SUPERFICIAL MANDIBULAR MUSCULATURE AND VOCAL SAC STRUCTURE IN THE ANURA

Thesis submitted for the Degree of
MASTER OF SCIENCE

by

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TABLE OF CONTENTS

SUMMARY

A systematic survey has been undertaken of the superficial mandibular musculature, vocal sac structure and associated myo-integumental lymphatic septa in nine anuran families. This study involved the examination, by microdissection, of ninety-five genera and three hundred and eighty-five species, so constituting approximately fifteen per cent. of the anuran fauna of the world.

The rationale of the approach was that evolution of vocal sacs, intruding above the superficial mandibular muscles of male frogs, had introduced a new functional role for those muscles during distension of the sacs. In the absence of any direct contact between the superficial muscles and deeper structures, modification of the musculature was considered to be a reflection of the new functional requirements.

The morphological data obtained supported the above hypothesis to the extent that the basic pattern of musculature, theoretically consistent with the primary functions of raising and lowering the floor of the mouth, is retained throughout the majority of members of the Archeobatrachia. Such members lack vocal sacs, and there is no evidence to suggest that they have ever been present.

It is proposed, for the first time, that vocal sacs have evolved on several occasions amongst 'modern' families of the sub-order Neobatrachia. A concept, vital to interpretation, that the vocal sac of the Archeobatrachian discoglossid *Bombina bombina* represents a primitive condition (Liu, 1935), and implicitly the type of structure from which other vocal sacs evolved, is refuted. The condition in *B. bombina* is demonstrated to represent an entirely independent evolutionary path, involving a different method of increasing the capacity of the buccal cavity as a resonance chamber.

Loss of vocal sac has occurred in many species including representatives of eleven genera studied. It is considered relevant that such loss is confined to those genera in which the vocal sac is customarily a unilobular and submandibular structure. It is argued that the more bizarre extremes of bilateral structures involve commitment to a more specialised adaptive path for which the penalty may be the reduction of evolutionary plasticity.

Consistency of the basic pattern of musculature throughout congeners is demonstrated and is considered a reflection of the conservative nature of such musculature. The only genus in which major divergence was recorded is *Rana*, which is probably a heterogeneous assemblage which will ultimately be subdivided into several genera. The geographic association of the divergence in musculature reported here may provide an indication of the nature of any future subdivisions of this genus.

The extent of the divergence in musculature between genera and families of the Neobatrachia are entirely consistent with modern concepts of the nature of the phylogenetic association of these families.

Hence there are similarities common to certain members of the Hylidae, Leptodactylidae and Rhinodermatidae, and between the Microhylidae and Ranidae.

Limited data on the ontogeny of musculature support the assumption that modification from the basic pattern reflect adult and not larval functions. The genetic basis of muscle variability involves an hiatus of knowledge beyond the scope of this thesis.

A systematic survey of lymphatic septa and of associated myo-integumental muscles indicate that the greatest inter-familial divergence occurs within the Archeobatrachia. Hence the association with the absence of vocal sacs may support the supposition that certain lymphatic septa have influenced, or have been influenced by, vocal sac evolution.

The evolution of anuran superficial mandibular muscles is examined in the light of the hypothesis of Jarvik (1963) that supplementary sheets constitute the persistence of submandibular dermal plates, changed from the bony form of those of the osteolepiform fishes that he considers their probable ancestors. This hypothesis is rejected, and the possible steps in the evolution of supplementary muscles have been reconstructed. From this approach it became possible to examine the phylogenetic relationships of families in which there was considerable morphological divergence (e.g. the Microhylidae) and to compare them with current opinions. In the case of the Papuan genera, a phylogeny derived from data on muscles was reasonably comparable with that derived from osteological data by Zweifel (1972).

The divergence in the muscles of the Anura included in the survey was demonstrably so profound that attempts to trace evolutionary trends throughout the Vertebrata are considered more complex and potentially hazardous than may have been recognised.

DECLARATION

I declare that this thesis contains no material which has been accepted for the award of any other degree or diploma in any University and, to the best of my knowledge and belief, contains no material previously published by any other person, except where due reference is made in the text.

Parts of the work have been published variously as follows: University of Kansas Publications of the Museum of Natural History (1971) 19 (4): 319-360; Journal of Natural History (1971) 5: 225-231; Herpetologica (1971) 27 (2): 150-152; Transactions of the Royal Society of South Australia (1971) 95 (1): 49-52; Records of the South Australian Museum (1972) 16 (9): 1-20. A part on the hylids of the West Indies undertaken in collaboration with Dr L. Trueb of the University of Kansas has been accepted for publication.

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CHAPTER 1 : GENERAL

INTRODUCTION

For many years zoologists and lay observers have been well aware that the mating calls of different species of frogs are distinguishable. However, within the last twenty years the significance of call differences has been appreciated, for it has been found that female frogs are attracted only to the call of conspecific males. This discovery implied that male mating call served as an effective pre-mating isolating mechanism, and has resulted in refined objective analysis of call structures in terms of such parameters as dominant frequency, pulse repetition rate and duration. Mating call spectrograms are now regarded as a highly desirable, integral component of the published descriptions of new species.

The amplification of sounds produced in the larynx is a logical adjunct to vocalisation to enable males to attract conspecific females from greater distances to the breeding sites. This need for a resonance chamber has resulted, in the males of most species, in the evolution of what are customarily termed vocal sacs. The vocal sacs most commonly occupy a submandibular position, and the external muscular wall of the sacs is provided by the superficial, ventral, mandibular and hyoid constrictors, so that these muscles are greatly distended when the sacs are inflated.

It follows that the superficial muscles in the mandibular region of the adult Anura have a dual role. There is firstly the primary function, common to both sexes, of raising the floor of the mouth as in oro-pharyngeal respiration, and the secondary one (in males) of protecting and restraining the vocal sac.

The evolution of the vocal sac may be influenced by the nature of the muscle architecture and the underlying skin. Similarly, other adjacent morphological structures, by virtue of their mobility or elasticity, may conceivably inhibit or determine the position and shape of the sacs. Conversely, it is equally plausible to postulate that existing muscle architecture is at least in part a reflection of the stresses induced by vocal sac inflation. Thus an holistic approach to the structures in the mandibular region is necessary to permit an interpretation of the evolution of these structures individually and collectively.

In addition, because superficial mandibular muscles are so accessible, and can be examined with minimal damage to specimens, any morphological divergence is of considerable interest as a character in anuran systematics, and as a phylogenetic index.

OBJECTS OF PRESENT STUDY

The objects of the present study are as follows:

1. To establish, by microdissection, the nature and extent of morphological divergence of superficial mandibular musculature, vocal

sacs and associated myointegumental lymphatic septa in adult anurans of selected families.

2. To examine the ontogeny of the muscles and vocal sacs.

3. To consider the various paths of evolution and the processes that may have influenced them.

4. To review the potential phylogenetic significance of the observed morphological divergence.

5. To compare the resulting conclusions on anuran phylogeny with current concepts.

LITERATURE SURVEY

The published data pertinent to a study of submandibular morphology have arisen from studies with varying objectives. In some instances the data are the result of specific investigation, but in others they are entirely incidental to the principal aims.

For example, data on vocal sacs have customarily been included in descriptions of new taxa, but it is clear that many contributors have not in fact examined the actual sacs, but have simply assessed their shape and position from external evidence such as modification of submandibular skin.

Early contributors, such as Gunther (1958) and Boulenger (1882), employed a broad classification of vocal sacs that has persisted with only slight changes to the present day. In their annotated monographs they described vocal sacs as "internal" or "external" and as "subgular" or "lateral". The term "external" implied that the underlying skin was folded or pleated in such a way that during vocal activity of the living animal it had been extended considerably. The lack of such modification resulted in the classification of "internal".

By far the most exhaustive survey of vocal sacs is that of Liu (1935) who tabulated their presence or absence in 559 species. He adopted the internal/external classification and recognised three principal categories:

1. A median subgular sac.
2. A paired subgular sac possessing a median division.
3. Paired lateral sacs.

The data that he assembled indicated numerous instances of convergence in the shape and position of the sacs, but were inadequate to permit any assessment of whether the examples involved strictly comparable structures.

The classical European anatomists of the nineteenth century produced the first descriptions of musculature. For example, Ecker (1864) and Weidersheim (1881) described the common European frogs *Rana temporaria* and *R. esculenta* in such detail that the gross anatomy of those species became the standard reference source. This was maintained despite the fact that Hoffman (1878) described the mandibular musculature of exotic animals such as *Pipa* and demonstrated that internal anatomy paralleled divergence in external morphology. However, only too frequently attention to the details of muscle architecture was clearly only cursory in comparison with the studies of osteology, which, at the turn of the century, was considered of prime importance in determining anuran phylogeny. This is well demonstrated in the work of Mehely (1901) on the New Guinea microhylid *Hylophorbus rufescens* (*Metopostira ocellata*). Beddard (1895a, *et seq.*) was the first contributor to draw attention to variation in superficial mandibular muscles, basing his observations on specimens received at the Zoological Gardens in London.

Until very recently the most extensive systematic survey of superficial mandibular muscles alone was that of Trewavas (1933) who described, and in many cases illustrated, their condition in sixty species representing thirty-six genera and ten families. Although the phylogenetic implications of her findings on the larynx (the principal topic of her investigation) were discussed and employed by many subsequent contributors, the possibly phylogenetic significance of the divergence in mandibular musculature that she demonstrated escaped attention.

One of the first frogs in which the vocal sac and the superficial mandibular musculature were studied together was the bizarre *Rhinoderma darwini* of Chili. They attracted interest because in that species the males carry developing tadpoles within the vocal sacs, a habit accompanied by gross development of the sac and the musculature surrounding it. Howes (1888) and Beddard (1908b) described the structures in detail, but their descriptions contained errors noted and corrected by Trewavas (1933).

Unusual animals continued to attract greater attention than the more generalised ones. Hence Devanesen (1922) reported the musculature and shape of the inflated vocal sac of *Uperodon (Cacopus) systoma*, Walker (1938) reported the morphology of the superficial mandibular musculature and vocal sac structure of the Mexican burrowing frog *Rhinophrynus dorsalis*, and Duellman (1956) provided the first detailed account of a hylid genus with bilateral vocal sacs (*Phrynohyas* of Central America).

Liem (1970) and Tyler (1971a) were the first contributors to investigate the application of divergence in superficial mandibular musculature and vocal sac structure as phylogenetic criteria at a generic level. Liem demonstrated divergence in the gross structure of these features in the Ranidae. He was concerned only with establishing the directions of evolutionary change to permit coding of character states for incorporation in the construction of phylogenetic trees. Tyler's approach differed in involving a more detailed comparative morphological study to determine the nature of divergence and its phylogenetic significance. From these features alone Tyler was able to demonstrate the long suspected heterogeneity of *Hyla*, leading him to propose the resurrection of *Litoria* to accommodate all Australo-Papuan species previously referred to *Hyla*.

Tyler (1972a) subjected the Australo-Papuan leptodactylid genera to similar analysis and concluded from that study that the sub-family

Cycloraninae was an artificial grouping of unrelated genera. Although this opinion conflicted with that reached by Parker (1940) and Lynch (1971), it has been supported by Watson and Martin (1973).

Data on larval musculature are available for relatively few anuran species and knowledge of muscle ontogeny is particularly limited. Interpretation of trends in muscle evolution is further complicated by the fact that the major adaptive shifts to extreme environmental conditions, such as fast-flowing streams, is reflected in highly specialised mouthparts. In addition to suctorial oral discs that have evolved in the inhabitants of these streams, other feeding mechanisms, varying from microphagy to cannibalism, similarly have produced gross differences in structure.

Of such bizarre extremes, published data are largely restricted to external morphology. Exceptions are Noble's (1929) description of the suctorial *Staurois ricketti*, which includes an account of the musculature, whilst Gradwell (1973) has described the muscle architecture and function of the sucker of *Ascaphus*.

Of the 'generalised' anuran larvae, Sedra (1950) provided a detailed account of the ontogeny of *Bufo regularis*, and Edgeworth (1911) and de Jongh (1968) *Rana temporaria*. More recently, Gradwell and Walcott (1971) described the relevant larval morphology of *Rana catesbeiana*.

One of the earliest authors to attempt a comparative ontogenetic study was Kesteven (1944) who undertook the task as part of a study of the evolution of cephalic muscles in vertebrates. He described the musculature of the Australian leptodactylid *Mixophyes* sp., but noted no major differences between that species, *Ranidella (Crinia)* sp., *Limnodynastes* sp., and the hylids *Litoria (Hyla) aurea* and *L. (Hyla) caerulea*. He stated, "The primordial cranial and branchial structures were so similar one to another and to those of *Rana*, that one is justified in making the assumption that the description here given of the muscles may be accepted as being truly and completely one of the muscles of the anuran tadpole generally." Unfortunately, this concept is demonstrably erroneous, as indicated here and by the findings of Severtsov (1968) and Starrett (1973).

One of the major areas of morphological divergence involves the larval interhyoideus muscle, which is customarily a single loop of transverse fibres. Noble (1929) noted separation of the interhyoideus into two separate elements in the African microhylid *Hoplophryne rogersi* (terming them the "subhyoideus" and "subhyoideus pars locomotorius", respectively). Similarly, his partially divided "M. subbranchialis" in *Staurois ricketti* may well represent the interhyoideus muscle.

Uncertain synonymies undoubtedly contributed to confusion about homologies, and Severtsov (1968) is apparently the first author to draw attention to the fact that division of the larval interhyoideus varies. He studied representatives of several families and reported: "The M. interhyoideus posterior is well expressed in the larvae of Pelobatidae, but absent in a series of investigated forms." The series comprised the pipid *Xenopus laevis*, the discoglossids *Bombina bombina* and *B. orientalis*, the ranids *R. temporaria* and *R. esculenta*, the bufonids *Bufo bufo* and *B. viridis* and the hylids *Hyla arborea* and *H. japonica*.

Starrett (1973) used the variation in the larval interhyoideus as a character in her subdivision of the Anura, but recorded two sheets only in the Microhylidae, a family which she referred to a separate sub-order (the Scoptanura). She did not cite Severtsov's paper, nor Gradwell and Walcott (1971) who observed comparable separation of the interhyoideus in larval *Rana catesbeiana*.

The first study of the ontogeny of a supplementary element of the intermandibularis is that of Tyler (1971a) who examined *Litoria aurea*, *L. ewingi*, *L. thesaurensis* and *L. wisselensis*. These observations were undertaken to determine the first appearance of the supplementary apical element. He recorded that the first fibres appeared at metamorphic climax and that final development was entirely post-metamorphic, so demonstrating adult and not larval function for that muscle element. Tyler (1972a) undertook similarly orientated studies on the atypical cycloranine leptodactylid *Cyclorana australis*, noting muscle ontogeny identical to the pattern in *Litoria*.

The ontogeny of the vocal sacs has been studied in the greatest detail in African frogs. Inger (1956) examined *Rana porosissima* and Inger and Greenberg (1956) *Bufo regularis*.

Data on anuran lymphatics were assembled and assessed by Kampmeier (1968). He provided a most detailed account of their distribution in *Ascaphus*, but fell into the common trap of assuming that Ecker's (1864) description of *Rana* was typical of the Anura. That there was variation in the subcutaneous myointegumental lymphatic septa of anurans was first noted by Tyler (1971b), who proceeded to demonstrate that two of these septa could influence the site of evolution of vocal sac structures and probably were functionally involved in the operation of vocal sacs.

Tyler (1971b) investigated the various forms of myointegumental contact, reported the role of the M. cutaneous pectoris in vocal sac evolution, and subsequently (1971c) reported that this muscle is confined to the ranid/hyperoliid/rhacophorid lineage.

Knowledge of the ontogeny of lymphatic septa is particularly limited. Kampmeier (1968) states that the subcutaneous sacs (and hence the septa) develop from primary lymph sinuses only during the latter stages of larval life and complete their development at metamorphosis. *Xenopus laevis* may be an exception, because Uehlinger and Beauchemin (1968) illustrate a larval mutant with gross hydrops and characterised by cutaneous distension constricted at sites corresponding to the positions of the dermal attachments of the septa in the adult.

Nothing is known of the ontogeny of the cutaneous pectoris, and I have been unable to locate any reference to it in published descriptions of larval musculature. A possible synonym is the M. diaphragmatobranchialis medialis reported by Noble (1929) in *Staurois ricketti*. This muscle arises from the base of the branchial skeleton (incipient post-pectoral region), immediately anterior to the M. rectus abdominus, and attaches upon the undersurface of the suctorial disc. This muscle is either lost at metamorphosis and subsequently replaced by the cutaneous pectoris arising only slightly posteriorly, or it is in reality the larval antecedent, which seems more likely. I have been unable to locate references to publications on the genetic basis of muscle variability.

MATERIAL AND METHODS

A total of approximately two thousand specimens, representing nine families, ninety-six genera and three hundred and eight-six species, were dissected. These are listed in Appendix 1. The vast majority are deposited in the collection of the South Australian Museum. The various sources of the specimens are listed in Appendix 2. Observations on adult specimens were made in air, employing a low power stereoscopic microscope. The orientation of mandibular muscle fibres was initially detected solely by means of a single spot light source directed across the muscles. Subsequently, it was found possible to highlight individual bundles of fibres by the addition of a laterally directed fluorescent light source, and to further clarify their orientation by employing the reversible iodine/potassium iodide muscle staining technique described by Bock and Shear (1971).

Drawings were prepared with the aid of a camera ~~L~~lucida or by scaled drawings from measurements obtained by the use of an eyepiece micrometer. Scales were not included on the final drawings because the objectives of demonstrating intergeneric variation in muscle architecture were in no way aided by such data.

Wherever possible, males and females of each species were dissected. Unless otherwise indicated, descriptions are based on adult male specimens.

The data sought systematically were as follows:

1. The presence, position and depth of the post-mandibular and pectoral, myointegumental (lymphatic) septa. Although these septa are extremely elastic in life and difficult to assess quantitatively, they were recorded as being short, moderate or deep in terms of the extent of the myointegumental separation permitted by them.
2. The shape of the musculus submentalis and the presence or absence of a median raphe.
3. The site of origin of the musculus intermandibularis. The extent of the muscle and the direction of its fibres; the presence or absence of aponeuroses or the existence of supplementary sheets (here termed elements).
4. The position and shape of any supplementary elements of the intermandibularis.
5. The extent of the musculus interhyoideus, the nature of its

contact with the M. intermandibularis, and the presence or absence of distinct lobes associated with the vocal sac *q.v.*

6. The site of origin of the M. interhyoideus (in representatives of each family).
7. The position and shape of the vocal sac apertures, and their size expressed as a proportion of the maximum length of the mandible.
8. The extent of the vocal sac above the interhyoideus or intermandibularis and interhyoideus, and its definition as one of the following: unilobular and median submandibular, bilobular submandibular, or bilobular supramandibular.
9. The existence of any additional supplementary submandibular muscles.
10. The existence of specialised myointegumental muscles communicating between the pectoral muscle block and adjacent skin.
11. The presence of any areas of direct myointegumental contact with adhesions present.
12. The presence of any bony processes on the mandible associated with the sites of origin of submandibular muscles.
13. The innervation of the submentalis, intermandibularis and interhyoideus (in a few representatives of each family).

