Leptobrachium*) *hasseltii* (*fide* BEDDARD) there are no œsophageal processes; in other species of *Megalophrys* there are two parallel processes.

The *constrictor* musculature of the larynx in *Megalophrys robusta* is exactly similar to the most generalized type in Leptodactylidæ, Ranidæ and Hylidæ. The specialization of the dilatator laryngis recalls, on the other hand, some of the more specialized Ranid larynxes.

NOBLE (1926) has described the Pelobatidæ as representing " a distinct advance over either Liopelmidæ or Discoglossidæ," and this certainly applies to the hyolaryngeal apparatus. A combination of the following three characters in this apparatus appears to be diagnostic of the family:—arytænoid without apical cartilage; cricoid ring incomplete dorsally; hyalia more or less reduced.

Leptodactylidæ.

The hyolaryngeal apparatus is here described in twelve species of Lepodactylidæ (= NOBLE's "Bufonidæ," excluding *Bufo*). Of these, the nine Neotropical species may be considered first.

In *Leptodactylus ocellatus*, *L. caliginosus*, *Crossdactylus gaudichaudi* and *Pleurodema bibroni* the apparatus is of a generalized type. The hyoid possesses all the typical processes, except anterior processes; the hyoglossal sinus is deep, extending backwards behind the origins of the alary processes. The hyoid muscles are attached to the lateral parts of the hyoid plate; an omohyoid and three posterior petrohyoid muscles are present. In the larynx, the arytænoid is simple, with moderate pulvinaria vocalia. The dilatator is simple, and constrictores anterior and posterior are differentiated, the anterior with a few fibres still sphincteric, ending in the raphe of m. constrictor externus, but with the main part attached to the hyo-arytænoid membrane, in *Crossodactylus* in part to the hyoid.

The most generalized of these is *Leptodactylus ocellatus*. In *L. caliginosus* the cricoid is incomplete mid-ventrally, a character which seems to have no evolutionary significance (*cf.* also *Crinia signifera*, fig. 27, and *Pseudohemisus longimanus*, fig. 72). The interior of the larynx in this species is apparently of an unusual type, but the significance of this cannot be judged until more is known of the vocal mechanism in the Anura. In *Crossodactylus* and *Pleurodema* the cricoid is of the type having an abruptly narrow lateral region and broad dorsal and ventral bands. The extreme manifestation of this tendency is found in *Edalorhina* and *Dendrobates*, where the cricoid is discontinuous laterally (at least in *Dendrobates*). *Crossodactylus* is distinguished by a broad m. constrictor posterior, which is attached in part to the pulvinaria, in part directly to the cricoid at each end. In *Pleurodema* on the other hand, the constrictor posterior is semi-tendinous.

Edalorhina perezi departs very little from the generalized plan, at least in the female, which alone is described here. It differs from *Pleurodema* in the relative size of hyoid plate and postero-medial processes, in having anterior processes of the hyalia, and in the absence of the ventral half of the constrictor laryngis posterior, which ends on a process of the cricoid that may correspond to the muscular process. The cricoid is peculiar in having an extra pair of processes between the bronchial processes.

Eupemphix nana and *Physalæmus cuvieri* have the larynx swollen and modified, in relation to the enormous vocal sac of the male, which extends into the abdominal lymph-space, so that the whole ventral subcutaneous region can be inflated with air. The close relationship to each other of *Eupemhix* and *Physalæmus* is well known, and is borne out by the structure of the larynx. H. W. PARKER (1927, p. 457) points out the relationship of both these to *Edalorhina*, and this is emphasized by a comparison of the larynx of the female in *Edalorhina* and *Physalæmus*. These are similar in all essentials, except that the ventral part of the constrictor posterior, tendinous in *Physalæmus*, is absent in *Edalorhina*, as it is in *Eupemphix*. The presence in the females

of an extra pair of processes of the cricoid is an expression of the tendency that causes the cartilage in the males to spread over almost the whole ventral wall of the larynx.

Eupemphix is characterized by loss of maxillary teeth. It has lost also the two hyoid muscles that so easily go, the omohyoid, and the second posterior petrohyoid.

The hyolaryngeal apparatus of the male *Pseudopaludicola falcipes* unites features of specialization which are found separately in other families, the Hylidæ being most strongly recalled. The large arytænoids, with thick pharyngeal and basal regions and thin intermediate zone, the cartilago basalis, and the paired procartilaginous " sesamoids " at the anterior ends of the constrictor externus are characteristic hylid features. As in most Hylas, the constrictor anterior remains mainly sphincteric. However, the shape of the hyoid, with shallow hyoglossal sinus and with the anterior process enclosing a fenestra, is quite unhylid, and recalls that of *Crinia*. The intimate hyo-cricoid union recalls some of the Brachycephalidæ. The division of the deep part of the dilatator laryngis into two slips, attached to the muscular process, is known elsewhere only in *Rana*. The loss of omohyoid and second posterior petrohyoid muscles has occurred often in Anura. This hyolaryngeal apparatus shows no resemblance to that of *Crossodactylus*, to which H. W. PARKER (1927) suggests that *Pseudopaludicola* may be related. The Hylid resemblances may not indicate a Hylid relationship, but show that the male *Pseudopaludicola* has the hyolaryngeal apparatus differentiated in the same way as the male Hylas. The ground-plan, as shown in the female, will probably prove to be different from the Hylid ground-plan, in which, however, there is no great constancy.

Of the Australian Leptodactylidæ studied, the specimen of *Mixophyes* is too young for consideration here. As already stated, *Crinia signifera* resembles *Pseudopaludicola falcipes* in the shape of the hyoid, although distinct postero-lateral processes are present ; a further likeness is the absence of the omohyoid, but the second posterior petrohyoid is present, though reduced in the male. The larynx of the male is much larger than that of the female, and, as in *Pseudopaludicola* and most Hylidæ, it is the arytænoids that are enlarged, whereas the cricoid is slender, more slender than in the female. However, no cartilago basalis was detected in dissection, the dilatator is simple, the cricoid has no muscular process, and in both sexes the cricoid ring is incomplete ventrally. The resemblances between the two genera are probably due to parallelism or convergence.

In both *Pseudopaludicola* and *Crinia* the constrictor anterior remains sphincteric, confluent in front with the constrictor externus ; the constrictor posterior is attached to well-developed pulvinaria, and acts as a " tensor chordarum."

The hyolaryngeal apparatus of *Helioporus* is of the generalized Leptodactylid type, with the peculiarity that the processes of the hyoid tend to spread in flat lobes of cartilage, which becomes thin at the edges and passes insensibly and irregularly into the surrounding membrane. In the larynx the broad lobate articular and cardiac processes of the cricoid are noticeable.

In *Limnodynastes*, although the hyoid is shorter and broader, the hyolaryngeal skeleton is essentially like that of *Helioporus*.

A family containing these eleven genera can hardly be said to be characterized by its hyolaryngeal apparatus. However, it is distinguished from the Discoglossidæ and from *Bufo* and some Brachycephalidæ in having distinct anterior and posterior constrictors differentiated; from the Pelobatidæ in having right and left sides of the cricoid continuous mid-dorsally; and from the Ranidæ and Rhacophoridæ by the absence of a cartilago apicalis of the arytænoid. *Pseudopaludicola* makes it impossible to define a Leptodactylid as against a Hylid larynx. Among the Brevicipitidæ, the members of the "*Gastrophryne*-group" (see below, p. 519) are distinguished from the Leptodactylidæ by the constant presence of a characteristic thickening of the hyoid plate between the postero-medial processes, and by the mode of attachment of the hyoid muscles. *Hemisus* differs from the Leptodactylidæ (and resembles the Ranidæ) in the presence of an apical cartilage of the arytænoid, and this is also true of *Breviceps adspersus*.

Hylidæ.

WILDER and BLUME recognized that in the Hylidæ the Anuran larynx exhibits extreme sexual differentiation, and this not only in size, but in the development in the male of sesamoid and other minute cartilages, which are absent in the female. The examples described in this paper further illustrate these facts (in spite of the fact that male and female of the same species are rarely available for comparison) and show also that in some species additional fibrous outgrowths of the wall of the larynx into its cavity may characterize the male, as in *Hyla rubra* (South America) and in the Australian Hylas.

The Australian Hylas provide a distinct type of larynx. *H. cærulea*, *H. ewingii* and *H. aurea* have in common the presence of a broad processus muscularis of the cricoid, and, in the males, of a paired bulbous prominence of the pulmonary end of the frenulum chordæ vocalis. In the remaining Anura a bulbous prominence of this type is known only in *Dendrophryniscus stelzneri*, a Brachycephalid, an example of convergence. Apparently, however, it is also present in the Hylid *Phyllomedusa moschata*, in which BLUME described a spherical procartilaginous mass that he took to represent the cartilago basalis. In this species, as also in *P. dacnicolor* (of which the female is described above, p. 448), the cricoid has a broad processus muscularis, which, at least in *P. dacnicolor*, lies *outside* m. constrictor laryngis posterior, as in the Australian Hylas and in few other Anura.* BLUME noted that *Phyllomedusa* stood apart from the remaining Hylidæ known to him, in the structure of the larynx, and also in the fact that the aditus is directed forwards and not dorsally. In this last feature it further resembles *H. aurea* and *H. ewingii* (but not *H. cærulea*).

Hyla cærulea and *H. ewingii* are peculiar in having the cartilago basalis ossified. *H. aurea* has no cartilago basalis, but the fibrous tissue of the frenulum, between the arytænoid and the bulbous prominence, is very dense, and is intimately united with the

* *Rana halecina* has a similar muscular process (*see* p. 475).

perichondrium of the arytænoid. This recalls BLUME's description of the same region in *Phyllomedusa moschata* (1930, p. 394).

Thus, in the structure of the larynx, the South American genus *Phyllomedusa* has more affinity with the Australian Hylas investigated than with other Hylidæ of South and North America and of the Old World. These, including *H. rubra* and *H. faber* of South America, have no processus muscularis of the cricoid, and the ventral half of m. constrictor posterior is tendinous, except in *Chorophilus feriarum*, where, according to WILDER, it is absent. The constrictor anterior is always narrow, and its main direction is antero-posterior; it is usually attached in front in its entirety to a median raphe with m. constrictor externus, thus exhibiting its most primitive condition, although in *H. versicolor* a few fibres are attached to the hyo-arytænoid membrane, and in *H. annectens* a few to the anterior end of the postero-medial process. Where sesamoid cartilages are present, these are evidently in the anterior and posterior raphes of this muscle, which is then not directly attached to the arytænoids, and is able to act as a sphincter around them. Even when the sesamoids are absent, as in most Anura, the median raphes are but loosely attached to the arytænoid, and the presence of the procartilaginous nodules is probably a strengthening of the raphes, correlated with the elongation of the arytænoid and the consequent acuteness of the angles round which the muscle must work.