The families selected for the systematic study were the Leiopelmatidae, Discoglossidae and Pelodytidae as representatives of archaic groups; the Rhinophrynidae, because it is a monotypic family containing a single and very highly specialised burrowing animal of dubious affinities to all other families except possibly the Pipidae; the Hylidae, Leptodactylidae and Rhinodermatidae, because the possibility of their evolution from a common stock has been postulated; and the Ranidae and Microhylidae, for the reason that applies to the Hylidae, Leptodactylidae and Rhinodermatidae.

TERMINOLOGY

In the literature the nomenclature of the superficial mandibular muscles varies considerably, and even in modern publications there is a regrettable lack of uniformity. The nomenclatorial criteria of authors frequently appear to be the accessibility of publications and personal preference, rather than uncertainty about homologies, priority of use, or the merit of the names in terms of whether they are appropriate or not in the descriptive sense.

I have followed Kesteven (1944) in employing the names submentalis, intermandibularis and interhyoideus, principally because that author demonstrated homologies with these structures in other vertebrates for which there is far greater uniformity in their use. The synonymy in the literature referred to in this thesis is listed in Table 1.

Nomenclature of the muscles situated ventral to the intermandibularis creates an almost insoluble problem. Liem (1970) coined the name "dentomentalis" for an elongate slender slip that he observed in many members of the Ranidae. Tyler (1971a) observed several distinct supplementary muscles in the Hylidae differing in their shape and position

TABLE 1

MUSCLE NOMENCLATURE OF PREVIOUS CONTRIBUTORS

Musculus submentalis

= intermandibularis anterior of Trewavas, 1933; de Jongh, 1968; and Severtsov, 1970.

Musculus intermandibularis

= intermandibularis anterior of Hoffman, 1878.

= intermandibularis posterior of Trewavas, 1933; de Jongh, 1968; and Severtsov, 1970.

= submaxillaris of Ecker, 1864; Beddard, 1908; Noble, 1929; Inger, 1956; and Liem, 1970.

= submaxillaris (part only) of Duellman, 1956.

Musculus interhyoideus

= intermandibularis posterior of Hoffman, 1878.

= subhyoideus of Beddard, 1908; Noble, 1929; Inger, 1956 and 1958.

= mylohyoid of de Watteville, 1874; and Liu, 1935.

= submaxillaris (part only) of Duellman, 1956.

Musculus cutaneous pectoris

= abdomino-cutaneous of Kein, 1850.

= abdomino-gutteral of Dugès, 1834.

= subcutaneous pectoris of Zenker, 1825.

of origin on the mandible. Because of the nature of the divergence in that family, he considered them to represent elements derived from the customary sheet of fibres, employing names that indicated the position of origin on the mandible: 'apical element', 'anterior element', 'anterolateral element' and 'posterolateral element'.

The studies reported here, in particular those on the Microhylidae, reveal an almost infinite variation in the number of supplementary elements and their position on the mandible. No arbitrary classification is really possible in that family. Within the Anura it is often difficult to find grounds for assuming that the strict criteria of homology can be fulfilled when comparing supplementary muscles in different families. Thus, as far as nomenclature is concerned, there are the alternatives of coining a number of new names for muscles or considering them all simply supplementary sheets that have completely differentiated from the parent muscle mass. I have adopted the latter course, with one exception which occurs in *Rhinophrynus dorsalis*. I have been influenced there by finding that the additional muscle arises from an epiphysis on the lateral surface of the mandible. Hence, in that particular instance, it seemed possible to exclude the concept of a supplementary muscle element in the process of migrating along the mandible. The muscle is now sufficiently static to have induced a change in the skeletal element from which it arises, and I have interpreted this as evidence of stability, and sufficient magnitude of evolutionary change, to merit recognition as a unique and new muscle. This I have named the M. mandibulomentalis. The action may imply an arbitrary quantification of the evolutionary process, but, in fact, it was only taken after a complete and conservatively biased assessment of the nature of divergence of anuran muscles in terms of their disposition, innervation and ontogeny.

The classification and nomenclature of vocal sacs follows Tyler (1971a), who proposed a system which avoided use of the inappropriate term "subgular" and involved names that indicated more precisely the site of the sac and its shape:

submandibular and either unilobular or bilobular;
supramandibular, bilobular.

The nomenclature of myointegumental lymphatic septa is that of Tyler (1971b), who favoured "postmandibular" and "pectoral".

Generic and specific names appearing in the text, tables and Appendix 1 are those in current use. Names in parentheses following those cited in the works of other authors are those employed by those authors.

THE MANDIBULAR SEGMENT OF THE ANURAN SKULL

I provide here a brief account of the morphology of the anuran mandibular segment to indicate the nature of the component structures and the areas in which major divergence occurs.

Skeletal and Myological Features

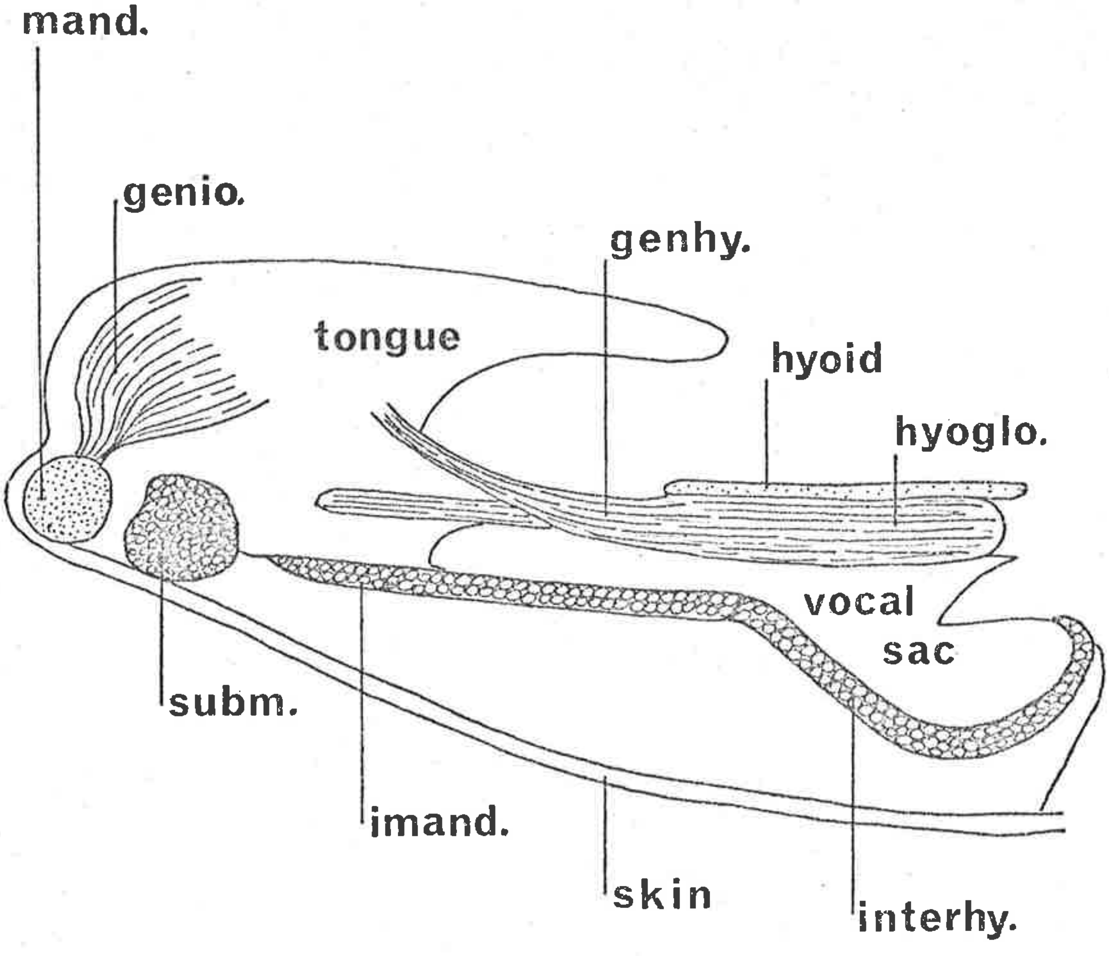
The skeletal elements of the mandibular segment of the anuran skull consist of the mandibles and the medially located hyoid. The mandibles are customarily slender, curved, compound edentulate structures rarely completely united at the mandibular symphysis. The hyoid is a complex and highly variable structure consisting primarily of a very thin plate, which is usually entirely cartilaginous, but partly or completely ossified in some species and bearing parahyoid bones in a few.

From the hyoid plate various cartilaginous or bony processes attach to associated structures but not to the mandible. However, muscular communication between the hyoid and the mandible occurs via the tongue, for anteriorly the genioglossus arises from the mandibular symphysis, whilst the geniohyoideii arise from the dorso-lateral lingual region of the mandible in an anterior position. The origin of the genioglossus is visible in the diagrammatic sagittal section (Fig. 1), but clearly not the geniohyoideii.

The M. submentalis is customarily an ovoid-shaped muscle whose fibres arise from the lateral surface of the mandible on each side of the mandibular symphysis. The fibres either traverse from one side to the other or meet at a median raphe.

The other two superficial, ventral, intermandibular constrictors consist of the M. intermandibularis and the M. interhyoideus. In its simplest form the intermandibularis comprises a thin muscle sheet arising

FIGURE 1: Diagrammatic sagittal section of mandibular region.



genio. = M. genioglossus; genhy. = M. geniohyoideus; hyoglo. = M. hyoglossus; imand. = M. intermandibularis; interhy. = M. interhyoideus; mand. = mandible; subm. = M. submentalis.

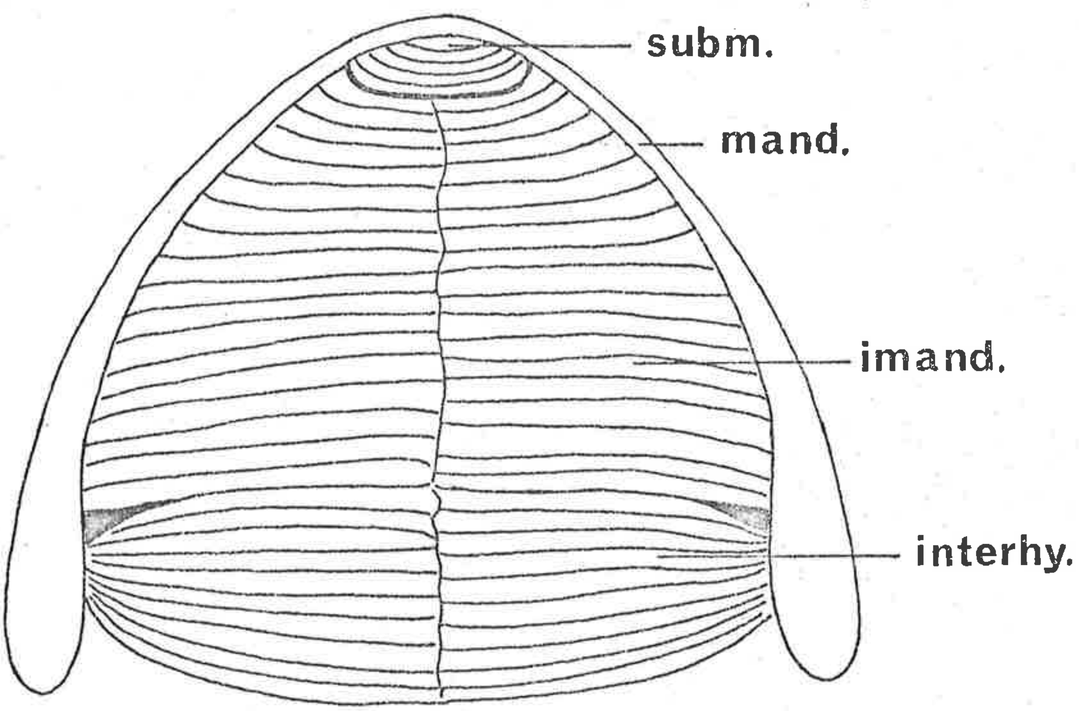
from the medial margin of the mandible, and extending along almost its entire length from the site of the submentalis to the anterior limit of the jaw articulation (Fig. 2). There is usually a simple median raphe, but median aponeurotic tendinous areas are not of uncommon occurrence. Variation in the morphology of the intermandibularis include the extent of the mandible from which it arises, its relationship to the submentalis, the orientation of the fibres in relation to the transverse plane, and the presence of supplementary elements completely separate from the customary sheet and lying ventrally to it (see Fig. 3).

The interhyoideus is equally variable in its structure. Most frequently its fibres arise from the anterior cornu of the hyoid at a position adjacent to the squamosal. The muscle broadens as it progresses inferiorly, and then expands into a flat sheet of which the anterior fibres fuse with the posterior fibres of the intermandibularis. However, in association with the vocal sac of male frogs (described below), the interhyoideus has evolved along a number of independent lines, most of which involve increasing the breadth of the interhyoideus and the length of most of its fibres.

Vocal Sac

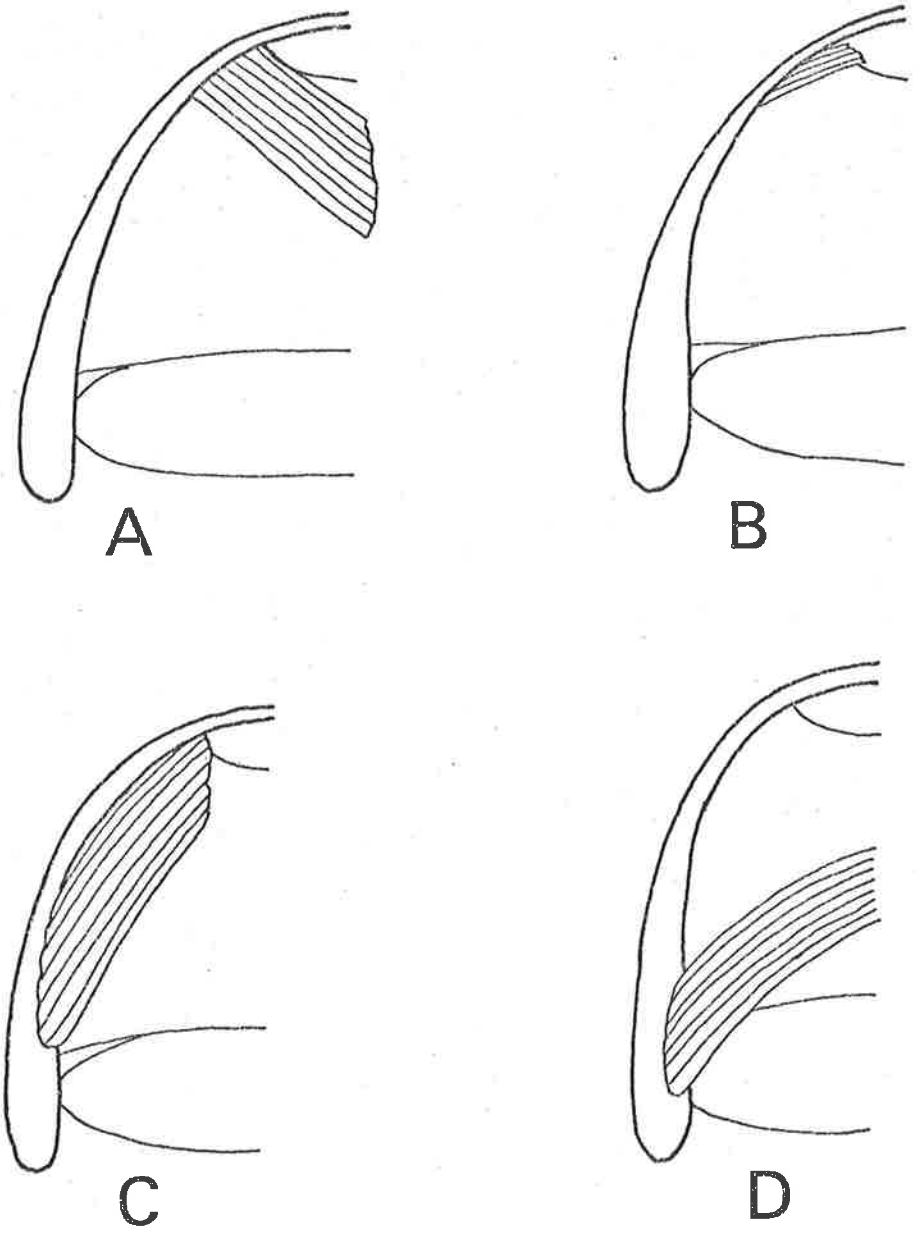
In the floor of the mouth there are, in male frogs, on each side of the tongue or approaching the jaw articulation, apertures representing separate evaginations of the mouth floor opening into a chamber (Fig. 4). This chamber most commonly intrudes between the geniohyoideii superiorly

FIGURE 2: Anuran superficial mandibular musculature.



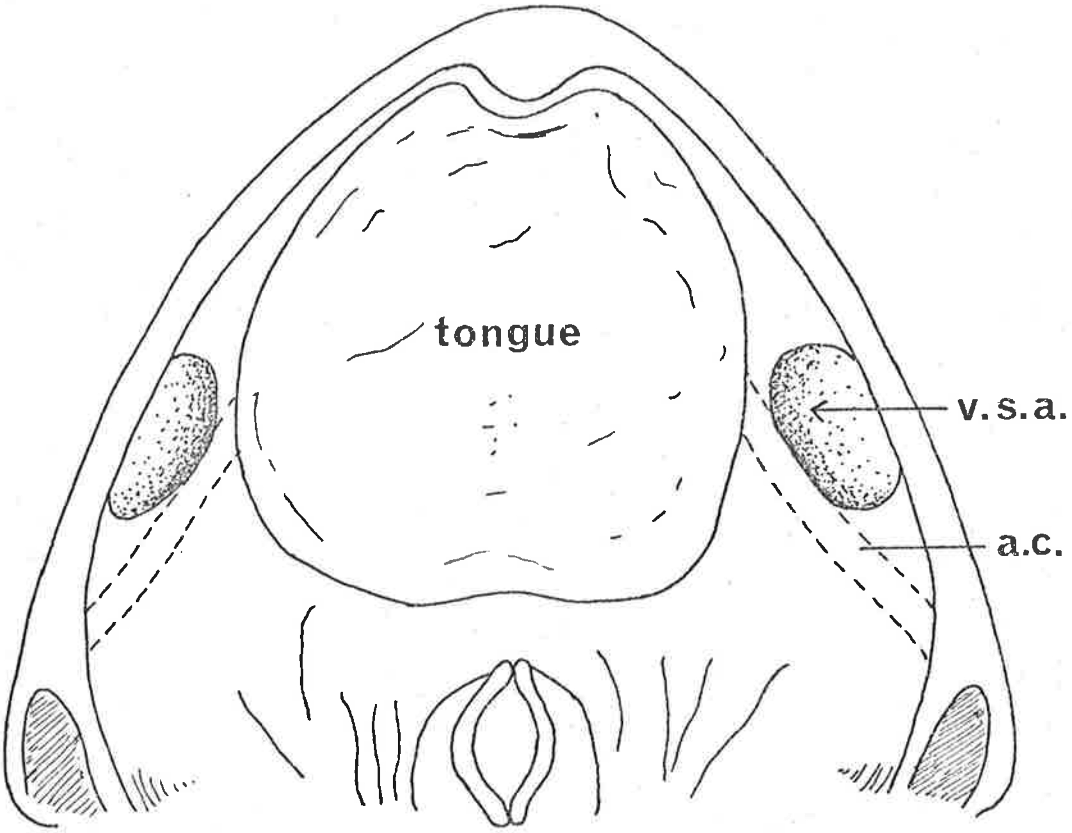
imand. = M. intermandibularis; interhy. = M. interhyoideus; mand. = mandible; subm. = M. submentalis.

FIGURE 3: Supplementary elements of the M. intermandibularis.



A = 'apical'; B = 'anterolateral'; C = 'mediolateral'; D = 'posterolateral'

FIGURE 4: Floor of mouth viewed from above.



a.c. = anterior cornu beneath tissue covering floor of mouth; v.s.a. = vocal sac aperture.

and the intermandibularis and interhyoideus inferiorly. This chamber is called the "vocal sac" and the apertures in the mouth communicating to it "vocal sac apertures". Examples of the variation in vocal sacs include a unilobular submandibular structure (Fig. 5A) and a bilobular supramandibular structure (Fig. 5B), so classified according to the position that they occupy when inflated with air.

Innervation

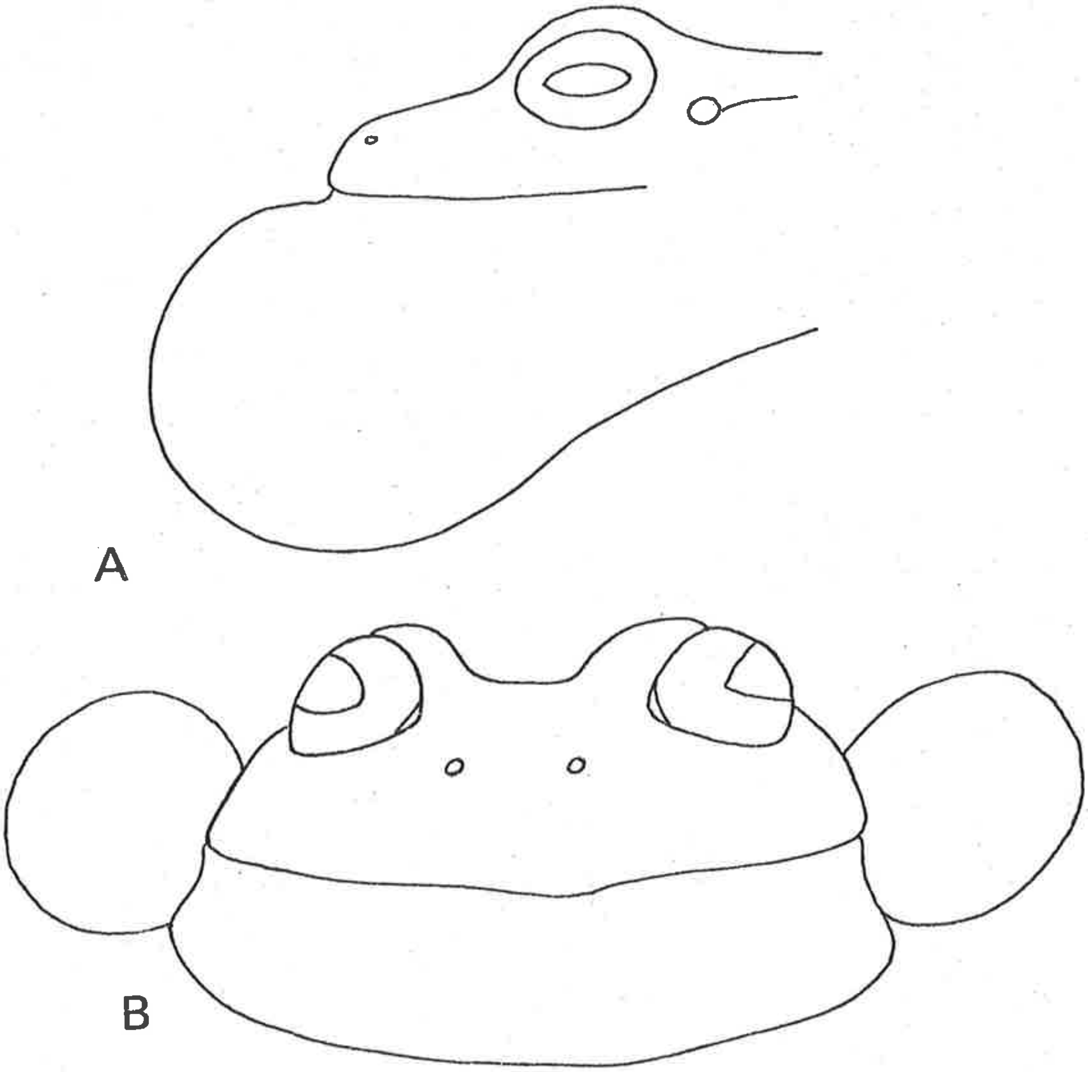
Two cranial nerves innervate the submandibular region: the submentalis and intermandibularis are supplied by the trigeminal, and the interhyoideus by the facial.

Submandibular and Pectoral Lymphatic Septa and Associated Muscles

In contrast with other vertebrates, the skin of all anurans, except *Rhinophrynus dorsalis*, is not intimately attached to underlying muscles but is freely separated, being connected only by numerous transverse or longitudinally orientated septa. There is therefore a series of discrete compartments between these tissues termed "subcutaneous lymphatic sacs". Because of the occasional presence of fluid in these sacs, Kampmeier (1969) visualised anurans as being maintained in a fluid medium despite their occupation of a terrestrial environment.

One lymphatic septum occurring in the submandibular region and another in the pectoral region are of relevance to the present study for two reasons: firstly, because it has been demonstrated that they are not

FIGURE 5: Inflated vocal sac structures.



A = unilobular submandibular form as in *Hyla* and *Litoria*.
B = bilobular supramandibular form as in *Rana ridibunda*.

uniformly distributed in the Anura, and, secondly, because it has been postulated that the septa are functionally involved in the evolution of the vocal sac structure (Tyler, 1971b).

The first of these septa is the post-mandibular septum, most commonly extending from the posterior extremity of the M. interhyoideus to the skin directly below it (Fig. 6A). There it produces a skin fold, noted by numerous taxonomists and termed the "pre-axillary fold" (Fig. 6B). The second septum is the pectoral septum communicating between the muscles of the anterior pectoral block and the adjacent skin. It, too, may produce a skin fold there: the "post-axillary fold" (Fig. 6B).

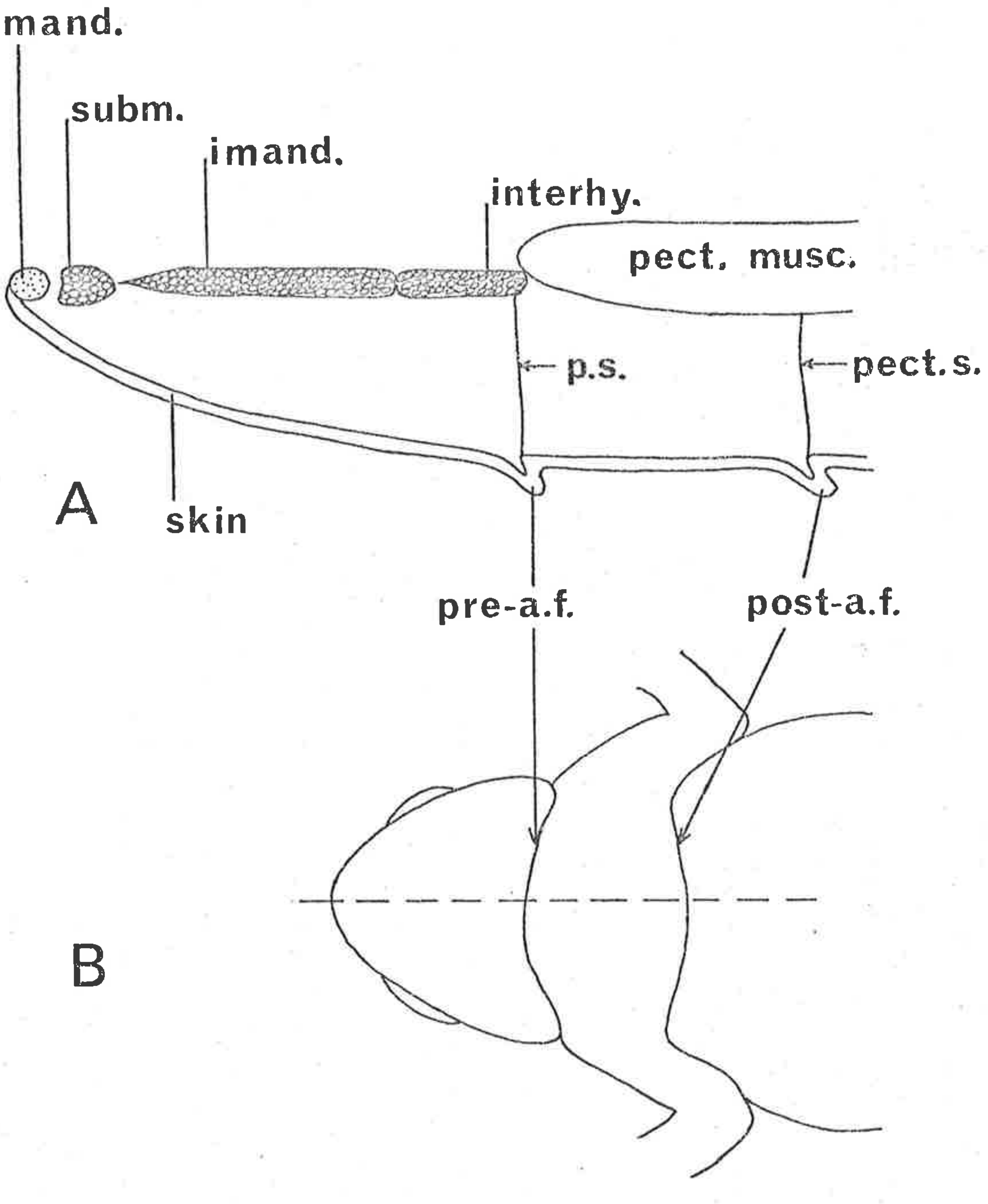
Known variation in these lymphatic septa involve the presence or absence of one or the other, the proximity of the two septa to one another and their respective depths.

In certain anuran families there are specialised muscles attached to the skin and communicating with underlying body musculature. Two such muscles have been reported: one in the pectoral region and the other in the inguinal. Attention is confined here to the former muscle which is known as the M. cutaneous pectoris. Synonyms are listed in Table 1.

The M. cutaneous pectoris constitutes an extremely thin rectangular sheet extending posteriorly from the surface of the anterior segment of the M. rectus abdominis, on each side of the mid-line. It passes anteriorly, usually traversing, but not adhering to, portions of the

FIGURE 6: Submandibular and pectoral lymphatic septa.
A = Sagittal section.
B = Anterior portion of head and body from ventral view.

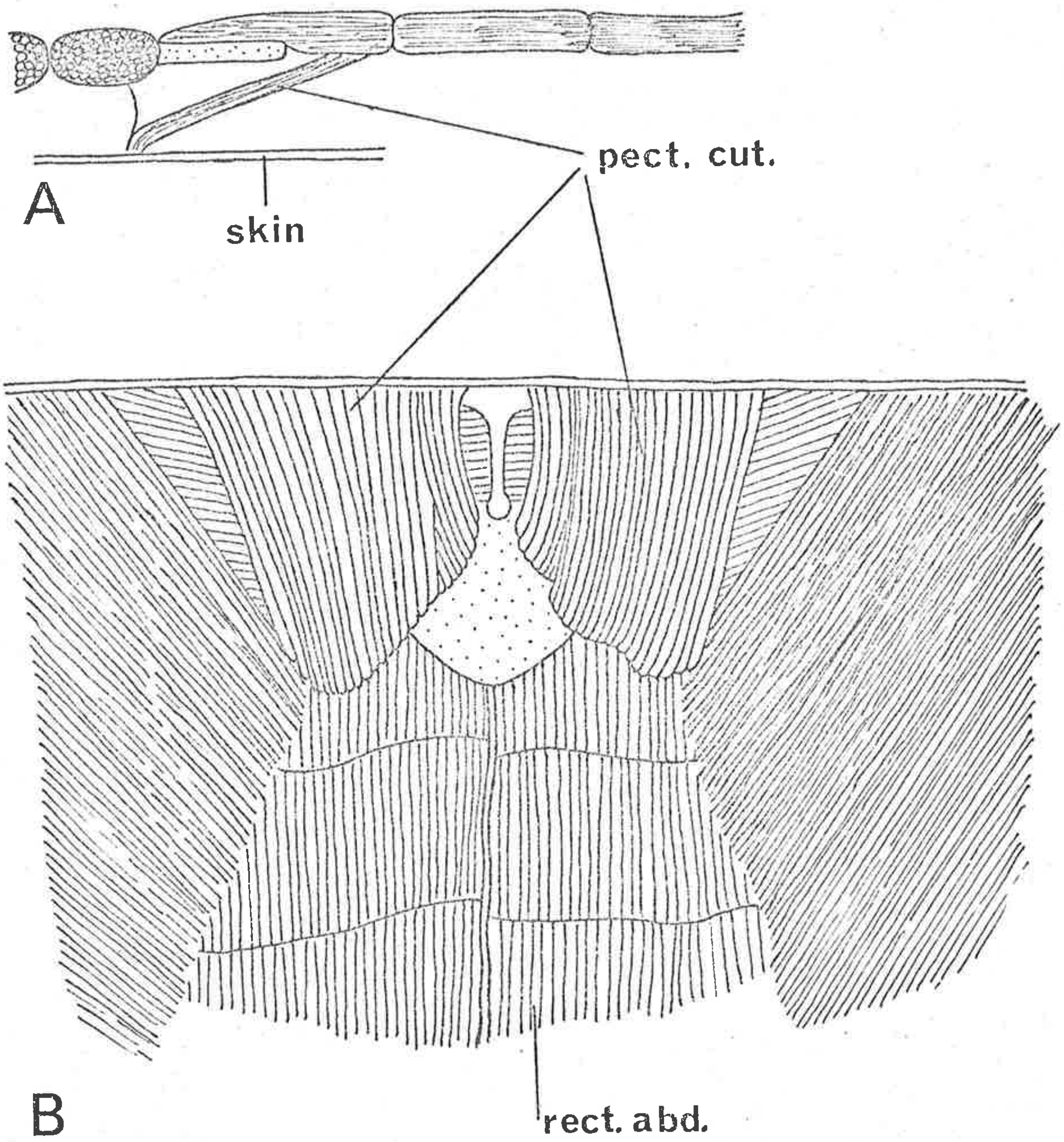
imand. = M. intermandibularis; interhy. = M. interhyoideus; mand. = mandible; pect. s. = pectoral septum; pect. musc. = pectoral muscle block; post-a.f. = post-axillary fold; pre-a.f. = pre-axillary fold; p.s. = postmandibular septum; subm. = M. submentalis.



M. pectoralis abdominalis, pectoralis sternalis and supracoracoideus superficialis.

Variation in the cutaneous pectoris principally is confined to its width, which is in turn associated with the depth of the pectoral lymphatic septum and the separation of the skin from the underlying tissues at this position. At the one extreme, the muscles on each side are medially only slightly separated from one another, diverge only slightly from the adjacent muscles and are associated with a short pectoral lymphatic septum; in the other, the muscles are widely separated, slender slips associated with a deeper pectoral lymphatic septum (Fig. 7).

FIGURE 7: Cutaneous pectoris muscle of *Ptychadena anchietae*.
A = Sagittal section through posterior portion of superficial mandibular and pectoral regions.
B = Ventral view of pectoral muscles extending anteriorly to level of pectoral septum.



pect. cut. = M. cutaneous pectoris; rect. abd. = M. rectus abdominis.

CHAPTER 2 : MORPHOLOGICAL DATA

SUPERFICIAL MANDIBULAR MUSCULATURE AND VOCAL SAC STRUCTURE

FAMILY: DISCOGLOSSIDAE

Four genera of discoglossids are currently recognised. Three of these are reported here. A rough sketch of the interhyoideus of *Bombina bombina* have been prepared by Liu (1935), but it is so inaccurate that I have described it here.

In *Alytes* and *Barbouroula* the submentalis is small, triangular and araphic. The intermandibularis lacks any supplementary muscles and consists of a simple sheet of transversely orientated fibres. The muscle bears a slender median aponeurosis in *Barbouroula,* but meets at a median raphe in *Alytes*.

The interhyoideus is poorly developed, comprising a transverse slip not extending posteriorly beyond the post-articular extremities of the mandibles. There is a triangular gap laterally between the intermandibularis and interhyoideus created by the failure of the borders of these muscles to unite. Vocal sacs are lacking in these genera.

In *Bombina bombina* the submentalis is of moderate size, triangular and araphic. The intermandibularis does not bear supplementary elements and lacks an aponeurosis. The posterior portion of the intermandibularis and the anterior portion of the interhyoideus are broadly separated from one another and are distended ventrally in bilateral, discrete bulges. The space between these muscles is occupied by a unique modification of the geniohyoideus lateralis. The superficial, ventral portion of the geniohyoideus lateralis broadens and divides to form several discrete supplementary heads. In the specimen illustrated (Fig. 8), portions of several of the heads are visible on the right side, but only one on the left. The extent of the separation, and hence of exposure, of the geniohyoideus lateralis varied in the specimens examined.

Bombina bombina lacks a vocal sac, but the floor of the mouth, corresponding to positions above the modified portion of the geniohyoideus lateralis, is folded longitudinally and depressed ventrally.

Bombina variegata differs from *B. bombina* in lacking the modifications of the geniohyoideus lateralis, and the associated changes involving the floor of the mouth and of the intermandibularis and interhyoideus.