WILDER did not recognize the homologies of the constrictor muscles of his Hylidæ with those of other Anura. The constrictor posterior, absent in *Chorophilus feriarum* and semitendinous in his other species, he called " tensor chordarum," a name which well describes its function, not only in the Hylidæ, but in most Anura in which it is differentiated. He mistook the constrictor anterior of Hylidæ for the constrictor posterior. This mistake led him to hope that the structure of the larynx might be diagnostic of the family, but it has not proved to be so. Even the presence in the male of sesamoid nodules and basal cartilages* is not universal in the species known, and is shared with *Pseudopaludicola*. There remains no constant character by which a Hylid larynx may be recognized as such, and distinguished from that of a Leptodactylid. Nevertheless, a cartilago basalis is present in the males of enough species, and the relationships to these of the species lacking it are sufficiently clear, to make it useful as additional evidence that the Hylidæ all over the world form a natural assemblage. No other member of the Anura Phaneroglossa, except *Pseudopaludicola falcipes*, is known to have a well-developed cartilage in this position, although much smaller nodules have been given the same name in *Alytes obstetricans* (BLUME, 1930) and *Rana esculenta* (GAUPP, 1901, KRAUSE, 1920, and BLUME, 1930).

* A possible homologue of the basal ossicles of *H. ewingii* and *H. cærulea* is found in *Pipa* (see GRÖNBERG, 1894, and RIDEWOOD, 1897 *a*), in which there is a pair of bony "outer arytænoids" surrounding the cartilaginous arytænoids proper, and prolonged into the cavity of the larynx as a pair of freely projecting bony rods. Like the basal cartilages and ossicles, these are found only in the male. If the basal ossicle of *H. cærulea* were to become enlarged, so as to appear in an external view of the larynx, and prolonged inwards into the bulbous prominence of the interior of the larynx, a condition very like that in *Pipa* would be attained. According to RIDEWOOD, however, the bony and cartilaginous parts of the arytænoid of *Pipa* form a single structure, not two, as is implied in GRÖNBERG's account.

Bufo

The hyolaryngeal apparatus of *Bufo* distinguishes it easily from any other Anuran genus except some of the Brachycephalidæ. The chief distinguishing characters are :—the curving of *m. hyoglossus* round the postero-medial edge of the postero-medial process, to be inserted on the dorsal surface of the latter, instead of, as is usual, the ventral ; the close connection of the lateral process of the cricoid with the postero-medial process ; the absence of a distinct *constrictor laryngis posterior*, the whole of the constrictor muscle except the *constrictor externus* having the relations of the *constrictor anterior* of many Anura ; and the absence of *pulvinaria vocalia*, probably dependent on the absence of a constrictor posterior.

In addition, the genus is characterized by a hyoid plate longer, often much longer, than it is wide, by the absence of anterior processes of the hyalia, and by stout, bent postero-medial processes with large cartilaginous ends. The arytænoids have acute apices, projecting forwards into the pharynx. The omohyoid muscle is weak, or, exceptionally absent, and there is usually no *petrohyoideus posterior secundus*.

The only other Anura (higher than the Discoglossidæ) which lack a constrictor posterior, are some of the Brachycephalidæ and *Chorophilus feriarum*. In the Brachycephalidæ this shows a true relationship to *Bufo* (see below, p. 516), but in *Chorophilus*, not only is there no other indication of relationship, but examination shows that we are dealing with quite a different state of affairs. In Hylidæ related to *Chorophilus*, the constrictor posterior is very tenuous, and it has disappeared in *Chorophilus* by atrophy. In *Bufo*, however, the extent of the " constrictor anterior," and the developmental evidence suggest that it is the whole of the constrictor (except the constrictor externus) which acquires an attachment to the postero-medial processes, and relinquishes the sphincteric condition as well as the possibility of becoming a " tensor chordarum."

Among the Leptodactylidæ, a condition of the constrictors approaching that of *Bufo* is found in *Crossodactylus* (p. 422, fig. 12). Here a large constrictor posterior is present, but only a few of its fibres are attached to the small pulvinaria. The rest of the muscle ends dorsally and ventrally on the cricoid. Its ventral ends are already widely separated, and it only remains for these to become attached to the hyoid to achieve the *Bufo* condition. A special relationship between *Crossdactylus* and *Bufo* is not suggested, for the hyoid and larynx of the former are otherwise much more generalized than in *Bufo*. The absence of the ventral half of the constrictor posterior in *Edalorhina* and *Eupemphix* might also be regarded as a first step towards the *Bufo* condition, but the shortened muscle does not acquire a hyoid attachment, and it is attached to well-developed pulvinaria at its pharyngeal end.

Brachycephalidae

NOBLE'S work (1926) on the pectoral girdle of the assemblage of South American toads which he unites in this family, considered with other osteological characters, led him to divide the family into three groups, of which the first consists of *Dendro-*

phryniscus, Oreophrynella, Atelopus and *Brachycephalus*, the second includes *Dendrobates*, and the third, including *Sminthillus* alone, is not represented in the present investigation.

NOBLE points out the similarity in general osteological characters between the first group and the genus *Bufo*, and it is now seen that this likeness extends to the structure of the larynx, except in *Brachycephalus*. In the other three genera, as in *Bufo*, there is no constrictor laryngis posterior, and in *A. ignescens* the attachment of the hyoglossus is in part, in *Oreophrynella* entirely, on the dorsal side of the postero-medial process. The absence of pulvinaria vocalia is probably here, as in *Bufo*, dependent on the absence of the posterior constrictors. The three genera further resemble *Bufo* in the long, rather narrow hyoid plate, with the insertions of the sternohyoid muscles reaching the middle line or nearly, in the bending dorsalwards of the postero-medial processes, in the well-developed lateral processes of the cricoid (in *Oreophrynella* intimately united with the hyoid), and in the absence (except in *Dendrophryniscus stelzneri*) of a middle posterior petrohyoid muscle. The omohyoid muscle, absent in this group, in *Bufo* is weak, occasionally absent. Compared with *Bufo*, the hyolaryngeal apparatus is of a lighter build, with more slender processes. The absence of bronchial processes in *Oreophrynella* is notable.

In *Brachycephalus*, resemblances in the hyolaryngeal apparatus to the other three genera are confined to the narrow shape of the hyoid plate and the absence of omohyoid and middle posterior petrohyoid muscles. The hyo-cricoid union, although intimate, is of a unique type, by means of spoon-shaped lateral processes. Of the attachment of the hyoglossus in this specimen nothing can be said. In contrast to the other three genera and to *Bufo*, a well-developed constrictor laryngis posterior is present, a generalized feature which suggests that, if there is a close relationship between *Brachycephalus* and the *Dendrophryniscus* group, the former must have diverged very early.

Another family in which the omohyoid and middle posterior petrohyoid are absent is that of the Brevicipitidæ, with which *Brachycephalus* was formerly included on account of its firmisternal shoulder girdle. A further resemblance to this family is found in the differentiation of the intermandibularis posterior of *Brachycephalus*. In other respects, however, the hyolaryngeal apparatus of *Brachycephalus* is quite unbrevicipitid, and the resemblances must be considered as due to convergence [*cf.* also the specialization of the intermandibularis of *Rhinoderma*, (BEDDARD, 1908 *b*) which is exactly like that of the Australian Hylas !].

Dendrobates has been placed by NOBLE in a separate group of his " Brachycephalidæ," a group which he believes to have been derived from *Crossodactylus*, by fusion of the coracoid cartilages. The hyolaryngeal apparatus of *Dendrobates* is of the Leptodactylid type, with a constrictor laryngis posterior. The hyo-cricoid union is of the *Bufo-Oreophrynella* type. A point of resemblance to the *Dendrophryniscus* group is offered by the absence of omohyoid and middle posterior petrohyoid muscles, but, as has already been noted, the loss of these muscles has occurred more than once in the Anura,

and by itself cannot be relied upon as indicating relationships. There is a rather striking general resemblance between the hyolaryngeal apparatus of *Dendrobates* and that of *Edalorhina perezi* (figs. 16 and 50).

In sum, a knowledge of the hyolaryngeal apparatus of five genera of the eight in NOBLE'S Brachycephalidæ gives little support to the inclusion of *Dendrobates* in the family, and makes doubtful any special relationship between *Brachycephalus* on the one hand and *Dendrophryniscus*, *Oreophrynella* and *Atelopus* on the other. It emphasizes, however, the relationship, pointed out by NOBLE, of the three last-named genera to *Bufo*.

It is not in the purpose of this paper, which deals with a single group of organs, to make major alterations in classification, but it is suggested that the absence of a posterior laryngeal constrictor, coupled with a number of other hyolaryngeal characters, would justify the retention of the family Bufonidæ, not for the miscellaneous collection of toothless arciferous forms which it previously comprised, but for *Bufo*, *Dendrophryniscus*, *Atelopus* and *Oreophrynella*. The alleged relationship of *Brachycephalus* to these should be reconsidered.

Rana, Megalixalus and Rhacophorus

The skeleton of the hyoid and larynx has now been described in nineteen species of *Rana*, five of *Rhacophorus* and one of *Megalixalus*. In all of these the arytænoid possesses an apical cartilage lodged in an incisura apicalis. BLUME'S microscopical investigations (1930) have shown that the apical cartilage is not always completely separate from the arytænoid, but the methods employed by me do not justify any statement about this detail. For the purposes of this enquiry it is sufficient to know that the apical cartilage and incisura are present in these genera, and are absent in all the arciferous families, in the Brachycephalidæ, and in most of the Brevicipitidæ (but see below, p. 520). In some arciferal forms the whole or a part of the dilatator is attached to the tough membranous lip of the aditus laryngis, above the edge of the arytænoid. Microscopic sections of *Physalæmus* show that in it there is a rod of dense cellular tissue which provides the actual attachment for the dilatator. It is possible to imagine the development of the apical cartilage by a chondrification and rounding off of this rod, especially if *Rhacophorus leucomystax* and *R. maculatus* be considered. In them the incisura is shallow, the prominentiæ are low, and the apical cartilage is laterally compressed. In *Rana*, however, the high prominentiæ suggest the origin of the apical cartilage from an arytænoid with a produced apex, the middle portion of which has become separated off. This is the view of the origin of the apical cartilage favoured by GOEPPERT (1898) and by BLUME (1930) on the evidence of those species of *Rana* in which it is continuous at one point with the arytænoid. At present, however, there seems to be no evidence which prevents us from reading the series in either direction.

The genus *Rhacophorus* is distinguished by the reduction of the alary process, with the correlated shifting forwards of the attachment of the genio- and omo-hyoid

muscles. The processes are present, but small in *Rh. leucomystax* and *maculatus*, absent in *Rh. goudoti* and *rhodoscelis*. In *Rh. dennysi* the hyalia also are reduced to short processes of the hyoid plate (FRAZIER, 1924).

In *Rana* there is a tendency for mm. dilatator laryngis and constrictor laryngis anterior to become, in part, attached to the muscular process of the cricoid. The arytæno-cricoid and hyo-cricoid slips of the dilatator have already been described by GAUPP and WILDER in *Rana esculenta*, *R. temporaria* and *R. clamitans*, and GAUPP also mentioned the minute slip of the constrictor anterior, which, in *R. esculenta* and *R. temporaria*, usually runs to the processus muscularis. *Rana halecina* and *R. erythræa* are similar to these in respect of the two muscles. In *R. labrosa* the dilatator has an arytæno-cricoid slip, but no hyo-cricoid. In *Rana fuscigula* the dilatator is simple, but a considerable division of the constrictor anterior is attached to the process. In *Rana greyi*, *R. kuhlii* and *R. limnocharis*, and also in a young specimen of *R. mascareniensis*, neither muscle is inserted on the process and the larynx-musculature is quite generalized. In *R. greyi* and *R. kuhlii*, however, the outer attachment of the dilatator extends on to the hyo-cricoid ligament.