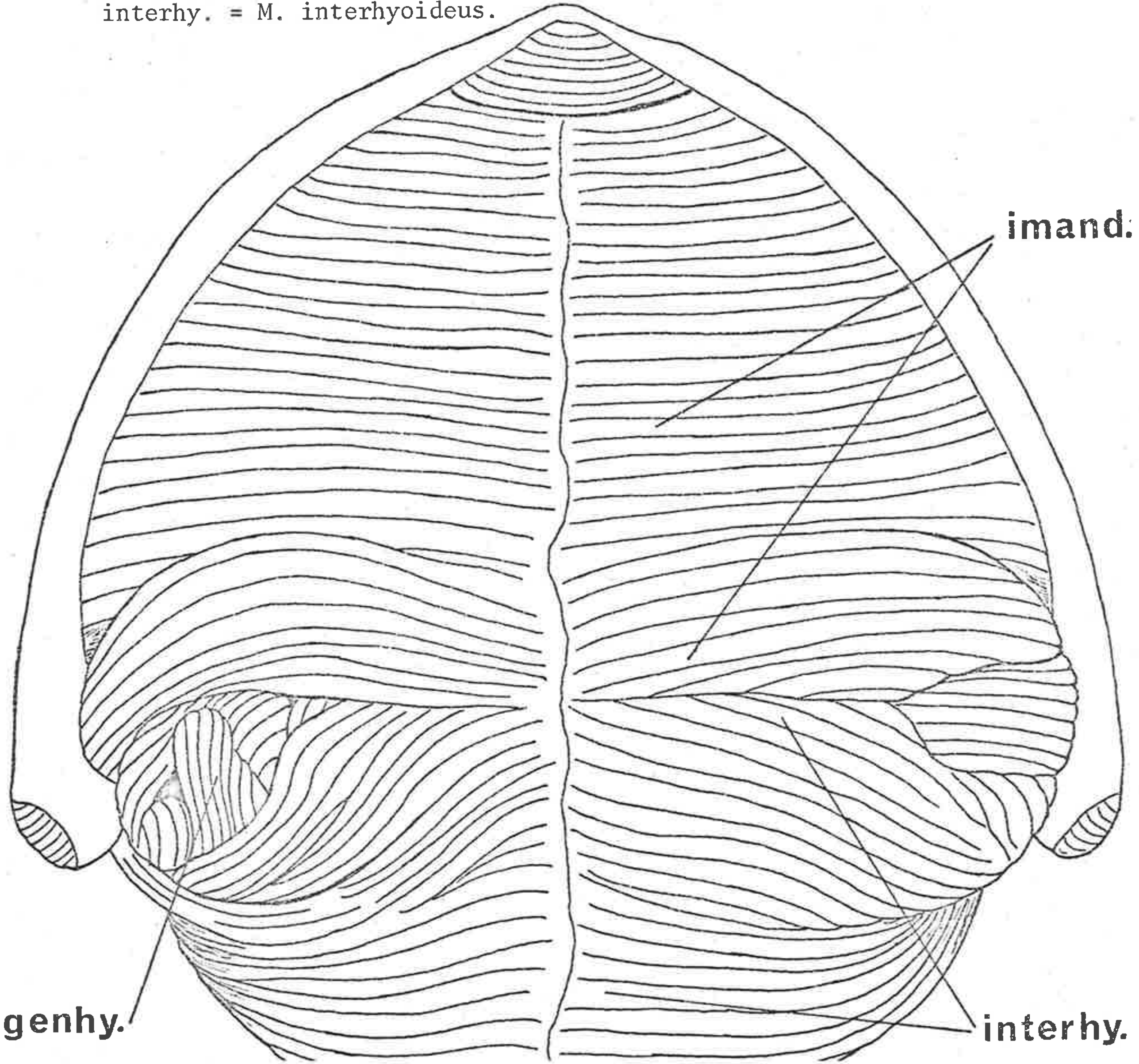
FAMILY: HYLIDAE

Duellman (1970) recognised thirty-one genera and approximately 450 species in this family. Of those genera, Tyler (1971a) surveyed the mandibular musculature and vocal sac structure of all except *Stefania*, and resurrected the genus *Litoria* from the synonymy of *Hyla*.

Subsequently, Trueb and Tyler (in manuscript) have erected the new genus *Calyptahyla* for *Hyla lichenata* of Jamaica, and resurrected

FIGURE 8: Superficial mandibular musculature of *Bombina bombina*.

genhy. = M. geniohyoideus; imand. = M. intermandibularis; interhy. = M. interhyoideus.



Osteopilus from the synonymy of *Hyla* for the West Indian species *septentrionalis*, *dominicensis* and *brunnea*. The only other generic change involving the Hylidae is that Tyler (in press) has transferred the genus *Chiroleptes* from the synonymy of the leptodactylid *Cyclorana* to the synonymy of the hylid genus *Litoria*.

To avoid extensive repetition of the morphological data in Tyler (1971a), I here present only a summary.

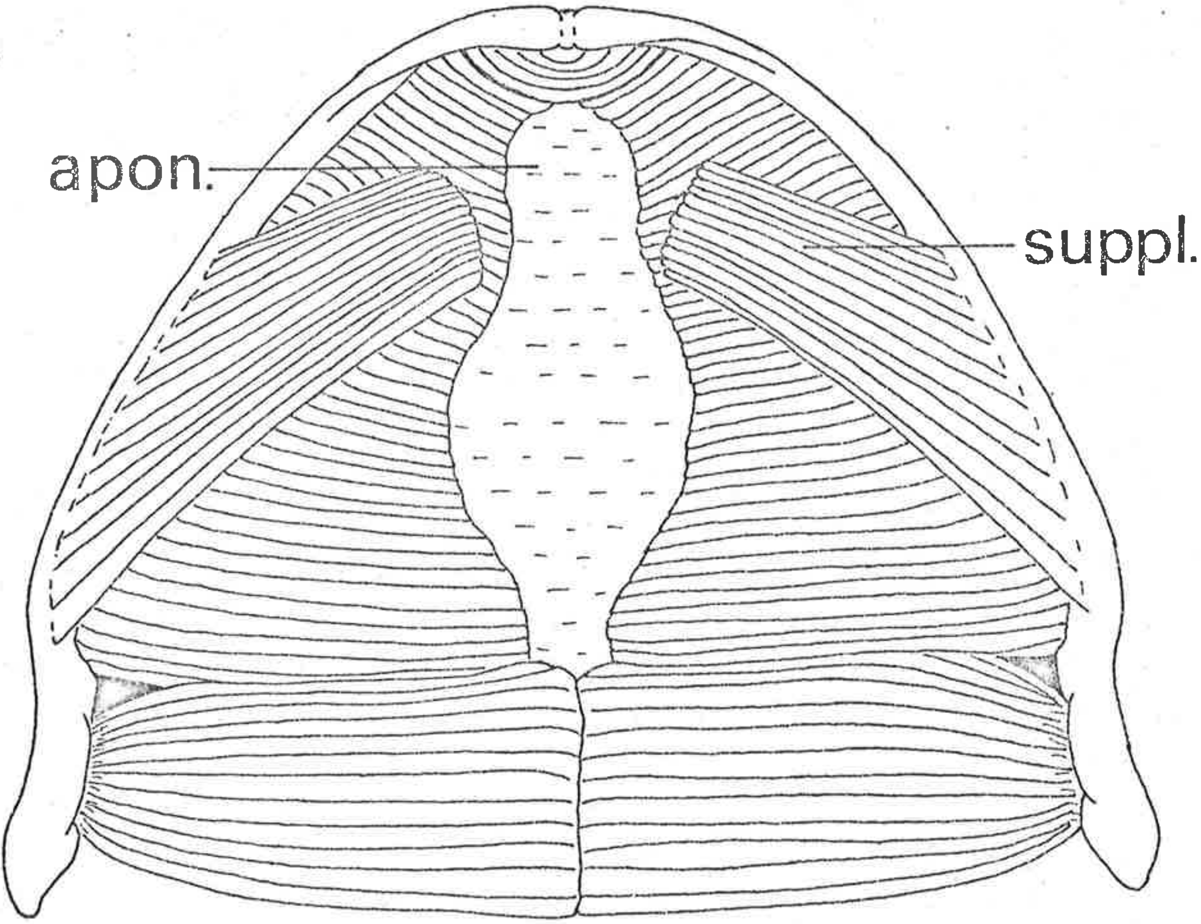
Sub-Family: Phyllomedusinae

Throughout this sub-family the submentalis is small, araphic and completely visible from the ventral aspect, being in no way underlain by anterior fibres of the intermandibularis.

The intermandibularis is differentiated to produce supplementary, posterolateral elements (Fig. 9). Each of these elements arises from the ventral surface of the mandible adjacent to the attachment of the mandibular adductor muscles and is attached to one or other of them by broad ligaments. The number of these adductor muscles varies from species to species, the muscle of variable occurrence being the superficial muscle (M. adductor mandibulae externus superficialis), whereas all exhibit the deep muscle (the M. adductor mandibulae posterior subexternus). In those species possessing both muscles, the ligament of the posterolateral element of the intermandibularis attaches to the M. adductor mandibulae posterior subexternus (Fig. 10).

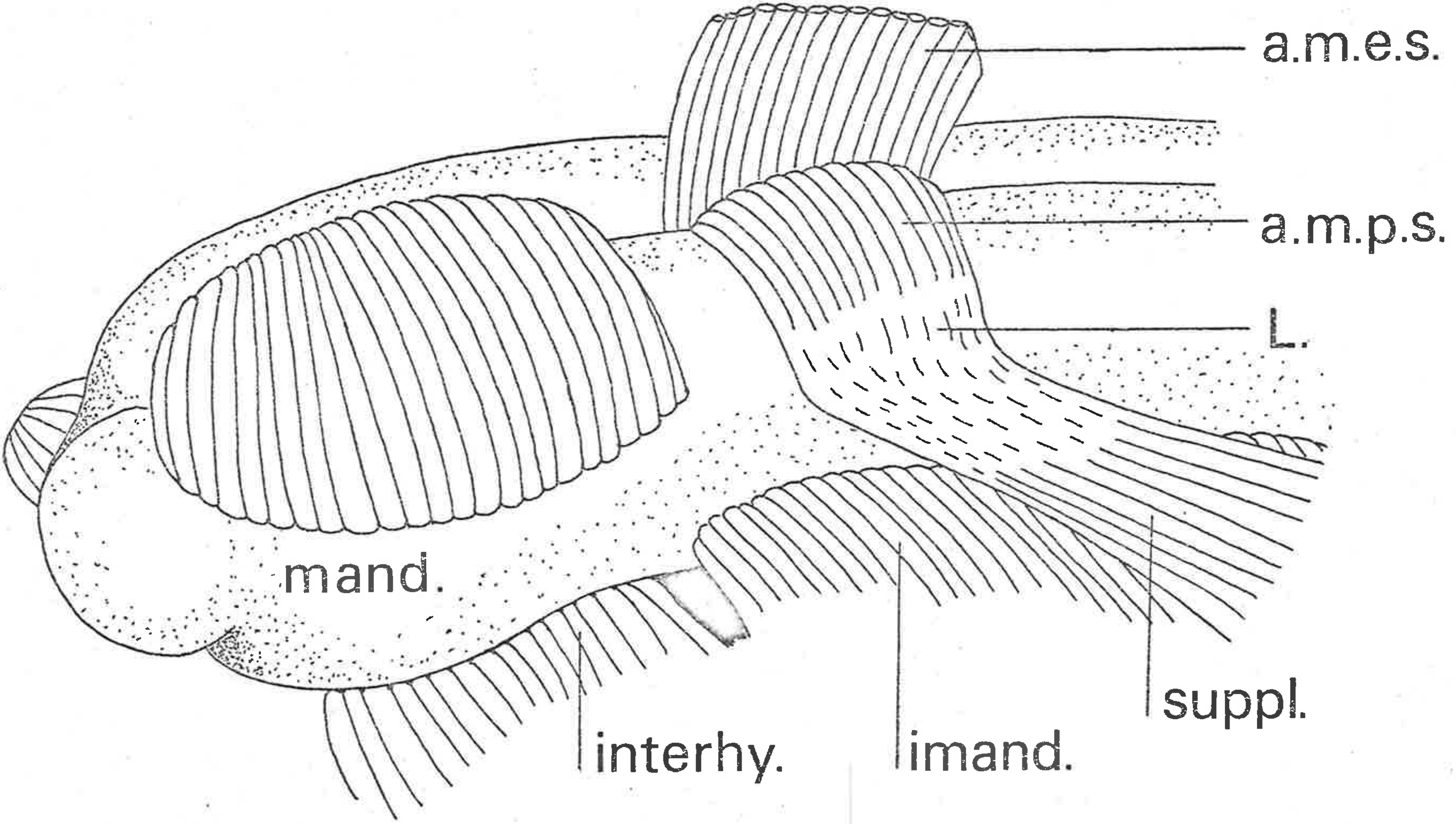
The posterolateral element of the intermandibularis passes

FIGURE 9: Phyllomedusine hylid superficial mandibular musculature.



apon. = median aponeurosis; suppl. = supplementary element of intermandibularis.

FIGURE 10: Articular extremity of mandible of *Phyllomedusa* from medial aspect.



a.m.e.s. = M. adductor mandibulae externus superficialis; a.m.p.s. = M. adductor mandibulae posterior subexternus; imand. = M. intermandibularis; interhy. = M. interhyoideus; L. = ligament; mand. = mandible; suppl. = supplementary element of intermandibularis.

anteromedially from its site of origin and attaches upon the customary element lateral to a broad, median aponeurosis.

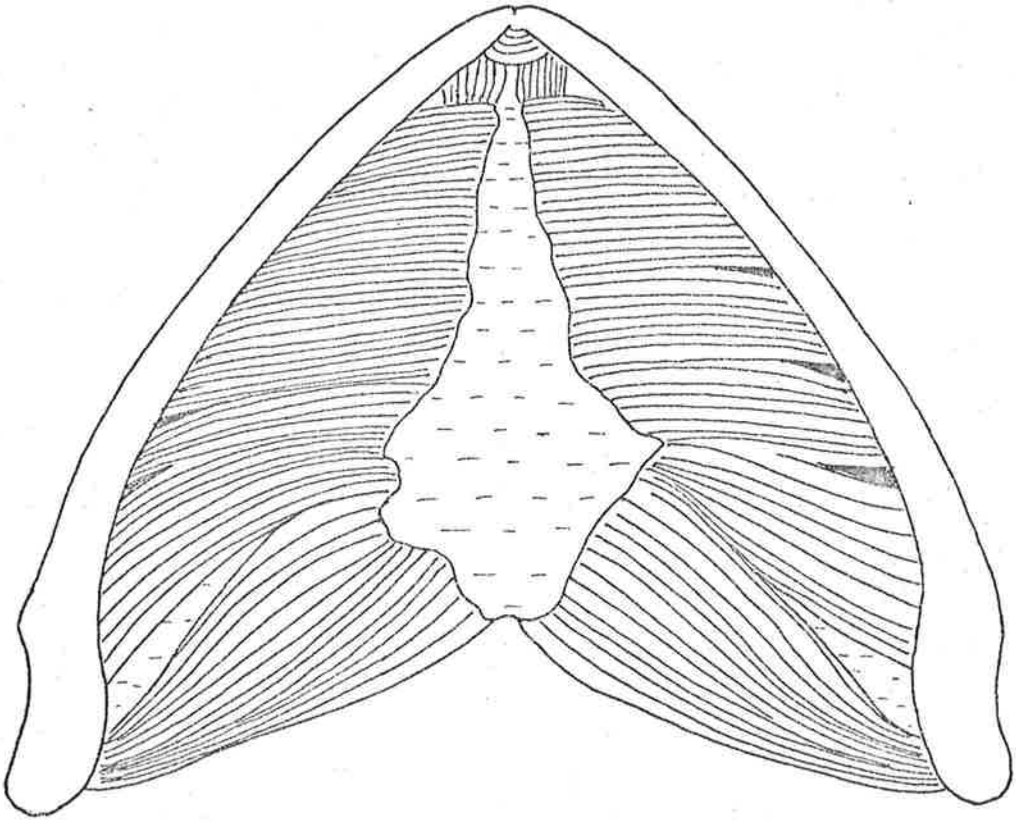
The interhyoideus is well developed, lacks folds and pleats, and shows no evidence towards bilobular development. *Phyllomedusa edentula* is unique in lacking a vocal sac. In all other species the vocal sac is situated principally above the interhyoideus, intruding above the intermandibularis only anterolaterally. The vocal sac apertures are customarily short slits, equivalent in length to approximately one-tenth of the length of the mandible. The position of the apertures in the mouth floor is directly above the site of origin of the posterolateral elements of the intermandibularis.

Sub-Family: Hemiphractinae

The submentalis is extremely small and araphic (Fig. 11). The intermandibularis is not differentiated and is poorly developed, being arrested anteriorly (so exposing the geniohyoideii) and composed of a sheet of muscle that is extremely thin in comparison with other hylid frogs of comparable dimensions. In addition, there is an exceptionally large median aponeurosis, and only limited contact between the most posterior fibres and the anterior portion of the interhyoideus.

The interhyoideus is similarly poorly developed, the opposing portions of this muscle being entirely separated by aponeurotic tissue confluent with that of the intermandibularis. The muscle fibres are inclined anteromedially.

FIGURE 11: Superficial mandibular musculature of *Hemiphractus panamensis*.



The hatched medial area is a vast aponeurosis.

There is no vocal sac in the four specimens examined.

Sub-Family: Amphignathodontinae

The submentalis is small, araphic in *Anotheca, Cryptobatrachus, Flectonotus, Fritziana, Gastrotheca* and *Nyctimantis*, but bearing a median raphe in *Amphignathodon*. The submentalis is completely visible, except in *Flectonotus* in which the most posterior fibres are underlain by the intermandibularis, and *Nyctimantis* in which it is obscured by dense, opaque, fibrous tissue.

The intermandibularis is not differentiated and median aponeuroses are present only in *Amphignathodon, Anotheca, Flectonotus* and *Nyctimantis*.

The interhyoideus is a simple sheet of transverse fibres in all genera, except *Gastrotheca* in which there is considerable anteromedial development (compensated by posteromedial development of the intermandibularis), and *Nyctimantis* in which there is similar anteromedial development and the development of a vast unilobular posterior lobe extending far beyond the extremities of the mandibles.

Vocal sacs are absent in *Anotheca, Cryptobatrachus* and *Gastrotheca ceratophrys*, but present in all other representatives of this sub-family examined. In *Flectonotus* the vocal sac extends above the entire area bounded by the intermandibularis and interhyoideus, but extends anteriorly only to the posterior half of the intermandibularis in the other species. Vocal sac apertures tend to be in the form of irregularly shaped holes, which are particularly vast in *Flectonotus* (aperture length approximately equivalent to one-third of the length of the mandible) and moderate in the remainder (equivalent to from one-fifth to one-sixth of the mandible length).

Sub-Family: Hylinae

Because of the numerical content and complexity of this sub-family, it is possible only to summarise at a generic level.

In *Acris* the submentalis is small and araphic. The intermandibularis is differentiated and the supplementary elements are of the apical type. The fibres of the supplementary element arise from the medial surface of the mandibles at their apex on each side of the submentalis. The fibres pass posteromedially and attach at a median raphe. The principal element of the intermandibularis lacks a median aponeurosis. The interhyoideus is well developed, forming a unilobular posterior lobe. The vocal sac extends anteriorly on a level with the posterior one-third of the intermandibularis, and the vocal sac apertures are slits equivalent in length to approximately one-quarter that of the mandible.