KRAUSE (1920) calls the arytæno-cricoid slip of the dilatator "*M. arylabialis*" and traces it as a fibrous strip into the pars basalis of the vocal cord. A similar muscle is present in *Pseudopaludicola falcipes* (p. 432), and, in *Megalophrys robusta*, what corresponds to a hyo-cricoid slip of the dilatator ends on the membranous wall of the larynx between arytænoid and cricoid; so that it is now clear that such a specialization of the dilatator is neither confined to *Rana*, nor is it universally present in the genus. The Ranidæ, in fact, possess a generalized larynx, the only characteristic feature of which, the apical cartilage, is shared with the related families of the Rhacophoridæ and Brevicipitidæ.

The shape of the cricoid exhibits some diversity within the genus *Rana*. The most usual shape is that found in *R. temporaria*, *R. kuhlii*, *R. halecina*, etc., in which the muscular process is a triangular eminence. FRAZIER shows it also in her *R. limnocharis* (1924, fig. 2), but this differs so much from my specimens of this species that it is probable that her specimen was wrongly identified. In my specimens of *R. limnocharis* the cricoid exhibits laterally a deep, narrow notch, instead of a process, and a shallower notch is present in *R. fuscigula*. In *R. nigromaculata* (FRAZIER, *tom. cit.*, fig. 4) the notch is shallow but is delimited by slender dorsal and ventral prominences. The presence of a notch is probably the most primitive condition, and was shown by MÄRTENS (1897) in an early developmental stage of *R. temporaria*. His next stage, in which the upper edges of the notch unite, enclosing a fenestra, is exhibited by the adult *R. plancyi* (FRAZIER, *tom. cit.*, fig. 6).

Cacosternum.

Cacosternum was included by BOULENGER (1882) in the Brevicipitidæ (Engystomatidæ), but the structure of the larynx offers little support to this opinion, and in this

paper it is therefore considered separately. The only specialized hyolaryngeal features that *C. capense* (see p. 483) shares with the Brevicipitidæ are the absence of a middle posterior petrohyoid, and the insertion of the first posterior petrohyoid, at the middle line. The shape of the anterior process of the hyale is of the generalized type found in many Brevicipitidæ, but also in other families. The arytænoid is of the type characteristic of Ranidæ, Rhacophoridæ and of *Breviceps* (*part.*) and *Hemisus* among the Brevicipitidæ, that is, with an incisura apicalis lodging a cartilago apicalis. Such eccentricities of shape and proportions as characterize the larynx here described might be expected in a male of almost any Anuran family in which sexual differentiation of the vocal apparatus is well marked.

If one were to judge from the hyolaryngeal apparatus alone, one would place *Cacosternum* near the stock from which the Ranidæ and Brevicipitidæ diverged.

Brevicipitidæ.

The eleven species, of eight genera, in which the larynx is here described, are representative of the whole geographical range of the family, and show a considerable diversity of habit and habitus. They are, nevertheless, well characterized by the structure of the hyolaryngeal apparatus, the underlying uniformity of which is more striking if two of the African genera, *Breviceps* and *Hemisus*, are left out of consideration.

There remain eight species, of six genera, namely, *Gastrophryne texensis* (N. America) *Microhyla inornata* (Farther India, Sumatra, Borneo), *M. ornata* (India, Farther India, S. China), *M. berdmorei* (Farther India, Sumatra), *Oreophryne celebensis* (Celebes), *Kaloula pulchra* (India, Farther India, S. China, Malay Archipelago), *Caluella guttulata* (Farther India) and *Pseudohemisus longimanus* (Africa and Madagascar). To them may be added *Microhyla okinavensis* (China) and *Cacopus systoma* (India), described respectively by Frazier (1924), and Devanesen (1922). In neither of these two is the whole hyolaryngeal apparatus described, but enough is known of both to justify their inclusion in this group, which may be called the "*Gastrophryne*-group."

The members of the "*Gastrophryne*-group" share the following features, in almost all of which they contrast sharply with other firmisternal families :—

1. The hyoid plate has a median ventral thickening of the cartilage between the origins of the postero-medial processes, and often a mid-ventral ridge in front of this.

2. The anterior process of the hyale is represented by a broader or narrower flange of thin cartilage along its convex edge.

3. The postero-medial process is bent at a sharp angle near the middle of its length, so that its posterior end is directed dorsally.

4. The arytænoid has no apical cartilage, nor a sharp apical notch.

5. The cricoid has no œsophageal process. (This is present in all Ranidæ, except in the males of one or two species where sexual differentiation of the larynx is marked.)

6. The bronchial processes are long, and either are recurved on the ventral surface

of the bronchus or root of the lung, or else end in an expanded, fenestrated plate of cartilage.

7. There is no omohyoid muscle.

8. There are only two posterior petrohyoidei.

9. The attachments of mm. sternohyoideus and petrohyoidei anterior and posterior are at or near the middle line, instead of at or near the lateral edges of the hyoid plate and postero-medial processes.

10. *Either* the hyoglossus has a slip, adjacent to the hyoid, which is attached with the bulk of the muscle to the posterior end of the postero-medial process, but ends anteriorly on the ventral surface of the hyoid plate, *or* m. constrictor laryngis anterior extends forwards below the hyoid plate to an attachment on its ventral surface. Contraction of the former of these muscles must have the effect of counteracting the sharp dorsal bend of the postero-medial processes, as far as their elasticity will permit, and so of depressing the larynx; the latter muscle depresses the larynx directly, using the posterior edge of the hyoid as a pulley. *Kaloula pulchra* is exceptional in the group in showing neither of these modifications, but the constrictor anterior ends in front on the *ventral* surface of the hyo-arytænoid membrane, which is unusual in Anura, and is the first step towards the second modification.