Data on the rare *Allophryne* are derived from a single, partly dissected female. From that specimen it is possible to establish only that the submentalis is elongate and araphic and that the intermandibularis is differentiated, having supplementary elements of the anterolateral type attaching upon the ventral surface of the submentalis, and that the principal element of the intermandibularis lacks an aponeurosis.

Aparasphenodon has a small araphic submentalis and an undifferentiated intermandibularis with a median aponeurosis. Although the interhyoideus is not well developed anteriorly or posteriorly, the sheet is folded and pleated, particularly adjacent to the mandible. The vocal sac is paired, medial adhesions separating each portion, entirely submandibular, and confined to the interhyoideus, except anterolaterally, where each extends as far as the limit of the posterior half of the intermandibularis. Vocal sac apertures are elongated holes on the mandibular margin and equivalent to approximately one-sixth of the length of the mandible.

The female *Argenteohyla* examined has a small araphic submentalis and, as in the preceding genus, the posteromedial portion is underlain by the intermandibularis. The intermandibularis lacks an aponeurosis and the interhyoideus is not well developed anteriorly or posteriorly. However, some bilobular posterior development of the interhyoideus in males is clearly indicated by Barrio's (1966) photograph of a calling male.

In *Calyptahyla* (Trueb and Tyler, in press) the submentalis is small and araphic. The intermandibularis is not differentiated and bears a slender, elongate aponeurosis. The interhyoideus is not developed anteriorly at the expense of the intermandibularis, nor posteriorly, but is extensively folded ventrally. The vocal sac is large and submandibular, occupying a position above the interhyoideus and the posterior half of the intermandibularis. The vocal sac apertures are small, circular holes, their diameter equivalent to approximately one-tenth of the diameter of the mandible length.

Corythomantis has an araphic submentalis and an intermandibularis which is not differentiated and lacks an aponeurosis. The interhyoideus is without posterior or anterior development, but is folded and pleated. The vocal sac is a bilobular postmandibular structure separated medially into two separate compartments. The vocal sac apertures are gaping holes equivalent in length to approximately one-fifth of the length of the mandible.

In Nearctic, Palaearctic and Oriental species of *Hyla* the submentalis is araphic and the posterior margin of this muscle is underlain by transverse fibres of the intermandibularis. The intermandibularis lacks an aponeurosis, and the interhyoideus is well developed anteriorly and posteriorly. The vocal sac is characteristically large and unilobular, anteriorly approaching the submentalis.

The numerous remaining Neotropical species of *Hyla* are morphologically diverse and I here only provide an indication of the extent of variation exhibited by them. They share only an araphic submentalis and an undifferentiated intermandibularis. Ventral attachment of the most anterior fibres of the intermandibularis upon the submentalis is present or absent.

Development of the interhyoideus most commonly results in the formation of a single median lobe. However, submandibular bilobular pouching of the muscle occurs in *H. brieni, H. catharinae, H. colymba, H. crospedospila, H. depressiceps, H. garbei, H. hayi, H. nasica, H. phrynoderma, H. pickeli, H. smaragdina* and *H. subocularis*. These range from slight bilobular development in *H. hayi* to distinct separation in *H. smaragdina*. Bilobular supramandibular development of the interhyoideus into lobes passing beneath the skin on the side of the head to the level of the tympanum occurs in *H. alboguttata*.

The variation of the development of the interhyoideus reflects the positions occupied by the vocal sacs. *Hyla marianae, H. pentheter* and *H. robertsorum* lack vocal sacs.

Vocal sac apertures are shorter in length and situated more posteriorly in the species possessing bilobular sacs than in those having unilobular sacs.

Limnaoedus has an araphic submentalis underlain posterolaterally by the anterior fibres of the intermandibularis. The intermandibularis is undifferentiated and lacks an aponeurosis. The interhyoideus is well developed anteriorly and posteriorly and the vocal sac is a vast structure extending anteriorly to a position mid-way above the intermandibularis. The vocal sac apertures are holes equivalent in length to one-quarter of the length of the mandible.

Litoria and *Nyctimystes* share an araphic submentalis, underlain anteromedially by the anterior fibres of the intermandibularis only in *L. freycinetti, L. nasuta* and *L. nigrofrenata*.

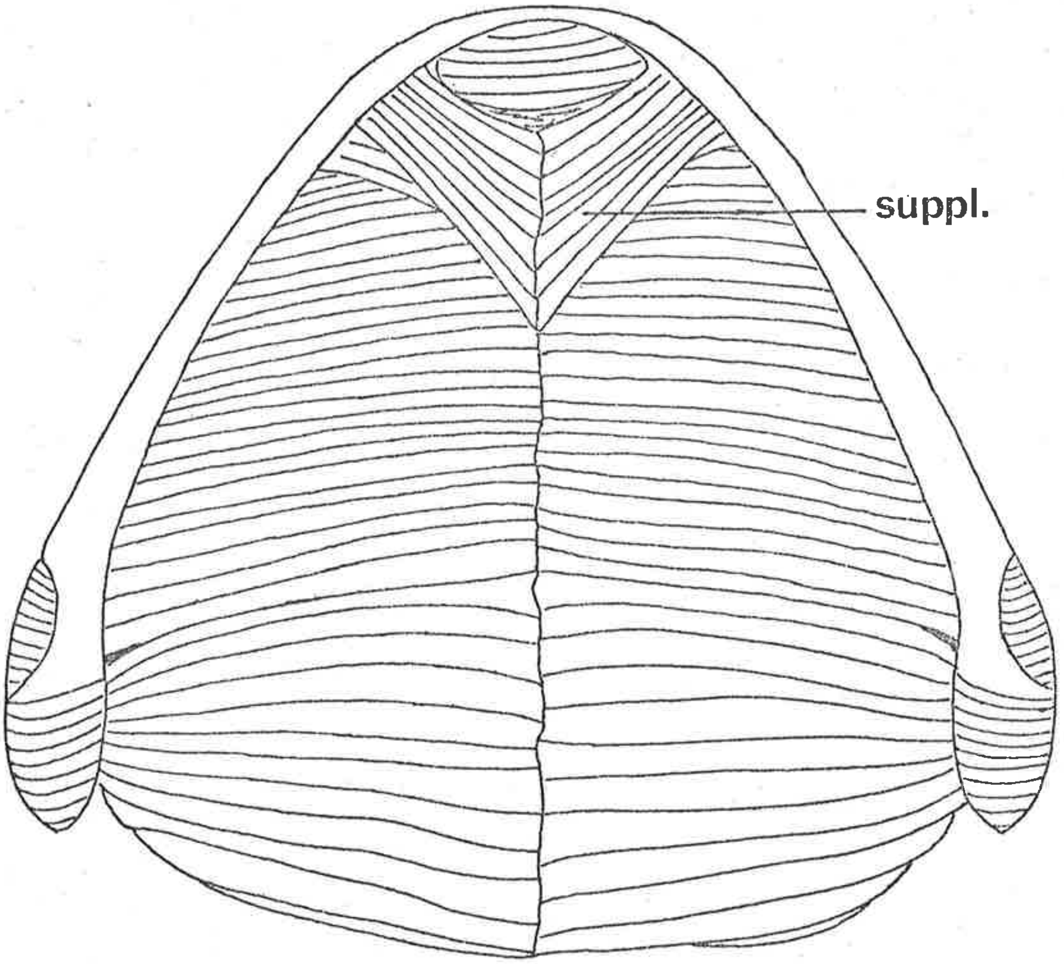
The intermandibularis is differentiated by the development of a supplementary apical element broadly comparable to that described for *Acris*. The interhyoideus is customarily moderately well developed (Fig. 12).

Vocal sacs are absent in *L. lesueuri*, *L. eucnemis*, *L. booroolongensis*, *L. genimaculata*, *N. avocalis*, *N. papua* and *N. tympanocryptis*. In the remaining species they are unilobular submandibular structures. An exception occurs in *L. infrafrenata*, where the position of the ossified episternum determines the shape of the inflated vocal sac (Tyler, 1971a, p. 337).

Vocal sac apertures are slits in *Nyctimystes*, and slits or gaping holes in *Litoria*. The only really aberrant aperture occurs in *L. citropa*, where it is an exceptionally small orifice located adjacent to the jaw articulation.

Osteocephalus, *Phrynohyas* and *Trachycephalus* share an araphic submentalis and an undifferentiated intermandibularis, and also have in common the development of supramandibular lobes of the interhyoideus. The supramandibular lobes vary from simple, slender, tubular extensions in *O. buckleyi*, *O. lepreuri* and *O. verrucigerus* to broad and usually extensively convoluted lobes in the other species. Vocal sacs are completely separated from one another, or possess slight communication via the posterior portion above the posterior portion of the interhyoideus. The vocal sac apertures vary considerably in relative size, being

FIGURE 12: Superficial mandibular musculature of *Litoria aurea*.



suppl. = supplementary element of M. intermandibularis.

equivalent to one-quarter to one-fifteenth of the length of the mandible. In *Osteocephalus* there is a two-fold variation associated with modification of the skin adjacent to the supramandibular lobes. Thus, in species possessing everted skin pouches, the apertures are double the length of those lacking them.

Osteopilus (of Fitzinger, resurrected by Trueb and Tyler, in press) is characterised by a differentiated intermandibularis of which the supplementary element is of the apical type. This apical element differs from that in *Litoria* and *Nyctimystes* in being intimately attached to the principal muscle over an extensive area.

The interhyoideus is well developed anteriorly, and has a well developed unilobular (*O. brunneus*) or slightly bilobular (*O. dominicensis* and *O. septentrionalis*) posterior margin.

The anteromedial limit of the vocal sac and size of the vocal sac apertures are similarly closely associated with the above divergence. In *O. brunneus* the vocal sac reaches an anterior position above the base of the apical element of the intermandibularis, and the aperture length is equivalent to one-third of the mandible length; in the remaining species the vocal sac is confined to the interhyoideus and the apertures equivalent to approximately one-tenth of the mandible length.

Phyllodytes has an elongate, araphic submentalis. The intermandibularis is not differentiated, bears a broad median aponeurosis, and anteriorly partly attaches upon the ventral surface of the submentalis.

The interhyoideus is well developed anteriorly and has a small, unilobular posterior lobe. The vocal sac occupies the area above the interhyoideus and the posterior half of the intermandibularis. The vocal sac apertures are large holes equivalent in length to approximately one-quarter of the mandible.

Plectrohyla has a small, araphic submentalis, of which the posterior border is transversely underlain by the intermandibularis. The intermandibularis is not differentiated and lacks an aponeurosis. The interhyoideus is slightly developed anteromedially in *P. ixil*, which possesses a vocal sac, and is not developed anteromedially in *P. guatemalensis*, which lacks one. The vocal sac is principally confined to the area above the interhyoideus, extending only slightly above the intermandibularis. The vocal sac apertures are long slits one-third of the length of the mandible.

The submentalis of *Pseudacris* is small and araphic. The intermandibularis is not differentiated, lacks an aponeurosis and anteriorly underlies the submentalis. The interhyoideus is conspicuously developed anteriorly and slightly developed posteriorly. The vocal sac occupies the area above the interhyoideus and the posterior half of the intermandibularis. The vocal sac apertures are exceptionally long slits, equivalent in length to approximately one-half of the length of the mandible.

In *Pternohyla* the submentalis is small and araphic. The intermandibularis is not differentiated and lacks an aponeurosis. The interhyoideus is developed slightly anteriorly but considerably posteriorly, forming a vast unilobular lobe. The vocal sac occupies the area above the interhyoideus and slightly more than the posterior half of the intermandibularis. The vocal sac apertures are long slits, equivalent in length to approximately one-third of the length of the mandible.

Ptychohyla has a small, araphic submentalis whose posterior border is traversed by the most anterior fibres of the intermandibularis. The intermandibularis is not differentiated and bears a median aponeurosis. The interhyoideus is slightly developed anteriorly and posteriorly, and bears numerous transverse, ventral folds. The vocal sac is confined to the area above the interhyoideus in *P. leonhardschultzei*, but extends anteriorly almost to the anterior extremity of the intermandibularis in *P. spinipollex*. The vocal sac apertures are narrow slits, equivalent in length to approximately one-quarter of the length of the mandible.

The submentalis of *Smilisca* is small and araphic. The intermandibularis lacks supplementary elements and lacks an aponeurosis. Anterior development of the intermandibularis is slightly arrested in *S. phaeota*, creating a very slight transverse gap between the submentalis and the intermandibularis. However, in *S. baudini* and *S. phaeota* the muscles are not so separated. The interhyoideus is developed slightly anteriorly at the expense of the intermandibularis. Posteroventrally the interhyoideus is developed into discrete bilobular pouches.

The vocal sac is principally confined to the interhyoideus and is a bilobular, submandibular structure. The vocal sac apertures are elongate slits commencing immediately posterior to the site of attachment of the geniohyoideus lateralis on the mandible and equivalent to one-third of the mandible length.

The submentalis of *Sphaenorhynchus* is rhomboid-shaped and araphic. The intermandibularis is differentiated, there being a very small and slender apical element arising from the medial surface of the mandible on each side of the site of origin of the submentalis. The customary element is large and lacks an aponeurosis. The interhyoideus is developed into a vast, unilobular and almost entirely postmandibular structure with pronounced folding and pleating.

The vocal sac is confined to the interhyoideus and is a unilobular, postmandibular structure. The vocal sac apertures are slits, equivalent in length to one-third of the length of the mandible.

In *Triprion* the submentalis is oval and araphic. The intermandibularis is not differentiated and the anterior fibres of this muscle attach upon the posterior fibres of the submentalis. The intermandibularis lacks an aponeurosis. The interhyoideus is developed posteriorly into two lobes and is extensively folded and pleated. This muscle is much thinner than the intermandibularis, the respective thicknesses in *T. s. spatula* being 0.7 mm for the intermandibularis against 0.25 mm for the interhyoideus.

The vocal sac is a submandibular bilobular structure confined to the area above the interhyoideus. The vocal sac apertures are slits, ranging from one-fifth to one-seventh of the length of the mandible.

FAMILY: LEIOPELMATIDAE

This family comprises three species of *Leiopelma* occurring in New Zealand and the monotypic *Ascaphus* of North America. All four species have been examined.

In all species of *Leiopelma* the submentalis is of moderate size, araphic, and completely visible from the ventral aspect. The intermandibularis is an undifferentiated muscle of transversely orientated fibres meeting at a median raphe and usually lacking an aponeurosis (present only in *L. hochstetteri*, Fig. 13). The interhyoideus is a simple, almost rectangular muscle.

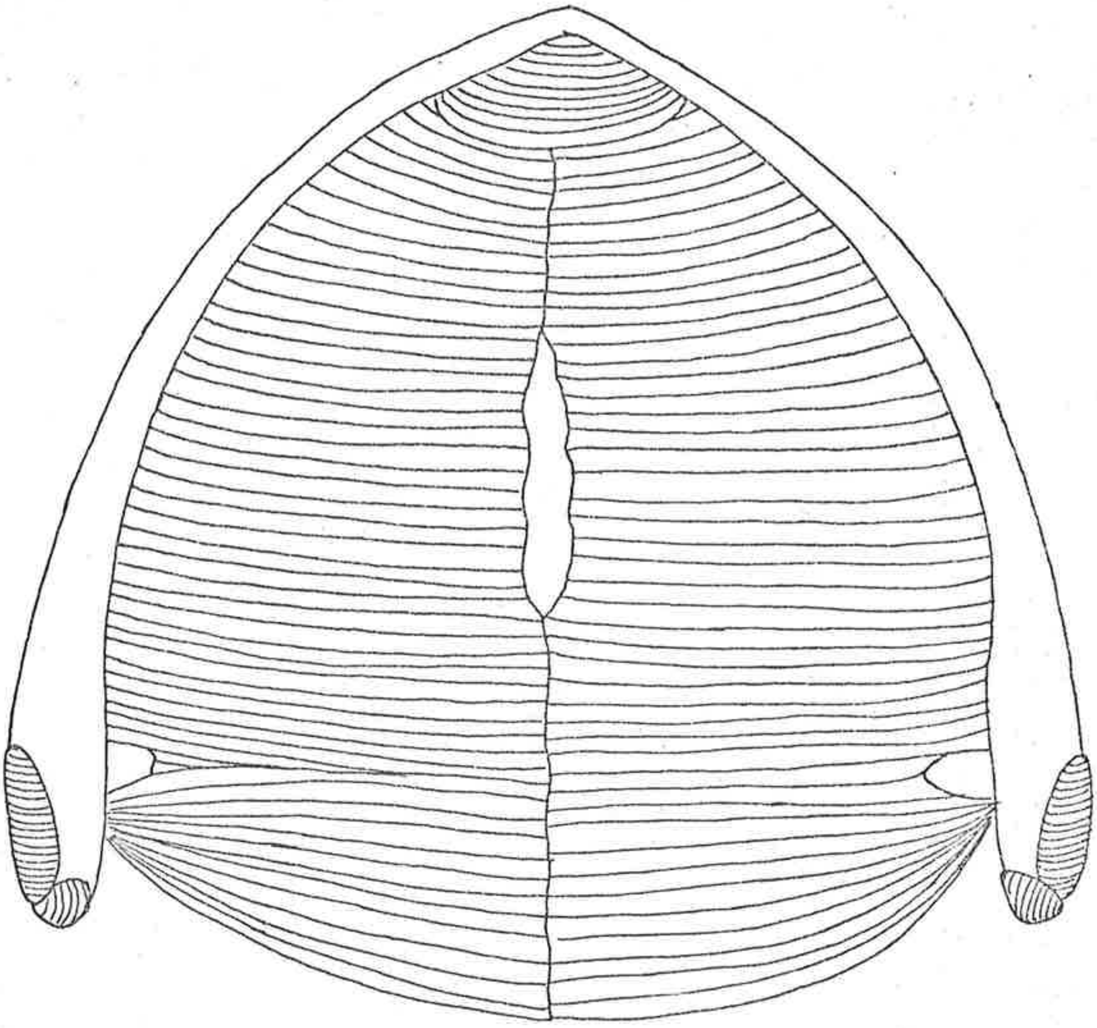
The musculature of *Ascaphus* differs only in that the anterior development of the intermandibularis is arrested, creating a transverse gap between the intermandibularis and submentalis.

Vocal sacs are absent in all members of the family.

FAMILY: LEPTODACTYLIDAE

Lynch (1971) recognised fifty-seven genera in his review of this family. Of these, Tyler (1972a) described the superficial mandibular musculature of all seventeen Australo-Papuan genera then recognised. Subsequent studies have drastically altered the number and content of the Australo-Papuan genera. *Assa* Tyler (1972b) was erected to accommodate *Crinia darlingtoni*, whilst Blake (1973) referred five of the remaining

FIGURE 13: Superficial mandibular musculature of *Leiopelma hochstetteri*.



Crinia species to *Geocrinia* and eleven to *Ranidella*. Blake also placed *Metacrinia* in the synonymy of *Pseudophryne*, and Liem (1973) described *Rheobatrachus*.

Lynch and other contributors in Vial (1973) favour placing the Australian genera and the South African genus *Heleophryne* in a separate family (the Myobatrachidae). This action is not followed here largely because of uncertainty about the status of the Hylidae (particularly in the Australo-Papuan genera), the possible origin of the Hylidae and Leptodactylidae from a common stock in Australia (first suggested by Tyler, 1970), leading to the real possibility that future major revisions may necessitate further changes in the names of families.

Sub-Family: Myobatrachinae

In *Assa*, *Crinia*, *Glauertia* and *Uperoleia* the submentalis is of moderate size, broadly oval and araphic. The intermandibularis is a single sheet of fibres arrested anteriorly, so creating a space between this muscle and the submentalis. A median aponeurosis is present in *Assa*.

In all genera the interhyoideus is large and well developed posteriorly, forming a median unilobular lobe extending far beyond the posterior extremities of the mandibles.

The vocal sac is large, extending above the interhyoideus and at least the posterior two-thirds of the intermandibularis in all species except *A. darlingtoni*. The apertures are elongate and in length equivalent to approximately one-third or one-half of the length of the mandibles.

In *Geocrinia, Pseudophryne* and *Ranidella* the submentalis is of small to moderate size, broadly oval and araphic. The intermandibularis is a sheet of uniformly, transversely directed fibres, except in *Pseudophryne*, where the anterior segment is composed of transverse fibres with posteromedially directed fibres superficial (ventral) to them. This differentiation is such that it is not possible to freely separate the fibres into separate sheets.

The interhyoideus is well developed: anteromedially with a compensatory reduction of the intermandibularis, and posteromedially forming a median, unilobular extension beyond the postarticular extremities of the mandibles. Development of the interhyoideus is most pronounced in those species with the most acutely angled mandibles. The vocal sac is largely confined to the area above the interhyoideus in *Pseudophryne*, but extends further anteriorly to intrude above the intermandibularis in *Geocrinia* and *Ranidella*. Vocal sac apertures are rather short in *P. nichollsi* (equivalent in length to one-fifth of the mandible length), but particularly long (equivalent to one-half) in the remaining *Pseudophryne* species and the representatives of *Geocrinia* and *Ranidella*.

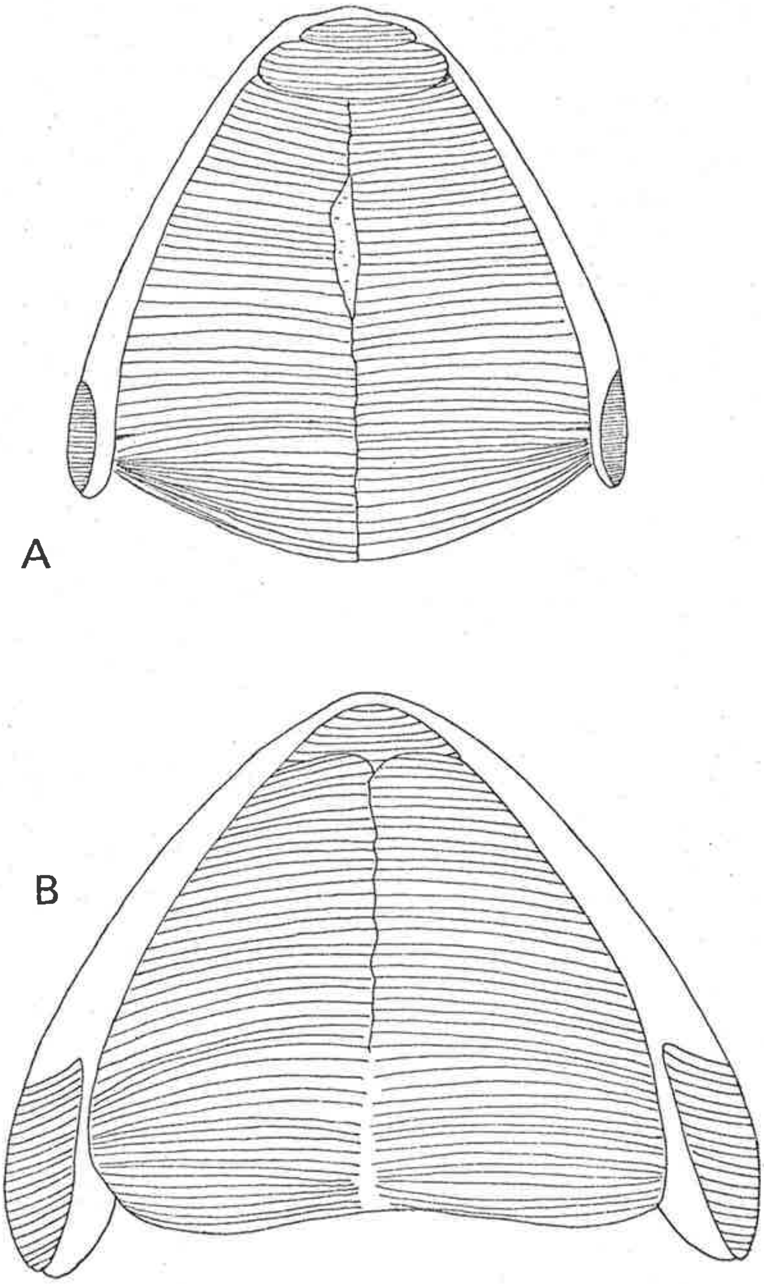
Myobatrachus is characterised by a small, elongate submentalis which is araphic. The intermandibularis is large and bears an anteromedial aponeurosis. The interhyoideus is well developed posteriorly and anteromedially underlies partly the intermandibularis. The posterior lobe of the muscle extends considerably beyond the postarticular extremities of the mandibles. The vocal sac is large, occupying the entire area above the interhyoideus and intermandibularis. The vocal sac apertures are moderate and slit-like, and equivalent in length to approximately one-quarter of the length of the mandible.

In *Rheobatrachus* the submentalis is rather large, rhomboid and araphic. The intermandibularis is a sheet of transversely directed fibres which anteriorly bears a slender aponeurosis and posteriorly meets at a median raphe.

The interhyoideus is poorly developed and confined to that area of the mandibles between the attachments of the jaw adductor muscles. The vocal sac is confined to the interhyoideus, and the vocal sac apertures are short slits equivalent in length to less than one-sixth of the length of the mandibles.

There is variation in the state of the submentalis in the species of *Taudactylus* examined. In *T. diurnus* and *T. rheophilus* it is simply large, broadly ovoid and araphic. In *T. acutirostris* (Fig. 14A) the muscle is composed of two distinct segments: a small and very slender anterior one, and a large and broadly oval posterior one. The latter portion is superficial in its attachment upon the mandible and can be readily dissected free to expose the geniohyoideus. The superficiality precludes a functional role common to the anterior segment, but the absence of a median raphe does eliminate the possibility of this latter

FIGURE 14: Superficial mandibular musculature.



A = *Taudactylus acutirostris*
B = *Adelotus brevis*

portion really representing a portion of the intermandibularis.

In all species the intermandibularis is thin and bears an extremely slender median aponeurosis. The interhyoideus is developed into a small, median postarticular lobe in *acutirostris* but not in *diurnus* and *rheophilus*.

A vocal sac is present only in *acutirostris* and *rheophilus*. It is largely confined to the area above the interhyoideus, and the vocal sac apertures are long slits following the medial margin of the anterior cornua, their anterior limit being the position at which the cornua pass above the medial border of the geniohyoideii lateralis.

Sub-Family: Cycloraninae

In *Adelotus* (Fig. 14B) the submentalis is large, broadly oval and araphic. The intermandibularis anteriorly underlies and attaches upon the posterior portion of the ventral surface of the submentalis. The intermandibularis lacks an aponeurosis.

The interhyoideus does not extend posteriorly beyond the postarticular extremities of the mandibles. Medially the most anterior are inclined slightly posteriorly. The vocal sac occupies the area above the interhyoideus and all except an anteromedial segment of the area above the intermandibularis. The vocal sac apertures are extremely long, extending on the medial border of the mandibles for a distance equivalent to approximately one-third of the total length of the mandible.

Cyclorana is the only anuran genus examined in which a specimen was found to have a submentalis bearing a median raphe (a single specimen of *C. cultripes*). In the remaining representatives of that and all other species the submentalis was araphic. The submentalis of *Cyclorana* is customarily rather small and ovoid.

The intermandibularis bears a supplementary element. The customary sheet of fibres has a median raphe and is entirely lacking contact with the submentalis, except in *C. dahli* in which the most anterior fibres of the intermandibularis pass anteromedially and attach upon the ventral surface of the submentalis. The supplementary element is of the apical form, arising from the medial surface of the mandible, immediately posterior to the submentalis. The fibres pass posteromedially and attach upon the median raphe of the customary element. (Comparable to the condition exhibited by hylids *Litoria* and *Nyctimystes*.)

The interhyoideus is well developed posteriorly, forming a large median lobe extending beyond the postarticular extremities of the mandibles. The vocal sac lies above the interhyoideus and posterior half of the intermandibularis. The vocal sac apertures are short slits equivalent in length to one-quarter of the length of the mandible.

In *Heleioporus* and *Neobatrachus* the submentalis is extremely large and oval or semicircular in shape. It is completely obscured from the ventral aspect by the intermandibularis whose anterior fibres cover its ventral surface. The intermandibularis is a large muscle with a median raphe and the interhyoideus a broad, rectangular slip (Fig. 15A).

Both of these genera lack vocal sacs, but the floor of the mouth between tongue and mandible is extensively folded and pleated.

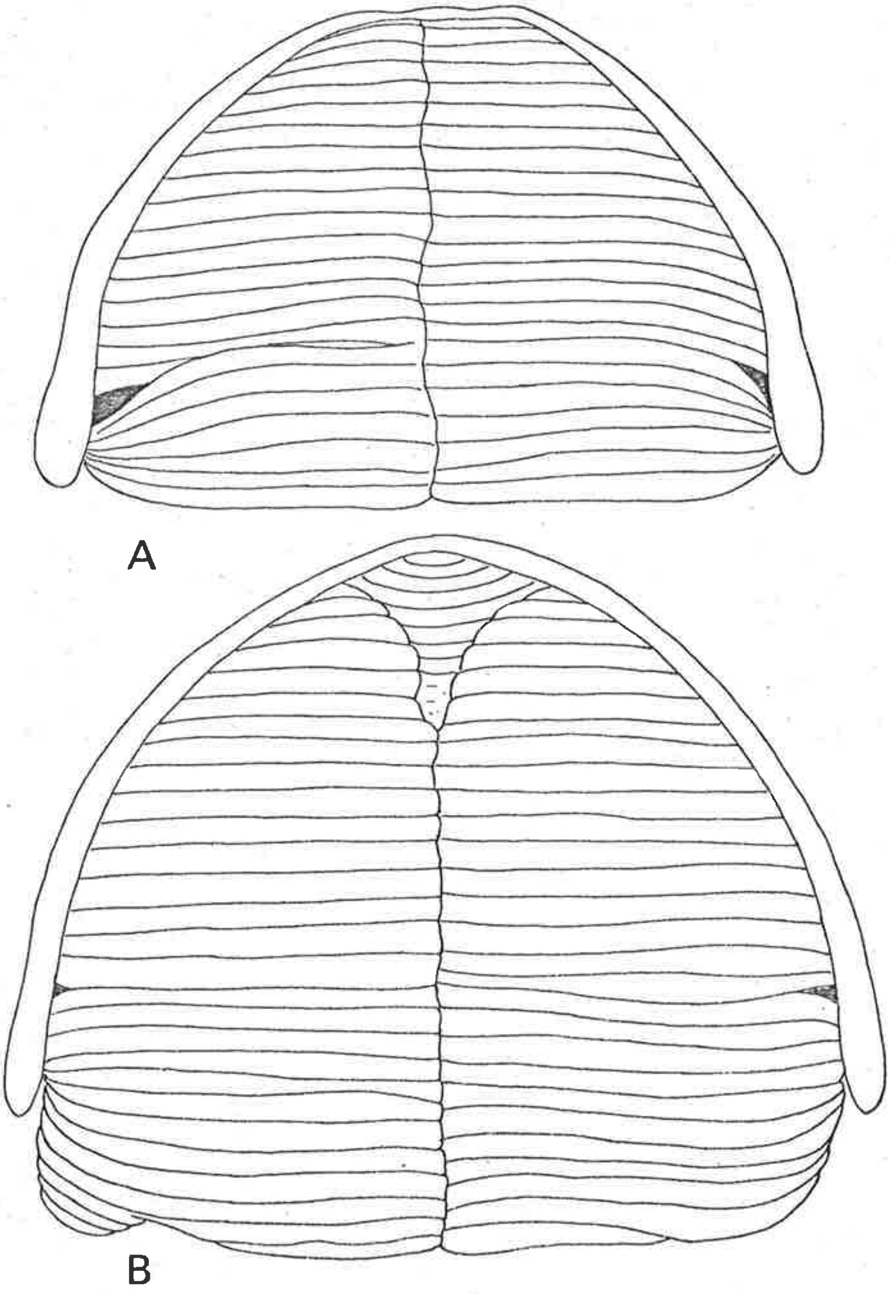
In *Kyarranus* the submentalis is of moderate size and very broadly oval in shape. The intermandibularis is composed of a single sheet of fibres, but the orientation is rather unusual. In the anterior one-third of the muscle they curve anteromedially and attach upon the posterior margin of the submentalis. The more posterior fibres are transversely directed.

Lechriodus has a moderately large submentalis whose posterior border is underlain by transversely directed fibres of the intermandibularis. The latter muscle bears a median aponeurosis. The interhyoideus is poorly developed, not extending posteriorly beyond the postarticular extremities of the mandibles. Vocal sacs are present in *L. fletcheri* and *L. papuanus*, extending above the interhyoideus and almost the entire intermandibularis. The apertures are of moderate size and equivalent in length to approximately one-third of the length of the mandible. The vocal sac is absent in *L. platyceps*.

The interhyoideus is well developed, and the vocal sac extends above the entire interhyoideus and intermandibularis. The vocal sac apertures are slit-like and in length equivalent to approximately one-quarter of the length of the mandible.

The large, broad, oval and araphic submentalis of *Limnodynastes* is obscured from the ventral aspect by the anterior fibres of the

FIGURE 15: Superficial mandibular musculature.
A = *Heleioporus inornatus*
B = *Limnodynastes tasmaniensis*



intermandibularis. The extent of the submentalis so obscured varies from species to species, with the extremes represented by *L. dumerili* and *L. spenceri*. In the former species the submentalis is largely hidden, with simply a V-shaped medial area exposed (Fig. 15B), whereas in the latter the visible portion is larger and almost semicircular. This difference is accompanied by differences in the orientation of the most anterior fibres of the intermandibularis, the *dumerili* condition reflecting a noticeable trend towards anteromedial orientation which is lacking in *spenceri*.

The intermandibularis bears a median raphe and the interhyoideus has a median postmandibular lobe most highly developed in some specimens of *spenceri*, where it underlies the anterior portion of the pectoral musculature.

The vocal sac is large, extending above the interhyoideus and intermandibularis. The apertures extend for almost the entire length of the intermandibularis.

In *Mixophyes* the submentalis is large, ovoid and araphic. The fibres of the intermandibularis are transversely directed and anteriorly underlie, and so obscure from ventral view, the posterior margins of the submentalis. The greater portion of the intermandibularis bears a median raphe, but there is a small aponeurosis located at the posterior extremity of the muscle.

The interhyoideus is of moderate size, rarely extending beyond the postarticular extremities of the mandibles. The vocal sac extends above the interhyoideus and laterally above the intermandibularis. The vocal sac apertures are long, extending for approximately one-third of the length of the mandibles.

In *Notaden* the submentalis is an elongate, ovoid shape which is rather compressed transversely. The intermandibularis is large and bears a median raphe; anteriorly it lies ventral to the posterior one-half of the submentalis.

The interhyoideus is vast, with bilobular and greatly convoluted supramandibular lobes. The fibres forming these lobes arise further proximally on the anterior cornua than is customary in Australo-Papuan genera. The vocal sac lies above the interhyoideus, extending into the lateral lobes and anteriorly above the intermandibularis. The vocal sac apertures are long, extending for a distance equivalent to one-third of the length of the mandibles.

Two separate segments of the submentalis are distinguishable in *Philoria:* a narrow anterior portion arising from the mento-meckelian bones (prominent in this genus), and a larger and broader posterior segment arising from the adjacent dentaries.

The anterior fibres of the intermandibularis pass anteromedially and underlie the posterior portion of the submentalis. The intermandibularis is of moderate size and bears a median raphe. The interhyoideus bears a prominent, median, unilobular, posterior lobe. The vocal sac lies above the interhyoideus and the posterior half of the intermandibularis. The vocal sac apertures are large, extending for a distance equivalent to approximately one-third of the length of the mandible.

Sub-Family: Heleophryninae

In *Heleophryne* the submentalis is of moderate size, ovoid and araphic. The intermandibularis consists of a single sheet of transversely orientated fibres meeting at a median raphe. The interhyoideus anteromedially underlies the intermandibularis, but this is the only noteworthy feature of this muscle.

The specimens examined are females. The only data on vocal sacs are Lynch's (1971) statement that they are median and subgular.

Sub-Family: Ceratophryinae

In *Ceratophrys* the submentalis is of moderate size, ovoid and araphic. The intermandibularis is a simple sheet of fibres meeting at a median raphe, and the interhyoideus rather poorly developed, posteriorly not extending beyond the postarticular extremities of the mandibles.

The only specimen available for study is a female. Lynch (1970) states that vocal sacs occur in this genus.

Sub-Family: Elosiinae

The submentalis of *Hylodes* is small, oval and araphic. The customary element of the intermandibularis is composed of transversely orientated fibres meeting at a median raphe. There is a supplementary muscle of the apical type lying ventral to the customary sheet. It arises from the medial surface of the mandible adjacent to the submentalis. Its fibres pass posteromedially and attach upon the median raphe of the customary sheet.

The interhyoideus is poorly developed and does not extend posteriorly beyond the postarticular extremities of the mandibles. The vocal sac lies above the interhyoideus and intermandibularis, and the apertures are elongate slits equivalent in length to approximately one-third of the length of the mandibles.

Sub-Family: Leptodactylinae

In *Leptodactylus* the submentalis is small, ovoid and araphic. The intermandibularis is exceptionally thin and anteriorly bears a small, median aponeurosis (detectable only by selective staining of muscles). The interhyoideus is poorly developed and does not extend posteriorly beyond the posterior extremities of the mandibles.

Data on vocal sacs from Lynch (1971) indicate that they vary from species to species: "males with median subgular or paired lateral vocal sacs or none."