The first and last of these ten characters are peculiar to the "*Gastrophryne*-group" and the others do not occur combined in any other family. The nearest approach to such a combination is found in *Bufo* and the *Dendrophryniscus*-group of the Brachycephalidæ, which differ from the Brevicipitidæ in their own hyolaryngeal peculiarities as well as in other characters.

Breviceps and *Hemisus* share with the *Gastrophryne*-group Nos. 3, 6, 7, 8 and 9 of these ten characters. Instead of No. 1, *Breviceps* has the postero-medial processes attached to a small, distinct posterior segment of the hyoid plate, and in *Hemisus* the proximal ends of the processes are expanded and form a broad bony plate narrowly divided in the middle line by a strip of cartilage. *Breviceps fuscus*, which has the posterior segment of the hyoid plate partially ossified* may perhaps be intermediate in this respect between *Hemisus* and other species of *Breviceps*.

In character No. 2 *Hemisus* agrees with the *Gastrophryne*-group, with the addition that the flanges of the hyale meet and fuse in the middle line. In the structure of the anterior process of the hyale, *Breviceps adspersus* appears to be intermediate between *B. gibbosus* and *Hemisus*.

In the presence in *Hemisus* and in *Breviceps adspersus* of an apical cartilage in an apical incisura of the artyænoid, we have a typical development of the most characteristic feature of the larynx of the Ranidæ and Rhacophoridæ. The incisura was evidently present in HENLE'S "*Engystoma gibbosum*," but in my specimen of *Breviceps gibbosus* the arytænoid has a simple, acute apex. The question arises as to whether incisura or apical cartilage is represented in the members of the "*Gastrophryne*-group." In

* DE VILLIERS, 1931 *b*, p. 173, fig. 7.

Kaloula pulchra and in *Pseudohemisus* the edge of the apical region of the arytænoid has a shallow concavity. The sharp notch described by FRAZIER in *Microhyla okinavensis* and that described in this paper in *M. inornata* do not seem to represent the Ranid incisura, but are at the posterior end of the aditus laryngis, and are probably connected with the median raphe of the most posterior petrohyoid muscle. More reminiscent of a Ranid arytænoid, or at least of that of *Rhacophorus* and *Cacosternum*, is the arytænoid of *Microhyla ornata*, in which there is a sharply differentiated flat apical region, which may represent an apical cartilage continuous with the arytænoid.

My specimen of *Rana labrosa* was given me by Mr. H. W. PARKER as showing a remarkable external resemblance to *Pseudohemisus*, and having the same distribution. However, the one has a typical Ranid larynx (p. 473 fig. 56) and the other a well-characterized Brevicipitid hyolaryngeal apparatus (p. 496, fig. 72).

Breviceps is like the *Gastrophryne*-group in lacking an œsophageal process (character No. 5). The curious condition of *Hemisus*, in which the œsophageal process is curved forwards above the larynx, serving for the attachment of part of the most posterior petrohyoid muscle, suggests the mode of disappearance of the process in other Brevicipitidæ, in which it is replaced by a linea alba.

The presence in both *Hemisus* and *Breviceps*, alone among the Anura, of a single, median thyroid gland is an indication of their relationship to each other.

It may be noted in passing that m. intermandibularis posterior is nearly always differentiated into longitudinal and transverse parts, and that a postero-lateral outgrowth of the mento-meckelian bone is usually present in this family.

The attachment to the ventral surface of the hyoid plate either of part of the hyoglossus, or of the constrictor laryngis anterior, is an interesting example of alternative structural modifications serving the same function, and that in nearly related species. For instance, in *Microhyla berdmorei* and *M. ornata* it is the constrictor which is modified, but *M. inornata* resembles *Gastrophryne texensis* and *Cacopus systoma* in having the hyoglossus modified.

Finally, whereas the Brevicipitidæ have been divided into a number of sub-families on certain skeletal characters (NOBLE, 1931), the structure of the hyolaryngeal apparatus emphasizes the underlying unity of the family, although, of the genera studied, *Breviceps* and *Hemisus* appear to stand apart from the others, and to be rather nearly related to each other.

Significance of hyolaryngeal characters.

It is now possible to arrive at certain conclusions as to the value of hyolaryngeal features as indicating relationship, or as functional modifications. The classification of the Anura is made difficult by the prevalence in the group of the radiating type of evolution, by which a given character may occur at the ends of two or more diverging series. In the structures under consideration the loss of omohyoid and of middle posterior petrohyoid muscles, often occurring simultaneously, is such a character. It

is constant in the Brevicipitidæ (both muscles absent), it occurs in *Eupemphix*, also in *Atelopus* and *Oreophrynella* (both muscles) in *Bufo* (petrohyoid) and in *Dendrophryniscus* (omohyoid), also in *Pseudopaludicola* (petrohyoid). In indicating relationships it is of use as an additional character only.

Into this category comes also incompleteness of the cricoid ring. This was formerly supposed to occur in *Discoglossus*, and to be a primitive feature. It is now known not to occur in adult *Discoglossus*. In the Pelobatidæ a dorsal gap appears to be constant and to be here a true indication of relationship, in spite of the fact that it has also been recorded in the unrelated *Rhacophorus dennysi* (FRAZIER, 1924). A ventral gap, however, is present in several unrelated species, namely, *Oreophrynella quelchii*, *Crinia signifera*, *Leptodactylus caliginosus* (but not *ocellatus*), *Pseudohemisus longimanus* and *Cacosternum capense*. A paired lateral break is present in *Dendrobates tinctorius* (BLUME, 1930) and perhaps in *Edalorhina perezi*.

In the shape of the hyoid there may be great diversity in related forms, but the Pelobatidæ are characterized by reduction of the hyalia (although this also is recorded in *Rhacophorus dennysi*, as well as in an old specimen of *Bufo marinus*), and the Brevicipitidæ, except *Breviceps* and *Hemisus*, have all, as far as is known, a ventral thickening of the hyoid plate.