The submentalis of *Pseudopaludicola* is small, ovoid and araphic. The customary element of the intermandibularis is very thin and bears a median raphe. There is a supplementary muscle arising from the medial surface of the anterior one-third of the mandible. It is extremely slender and passes anteromedially adjacent to the mandible to attach upon the ventral surface of the submentalis.

The intermandibularis is moderately well developed, with a median, and slightly bilobular, posterior margin extending slightly beyond the posterior extremities of the mandibles. The vocal sac lies above the interhyoideus and intermandibularis, and the apertures are slits equivalent in length to one-quarter of the length of the mandible.

Sub-Family: Telmatobiinae

In *Cycloramphus* the submentalis is of moderate size, ovoid and araphic. The intermandibularis is a simple sheet of fibres meeting at a median raphe. In *C. dubius* they underlie the posterior portion of the submentalis, whereas in *C. asper* there is no such anterior occupation. In both species examined the interhyoideus is poorly developed and does not extend beyond the postarticular extremity of the mandibles. The vocal sac lies above the interhyoideus and the intermandibularis, and the vocal sac apertures are slits extending for approximately one-quarter of the length of the mandibles.

The submentalis of *Eleutherodactylus* is of moderate size, ovoid and araphic. The intermandibularis is a simple sheet, and the only noteworthy feature is that the most anterior fibres are orientated anteromedially. The interhyoideus is poorly developed and does not extend posteriorly beyond the postarticular extremities of the mandibles. The vocal sac is situated above the interhyoideus and the posterior two-thirds of the intermandibularis, and the vocal sac apertures are slits extending for approximately one-quarter of the length of the mandibles.

In *Thoropa* the submentalis is of moderate size, ovoid and araphic. The intermandibularis is comparatively thin and bears a rather broad, median aponeurosis occupying the anterior two-thirds of the muscle. The interhyoideus is moderately well developed, extending posteriorly slightly beyond the postarticular extremities of the mandibles. The vocal sac lies above the interhyoideus and the posterior one-half of the intermandibularis, except the median portion, where it does not occupy the aponeurotic area. The vocal sac apertures are slits equivalent in length to approximately one-quarter of the length of the mandible.

Hylactophryne and *Ischnocnema* have a moderate, araphic submentalis. The intermandibularis lacks supplementary elements. The most anterior of the fibres of the intermandibularis attach anterolaterally upon the ventral surface of the submentalis. The interhyoideus lacks pronounced posteromedial development, but the single representatives of each genus available is a female, hence such development associated with presence of the vocal sac cannot be excluded.

FAMILY: MICROHYLIDAE

Parker (1934) reviewed this family and recognised forty-three genera and one hundred and eighty-five species. At least two hundred and forty species are now recognised, but the sub-familial disposition of many genera has been seriously questioned by Savage (1973). The major centres of the family are New Guinea and Madagascar. Of the genera included here the New Guinea ones have received close attention. Mehely (1901) has illustrated but not described the musculature of *Hylophorbus (Metopostira)* and Beddard (1908c, 1908a) has described *Hemisus* and *Breviceps* in detail.

Sub-Family: Asterophryinae

The submentalis of *Asterophrys* is a small, triangular muscle arising from the medial surface of the mento-meckelian bone (Fig. 16A).

The customary element of the intermandibularis bears a median aponeurosis along its entire length. The aponeurosis is very broad anteriorly. A supplementary element arises from the ventral surface of the mandible near its posterior extremity, passes forwards parallel to the mandible and attaches upon the most anterior fibres of the intermandibularis.

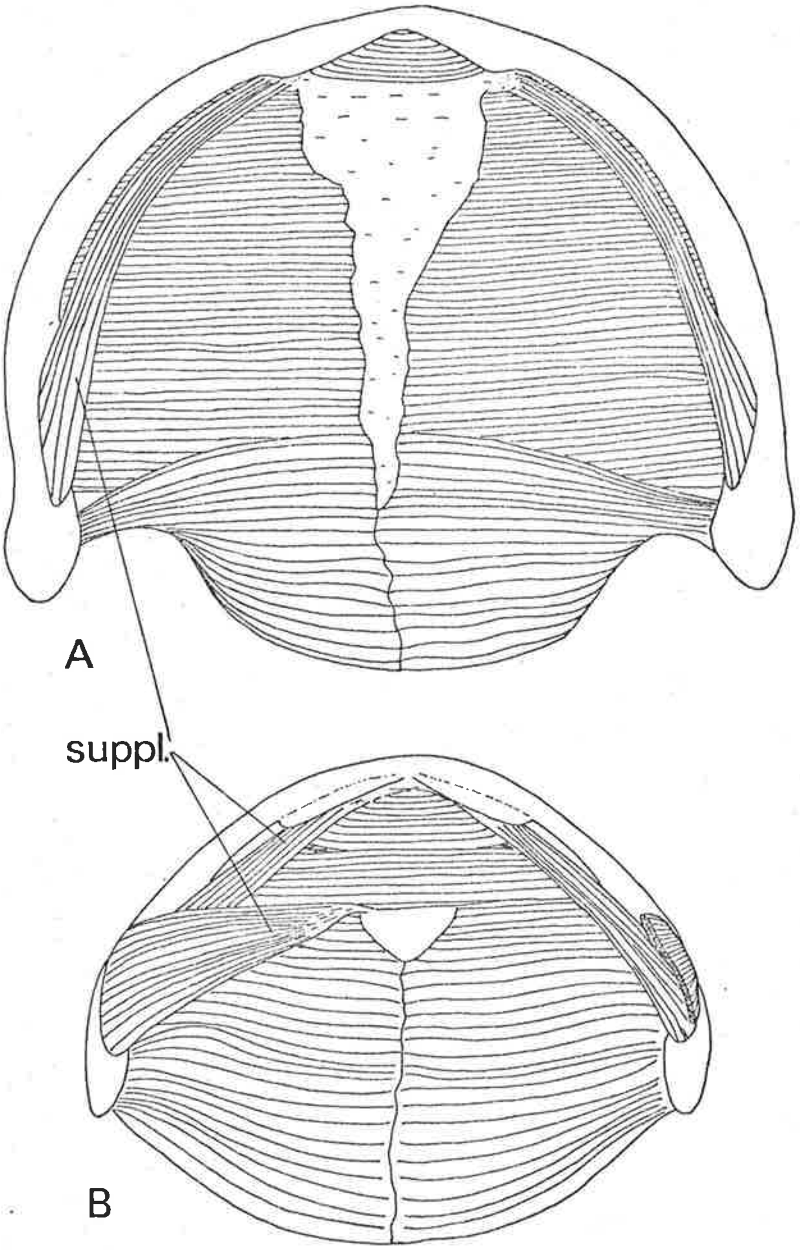
Anteriorly the interhyoideus partly underlies the intermandibularis and posteriorly forms a small median lobe. The anterior one-third of the muscle bears a median aponeurosis.

The only specimen of this monotypic genus available for dissection is a female, so that no data are obtainable on the vocal sac.

In *Barygenys* the submentalis is a moderately sized, araphic, triangular-shaped muscle between the mento-meckelian bones (Fig. 16B).

There are four additional muscle elements that may all represent portions of the intermandibularis. Progressing posteriorly according to their site of origin from the mandible, two arise from the medial surface. The first is a rectangular slip arising from a position immediately

FIGURE 16: Superficial mandibular musculature.
A = *Asterophrys turpicula*
B = *Barygenys atra*



suppl. = supplementary elements of M. intermandibularis.
Note most superficial element on left side of *Barygenys* removed.

posterior to the site of origin of the submentalis. The customary muscle is posteriorly adjacent to it. Anteriorly the fibres are medially arrested, producing an aponeurosis in the shape of an inverted cone.

There are two ventral superficial elements, of which the deepest is in the form of a thin, elongate slip arising from the ventral surface of the mandible near its posterior extremity. It passes anteromedially along the medial margin of the mandible and attaches, via a slender ligament, upon the lateral margins of the submentalis. The most superficial muscle arises from the ventral, or from the ventral and lateral surfaces of the mandible, superficial to the site of origin of the muscle described above. The ventral site occurs in *B. cheesmanae*, but in the figured species (*B. atra*) a portion of the muscle in part overlies the site of origin of the adductor mandibulae externus superficialis. The muscle attaches upon the superior margin of the aponeurosis of the customary element via a very slender ligament. Thus, from its broad site of origin, the muscle tapers to form a triangular shape, with the most anterior fibres orientated transversely and the most posterior anteromedially.

The interhyoideus is moderately well developed with a unilobular posterior lobe.

The vocal sac is situated above the interhyoideus, and the vocal sac apertures are broadly oval spaces located adjacent to the mandible, near the posterior border of the customary element of the intermandibularis.

The submentalis of *Hylophorbus* is small, obtusely triangular and araphic (Fig. 17). The customary sheet of the intermandibularis is a large, thin muscle of transversely orientated fibres and bears an elongate posteriorly-tapering aponeurosis for almost its entire length. A small, supplementary, anterolateral element arises from the medial surface of the anterior portion of the mandible and attaches upon the ventrolateral margin of the submentalis.

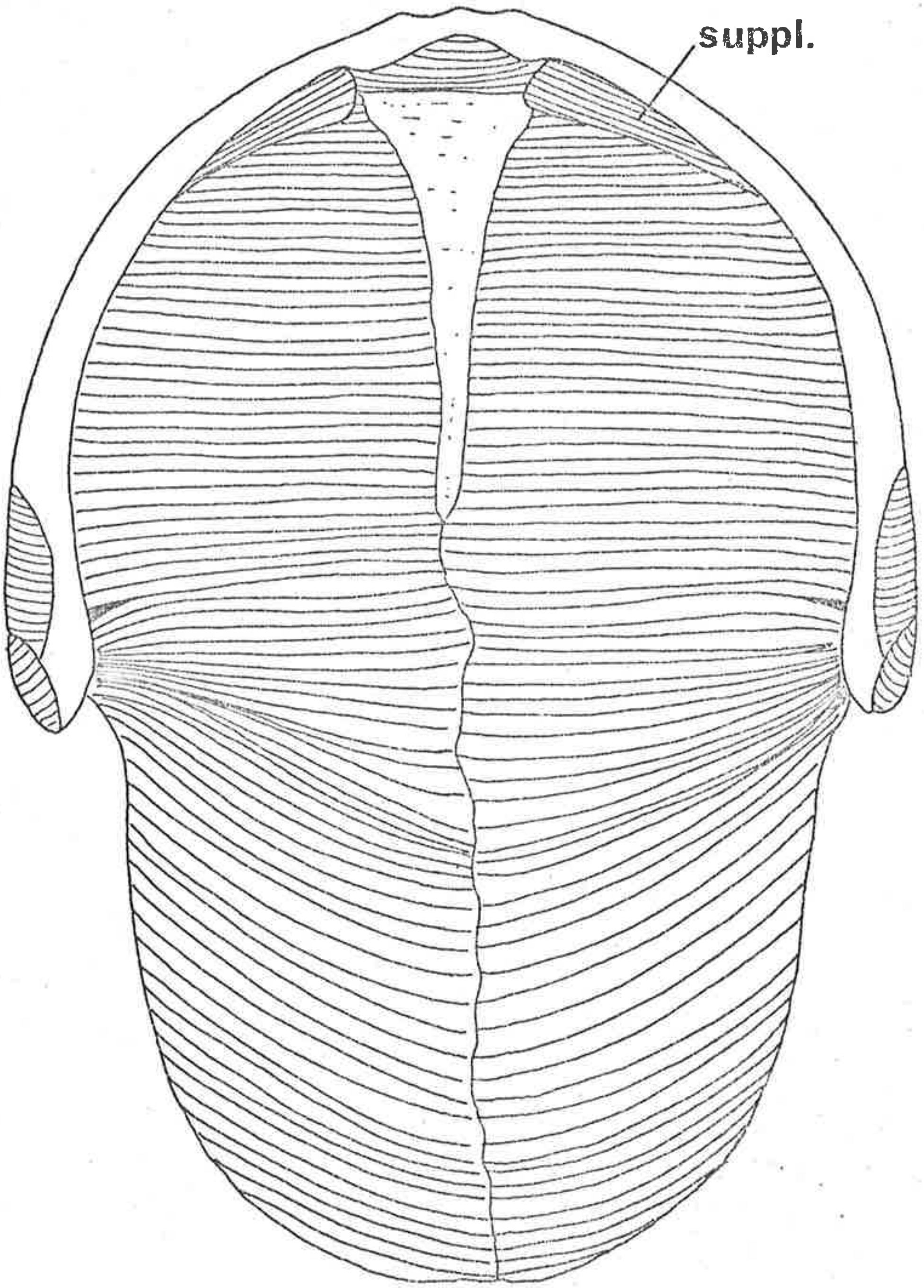
The interhyoideus extends posteriorly into a vast unilobular lobe partly overlying the ventral pectoral muscles. The vocal sac is confined to the interhyoideus, and the vocal sac apertures are oval holes, inclined slightly anteromedially, bordering the mandible near the posterior extremity of the intermandibularis.

The submentalis of *Pherohapsis* is an oval, araphic muscle of moderate size (Fig. 18). The intermandibularis bears a broad median aponeurosis anteriorly. The most anterior fibres of the intermandibularis diverge from the remainder in passing anteromedially to attach upon the lateral ends of the ventral surface of the submentalis.

The interhyoideus is a vast muscle. Anteriorly the fibres pass anteromedially and underlie the intermandibularis; posteriorly the muscle develops into a large, unilobular lobe.

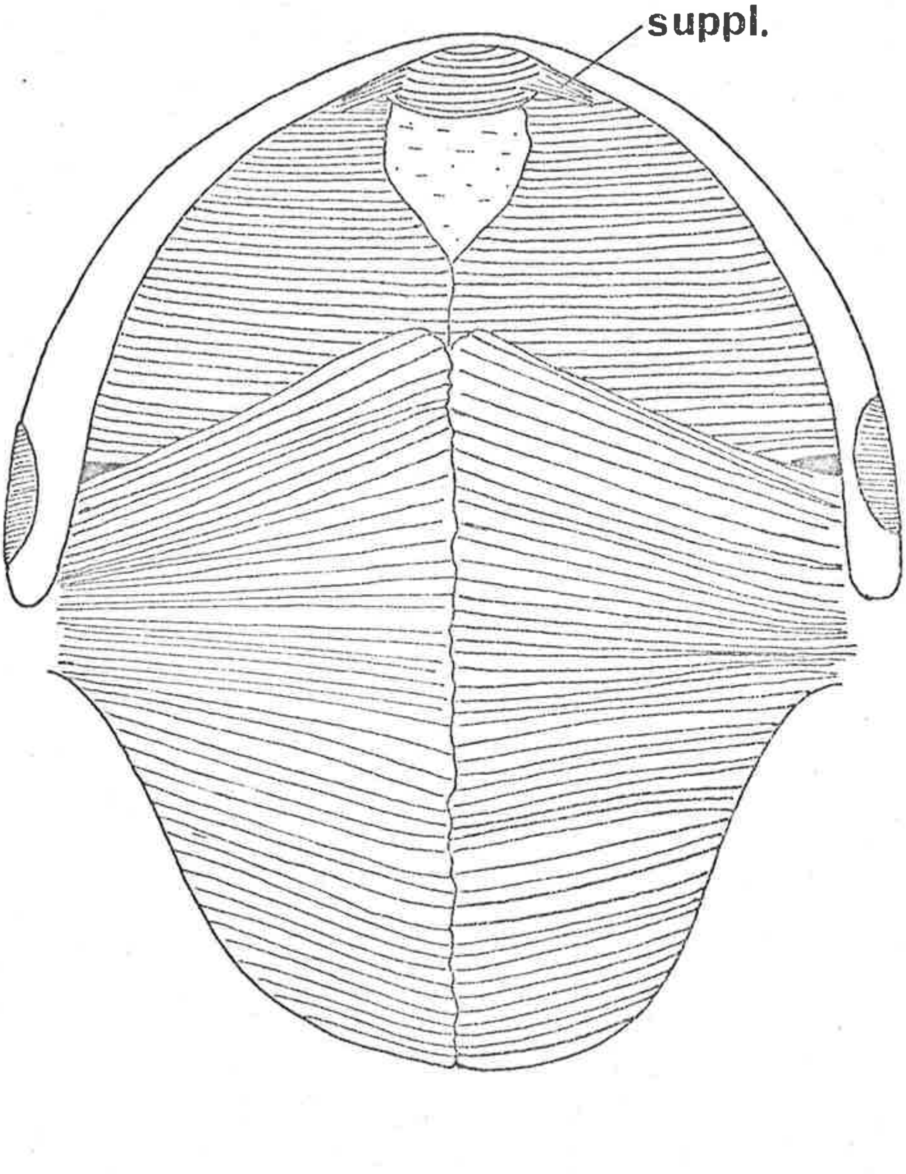
The vocal sac lies above the interhyoideus and greater portion of

FIGURE 17: Superficial mandibular musculature of *Hylophorbus ocellata*.



suppl. = supplementary element of M. intermandibularis.

FIGURE 18: Superficial mandibular musculature of *Pherohapsis menziesi*.



suppl. = supplementary element of M. intermandibularis.

the intermandibularis. The vocal sac apertures are holes extending from the mandible to the cornua adjacent to the posterior end of the intermandibularis. Each aperture length is equivalent to approximately one-quarter of the mandible.