The anterior process of the hyale, when it projects forward as a bar, is said to assist the respiratory movements by acting as a valve for the nostril (NOBLE, 1931). Unfortunately the possibility of this function being served by it was not known by me until the dissections for this work were completed, but in its other shapes (*e.g.*, as in the Brevicipitidæ) this would seem to be excluded. It would be interesting to know if its absence in so many species is correlated with some modification of the respiratory movements as known in species of *Rana*.

The presence of an apical cartilage of the arytænoid would seem to permit of a partial opening of the *aditus laryngis*, probably in connection with vocal activity. It is perhaps following upon this that subdivision of the dilatator has occurred in the more specialized species of *Rana*. The apical cartilage is a structure probably of equal interest from functional and phylogenetic points of view, for its reliability in classification is considerable.

The function of the cartilago basalis is more difficult to suggest. In a well-developed form, it was thought to be confined to the Hylidæ, but it is now seen to be typically present also in *Pseudopaludicola falcipes*. That it is related to voice production may be conjectured from its presence in the male alone. It is unreliable as an aid to classification.

From the phylogenetic point of view the differentiation of the laryngeal muscles is perhaps the most interesting feature here revealed. The main facts were known before, but the range of their application is first seen now. The Discoglossidæ and *Liopelma* may be said figuratively to be in an experimental stage as regards the constrictor musculature. In other Phaneroglossa a constrictor externus is always present.

The remainder of the constrictor is differentiated in all except *Bufo*, *Dendrophryniscus Atelopus*, and *Oreophrynella*, into anterior and posterior parts. The posterior becomes attached to the ends of the vocal chords, with the intermediacy of the pulvinaria vocalia, and is thus specialized as a tensor chordarum. The anterior remains a ring-muscle in some members of each group, but shows a tendency to become attached to the postero-medial processes, and thus to serve as a *depressor laryngis*. It is thus that the whole muscle, representing both anterior and posterior constrictors, becomes specialized in *Bufo*, and the three related genera, which all lack a tensor chordarum. In *Chorophilus feriarum* the tensor chordarum appears to have atrophied secondarily, as stated above (p. 514).

The differentiation of the constrictor musculature is thus of real value in classification, but serves only to define major groups.

The works of Grönberg and Ridewood show that in the Aglossa constrictores anterior and posterior are not differentiated. A constrictor externus is present in *Pipa* but is apparently unrepresented in *Xenopus*.

In a relatively uniform group like the Anura, it not infrequently happens that an extension of knowledge, although it throws light on the inter-relationships of the forms studied, does not to the same degree facilitate definition of groups. This position is arrived at as the result of the study of the Anuran larynx. Nevertheless, the attempts made to define the families on hyolaryngeal characters are not without some success. The groups in which these structures are most characteristic are (i) *Bufo* and related genera, (ii) the "*Gastrophryne*-group" of Brevicipitidæ, and (iii) the Firmisternal families Ranidæ and Rhacophoridæ. These groups are not of equal value, and only the third corresponds to a previously recognized family, but the conceptions involved are not in conflict with suggestions made on other evidence, for NOBLE has already hinted at a relationship between *Bufo* and the section of his "Brachycephalidæ" to which *Dendrophryniscus*, etc., belong, and *Breviceps* and *Hemisus* are known to stand apart from other Brevicipitidæ.

Summary.

1. The skeleton and muscles of hyoid and larynx are described in sixty species of Anura Phaneroglossa.

2. The tensor mechanism of the vocal chords is described, and the function of the pulvinaria vocalia is deduced from their structural relationships and from the conditions associated with their absence.

3. In the Discoglossidæ and *Liopelma* there is a parahyoid bone, single or paired, distinct or invading the cartilage of the hyoid plate; the geniohyoid does not extend backwards on the surface of the hyoglossus; a constrictor laryngis posterior is not differentiated and there are no pulvinaria vocalia. In *Bombina* there is no constrictor laryngis externus; in *Discoglossus* and *Alytes* a constrictor externus is differentiated

from the ring-muscle, but remains ventral as in larvæ of other Anura; in *Liopelma*, an additional dorsal slip of the constrictor acquires a hyoid attachment.

4. In all Anura except the Discoglossidæ and *Liopelma* the internal division of the geniohyoid extends backwards on the surface of the hyoglossus, to the end of the postero-medial process.

5. In the Pelobatidæ the hyale is reduced and the cricoid is discontinuous mid-dorsally; the constrictor laryngis consists of external, anterior and posterior divisions, the last attached to pulvinaria vocalia and forming a tensor chordarum.

6. In the Leptodactylidæ the hyalia are complete; the cricoid is complete mid-dorsally but may be discontinuous mid-ventrally; constrictores laryngis externus, anterior and posterior are differentiated. The hyolaryngeal apparatus shows great diversity within the family, but the most aberrant types are found in males with vocal sacs.

7. The hyolaryngeal apparatus of the Hylidæ cannot be distinguished from that of the Leptodactylidæ. Sexual differentiation is usually strongly expressed. In the males a basal cartilage is frequently present, and sesamoid nodules of vesicular cartilage may strengthen the tendons of some laryngeal muscles. The larynx of *Phyllomedusa* is strikingly similar to that of some Australian Hylas.

8. The genus *Bufo* is characterized by the absence of a constrictor posterior and of pulvinaria vocalia. The constrictor anterior forms a broad transverse band attached at each side to the postero-medial process of the hyoid. The hyoglossal muscle is attached to the dorsal side of the postero-medial process. There are usually only two posterior petrohyoid muscles.

9. Among the "Brachycephalidæ," *Dendrophryniscus*, *Atelopus* and *Oreophrynella* have the hyolaryngeal characters of *Bufo*, except that in *D. stelzneri* the attachment of the hyoglossus is ventral and there are three posterior petrohyoidei. In addition, the omohyoid muscle is absent. The cartilages are on the whole more slender than in *Bufo* and the bronchial processes are slender or even (in *Oreophrynella*) absent.

10. Of the remaining Brachycephalidæ, *Brachycephalus* and *Dendrobates* are examined. In essentials the larynx in both these is Leptodactylid in character, that of *Dendrobates* resembling *Edalorhina*. It is suggested that neither of these is very closely related to the genera named under 9 above.

11. The Ranidæ and Rhacophoridæ are characterized by a cartilago apicalis of the arytænoid. This is constant in the twenty-five species so far investigated and is present also in *Cacosternum capense*. It may be separate, or narrowly continuous with the arytænoid (Blume). Elsewhere in the Anura it is found only in *Hemisus* and in one species of *Breviceps*.

12. *Rhacophorus* is further specialized in the reduction or absence of the processus alaris of the hyoid, and in one species the hyale is also reduced (Frazier, 1924).

13. In *Rana* the pulvinaria vocalia are usually very large, and to the muscular process of the cricoid are attached parts of from one to three laryngeal muscles.

14. *Cacosternum capense* exhibits no important Brevicipitid features in the larynx, which is of a generalized Ranid type, but with certain peculiarities of its own. It has lost the middle posterior petrohyoid muscle.

15. In the Brevicipitidæ there is no omohyoid muscle, the posterior petrohyoidei number only two, the hyoid muscles are attached near the middle line, the bronchial processes are well developed, branched or ending in an expanded, fenestrated plate. If *Breviceps* and *Hemisus* be excepted, the remaining species investigated resemble each other in the shape of the hyoid, which has a median posterior ventral thickening, and (except *Kaloula*) in the attachment either of part of the hyoglossus or of the constrictor laryngis anterior to the ventral surface of the hyoid.

16. *Breviceps* and *Hemisus* show affinity to the other Brevicipitidæ in the hyoid musculature and in the bronchial processes. *Hemisus* and *B. adspersus* resemble the Ranidæ and Rhacophoridæ in possessing an apical cartilage of the arytænoid. They show relationship to each other in the shape of the hyalia and in having the thyroid gland single and median. Each has its own conspicous peculiarities, notably the long bronchi of *Breviceps adspersus*, and the nature of the junction of the postero-medial processes to the hyoid in both.

17. The functional and phylogenetic significance of Anuran hyolaryngeal features is discussed.

ABBREVIATIONS USED IN THE FIGURES.

a. l. ... ... aditus laryngis.
a. pulm. ... ... pulmonary artery.
ar. ... ... arytænoid.
br. ... ... bronchus.
ca. ap. ... ... apical cartilage of arytænoid.
ca. bas. ... ... basal cartilage of arytænoid.
ca. v. ... ... ventral thickening of hyoid plate.
c. ca. ... ... calcified cartilage.
c. l. a. ... ... constrictor laryngis anterior.
c. l. ext. ... ... constrictor laryngis externus.
c. l. p. ... ... constrictor laryngis posterior.
cr. ... ... cricoid.
c. v.... ... ... vocal chord.
dil. ... ... dilatator laryngis.
fren. ... ... frenulum.
g. hy. ... ... musculus geniohyoideus.
g. hy. lat. ... ... musculus geniohyoideus lateralis.
g. hy. med. ... musculus geniohyoideus medialis.
hy. ... ... hyale.
h. gl. ... ... musculus hyoglossus.
i. hy. ... ... musculus interhyoideus.
i. man. a. ... ... musculus intermandibularis anterior.
i. man. p. ... ... musculus intermandibularis posterior.

l. h. ar. ... ... hyo-arytænoid ligament.
l. h. cr. ... ... hyo-cricoid ligament.
l. j. ... ... lower jaw.
l. i. cr. ... ... inter-cricoid ligament.
man. ... ... manubrium.
mem. h. ar. ... hyo-arytænoid membrane.
mem. h. gl. ... hyoglossal membrane.
mem. thy. ... ... thyroid membrane.
m. æs. ... ... œsophageal portion of musculus obliquus internus.
o. hy. ... ... musculus omohyoideus.
os. bas. ... ... basal ossicle.
par.... ... ... os parahyoideum.
pet. hy. a. ... ... musculus petrohyoideus anterior.
pet. hy. p. 1 ... musculus petrohyoideus posterior primus.
pet. hy. p. 2 ... musculus petrohyoideus posterior secundus.
pet. hy. p. 3 ... musculus petrohyoideus posterior tertius.
pr. a. ... ... anterior process of hyale.
pr. al. ... ... alary process (of hyoid plate).
pr. art. ... ... articular process (of cricoid).
pr. br. ... ... bronchial process (of cricoid).
pr. card. ... ... cardiac process (of cricoid).
pr. lat. ... ... lateral process (of cricoid).
pr. m. ... ... muscular process (of cricoid).
pr. æs ... ... œsophageal process (of cricoid).
pr. p. lat. ... ... postero lateral process (of hyoid plate).
pr. p. med. ... postero-medial process (of hyoid plate).
prom. ap. ... ... prominentia apicalis of arytænoid.
p. v. ... ... pulvinar vocale.
s. hgl. ... ... hyoglossal sinus.
seg. p. ... ... posterior segment of hyoid plate.
st. hy. ... ... musculus sternohyoideus.
st. hy. d. ... ... musculus sternohyoideus pars dorsalis.
t. c. l. p. ... ... tendon of m. constrictor laryingis posterior.
t. dil. ... ... tendon of m. dilatator laryngis.
thy. ... ... thyroid gland.
v. pulm. ... ... pulmonary vein.

The areas of insertion of the muscles are labelled as the muscles themselves.

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