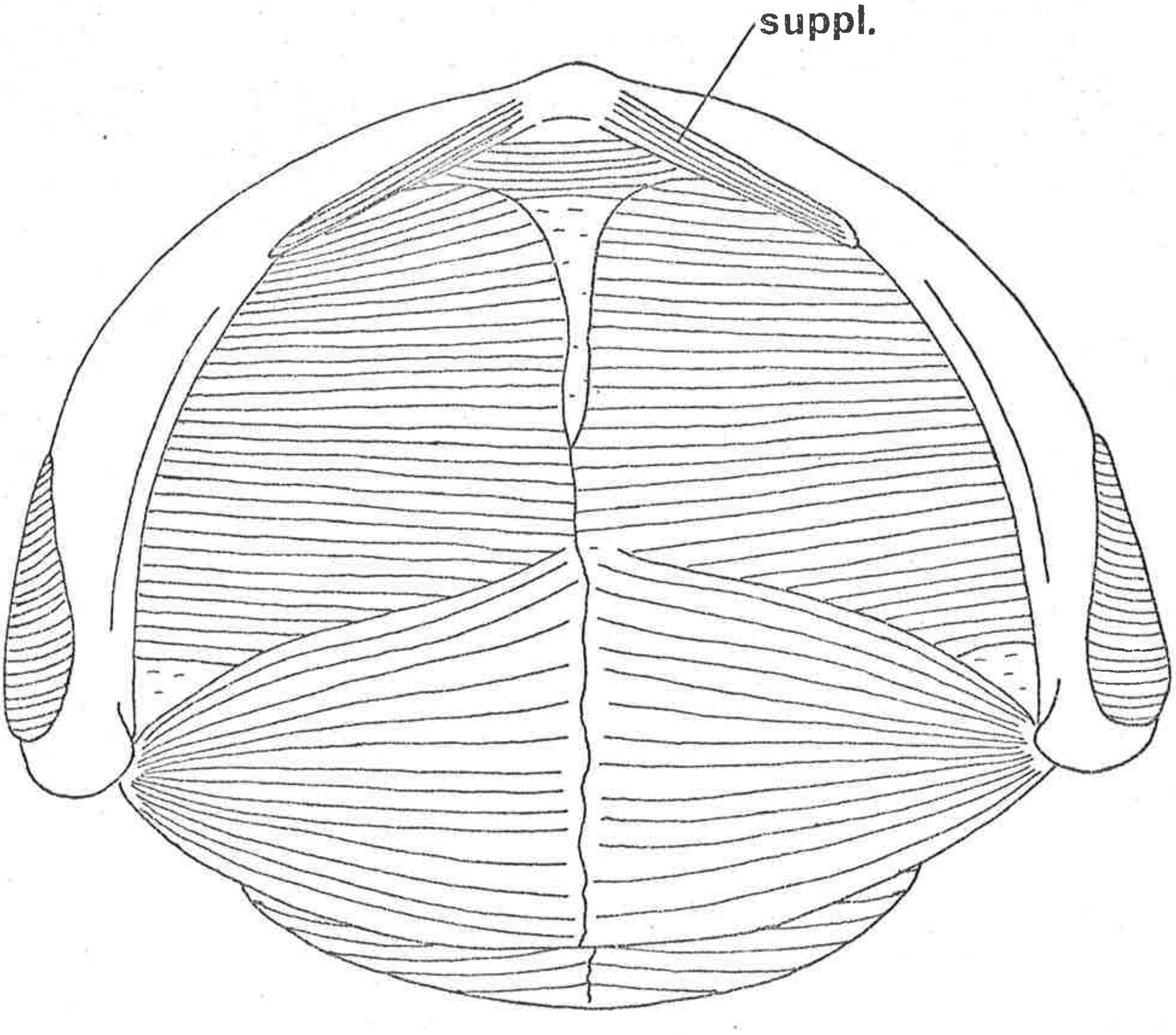
Phrynomantis has a submentalis which is elongate and araphic (Fig. 19). The customary sheet of the intermandibularis is arrested anteromedially, bearing an elongate aponeurosis which extends posteriorly for approximately one-half of the length of the muscle. The most anterior fibres of this sheet underlie the posterolateral margin of the submentalis. A small, slender supplementary sheet of the intermandibularis arises from the medial surface of the mandible, passes anteromedially over the site of origin of the submentalis and attaches upon the ventral surface of the mandible on each side of the symphysis.

The interhyoideus anteriorly underlies the posterior one-third of the intermandibularis and attaches at the median raphe of that muscle. Posteriorly the interhyoideus forms a moderately sized unilobular lobe, commonly bearing a single transverse fold near its posterior extremity.

The vocal sac is confined to the area above the interhyoideus. The vocal sac apertures are slit-like in *P. humicola*, *P. lateralis*, *P. robusta* and *P. wilhelmana*, whereas they are gaping holes in the mouth floor in *P. personata* and *P. stictogaster*.

In *Xenobatrachus* the submentalis is large and araphic (Fig. 20B). The customary element of the intermandibularis is a thin sheet of

FIGURE 19: Superficial mandibular musculature of *Phrynomantis stictogaster*.



suppl. = supplementary element of M. intermandibularis.

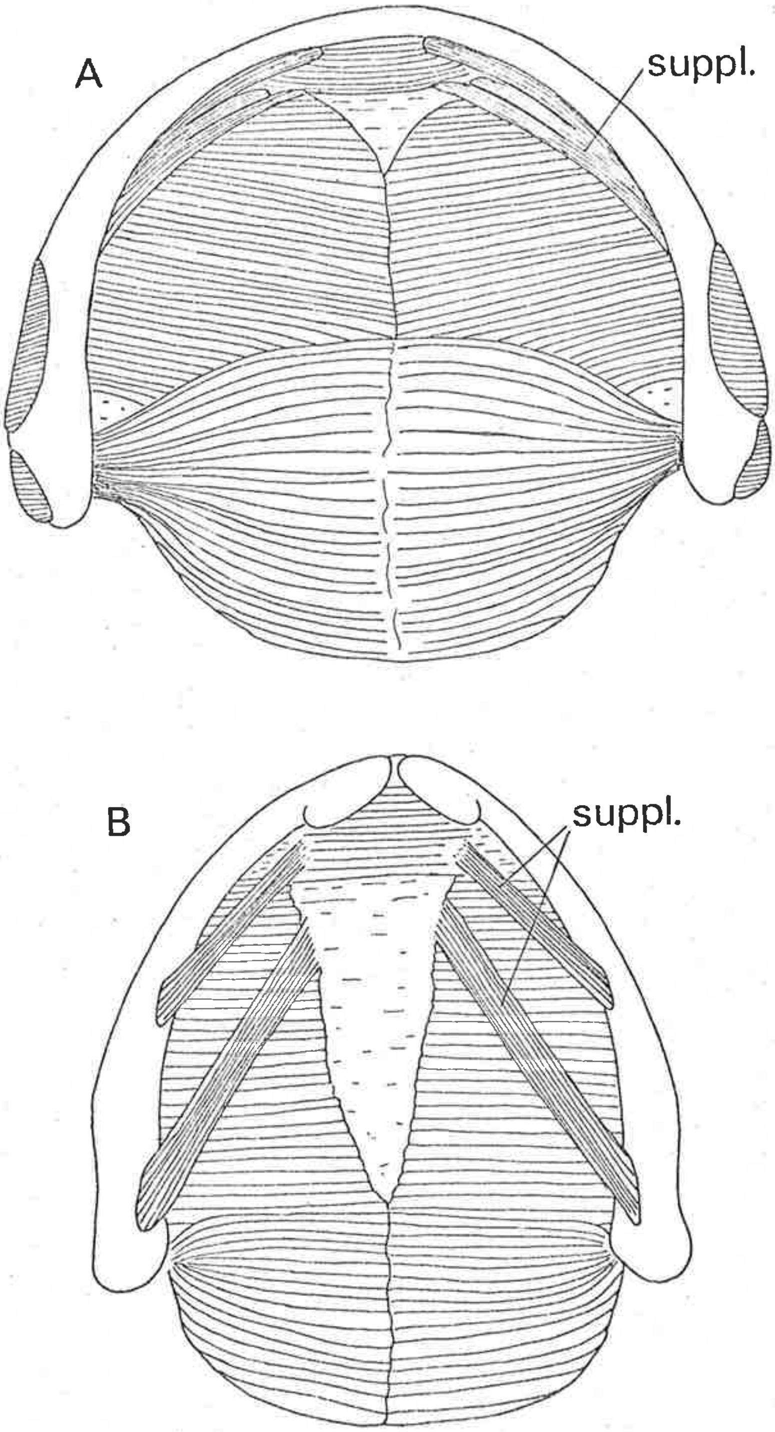
transversely orientated fibres medially separated by an aponeurosis which is broad anteriorly and gradually tapers posteriorly to exhibit a triangular shape. Two separate supplementary elements of the intermandibularis occur in this genus, each constituting an elongate, rectangular sheet. The most anterior arises from the medial surface of the median portion of the mandible, passes anteromedially and attaches upon the ventral surface of the submentalis. The posterior arises from the ventral surface of the mandible, passes anteromedially and attaches upon the customary element of the intermandibularis adjacent to its median aponeurosis.

Xenobatrachus rostratus and *X. mehelyi* differ from the figured species (*X. obesus*) to the extent that the posterior of the two supplementary sheets is considerably broader.

The interhyoideus is of moderate size and is developed posteriorly into a unilobular lobe. The vocal sac is confined to the interhyoideus. The vocal sac apertures are oval in shape and located adjacent to the mandible above the posterior extremity of the intermandibularis.

The submentalis of *Xenorhina* is a slender, elongate, araphic muscle (Fig. 20A). The customary element of the intermandibularis is arrested medially forming an inverted triangular aponeurosis. There is a supplementary element of the intermandibularis arising from the medial surface of the mandible, at a position slightly within the posterior half of the bone. This element passes forward adjacent to the medial surface

FIGURE 20: Superficial mandibular musculature.
A = *Xenorhina doriae*
B = *Xenobatrachus obesus*



suppl. = supplementary elements of M. intermandibularis.

of the mandible and divides into three distinct heads. The medial and central of these heads attach via slender ligaments to the posterior fibres of the submentalis, whereas the lateral passes further anteriorly to attach upon the superior segment of the submentalis.

The interhyoideus is a moderately sized muscle anteriorly underlying the intermandibularis. Posteriorly it develops into a unilobular lobe.

The vocal sac is confined to the interhyoideus. The vocal sac apertures are in the form of gaping holes.

Sub-Family: Brevicipitinae

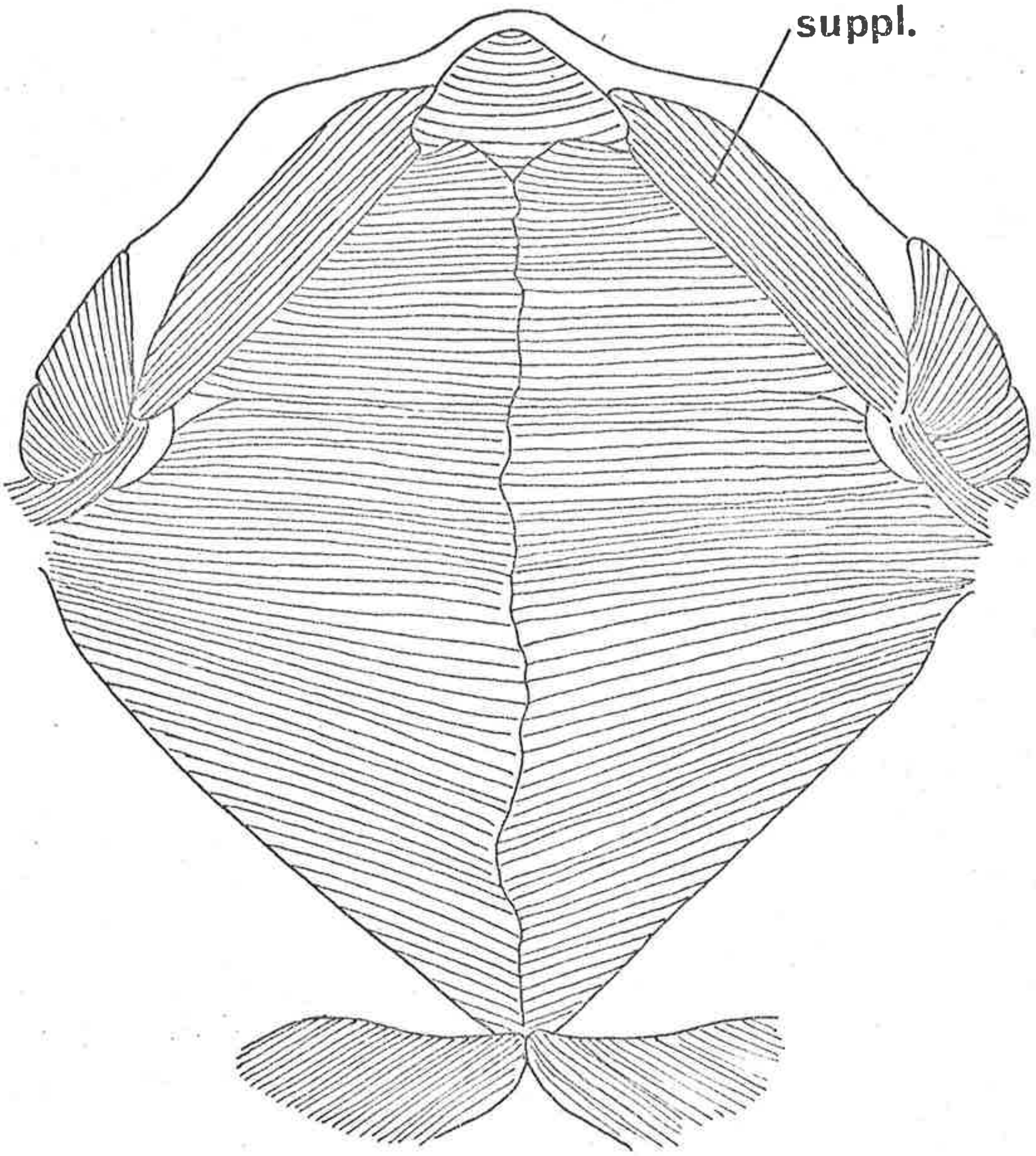
In *Breviceps* the submentalis is of moderate size, triangular and araphic (Fig. 21). The intermandibularis lacks a median aponeurosis; the most anterior fibres of this muscle pass slightly rostral and attach upon the ventral surface of the submentalis, but the remainder are transversely orientated.

A longitudinal, supplementary muscle of unknown identity arises from the ventral surface of the mandible beneath the site of the jaw articulation, passes anteromedially ventral to the mandible and intermandibularis, and attaches upon the ventral surface of the submentalis.

The interhyoideus is an enormous fan-shaped muscle forming a vast, triangular posterior lobe which, at its posterior extremity, attaches to the proximal tip of the sternum.

The vocal sac is situated above the interhyoideus and the posterior

FIGURE 21: Superficial mandibular musculature of *Breviceps poweri*.



suppl. = supplementary element of M. intermandibularis.

portion of the intermandibularis. The vocal sac apertures are slits adjacent to the mandible and with a length equivalent to approximately one-quarter of the length of the mandible.

Sub-Family: Cophylinae

The submentalis of *Rhombophryne* is a large, ovoid, araphic muscle. In association with the exceptionally obtuse mandibles, the fibres of the intermandibularis pass posteromedially and are separated medially by a broad aponeurosis. The intermandibularis is differentiated anteriorly by development of anterolateral elements which, as a consequence of the shape of the mandibles, are inclined only slightly from a transverse path and attach upon the ventral surface of the submentalis.

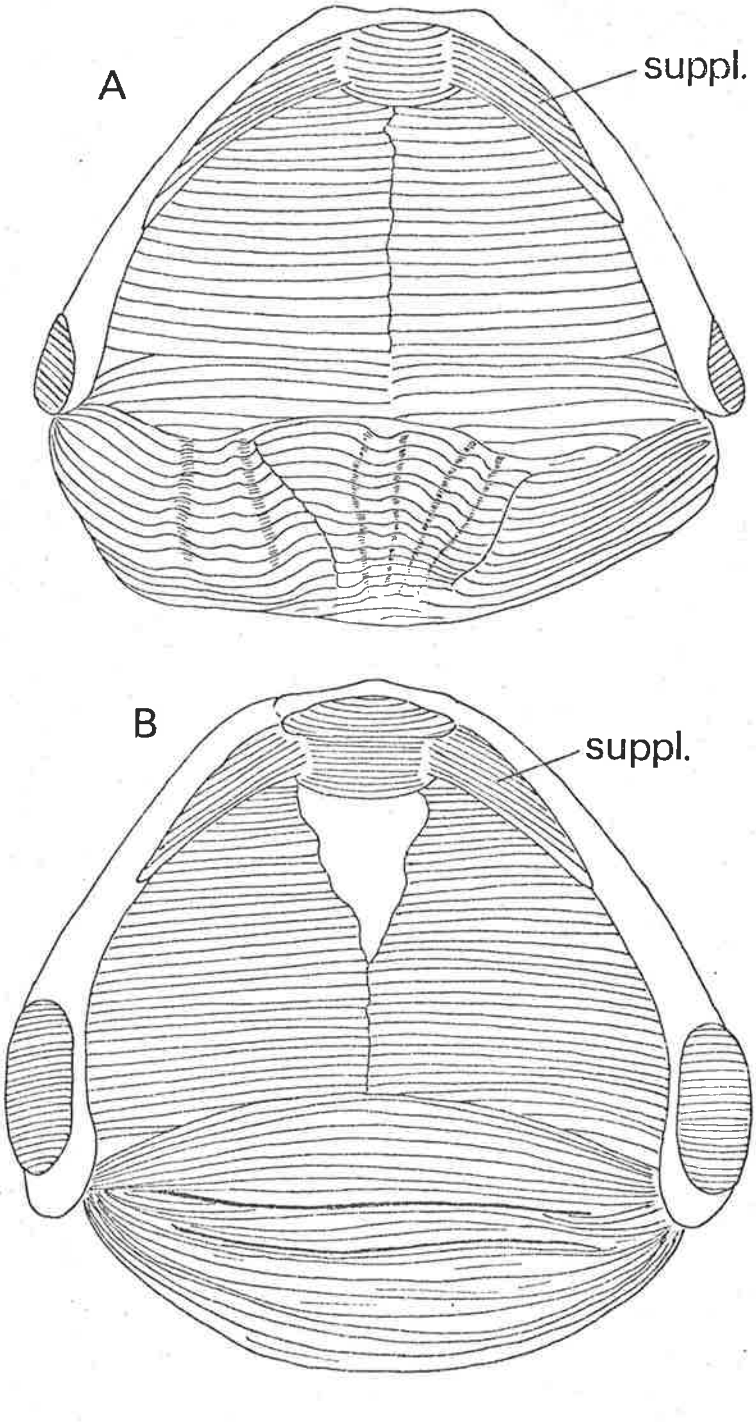
The interhyoideus is a vast muscle anteriorly underlying the intermandibularis and anteromedially approaching the submentalis. Posteriorly it extends into a large, unilobular lobe extending far beyond the extremities of the mandibles.

The vocal sac apertures are short slits above the posterior extremity of the intermandibularis, and the vocal sac lies above the interhyoideus.

Sub-Family: Microhylinae

The submentalis of *Kaloula* is of moderate size, oval and araphic (Fig. 22A). The intermandibularis is well developed, with a transverse orientation of the fibres and no median aponeurosis. There is a supplementary element of the intermandibularis arising from the ventrolateral, lingual margin of the mandible and attaching upon the ventral surface of

FIGURE 22: Superficial mandibular musculature.
A = *Kaloula picta*
B = *Cophixalus riparius*



suppl. = supplementary elements of M. intermandibularis.

the submentalis. The length of this supplementary element is equivalent to approximately one-half of the length of the mandible.

In *K. conjuncta negrosensis* the interhyoideus anteromedially intrudes slightly into the area normally occupied by the intermandibularis, but the border of these muscles is contiguous and there is no overlap of the respective sheets. In *K. picta* there is no such intrusion.

Posteriorly the interhyoideus of *Kaloula* forms a unilobular lobe, ventrally folded and pleated. The vocal sac is a vast structure extending above the intermandibularis and the interhyoideus, and the vocal sac apertures are elongate slits located above the intermandibularis and equivalent in length to approximately one-third of the length of the mandible.

Sub-Family: Sphenophryninae

Throughout the sub-family the submentalis is of moderate size and araphic (Fig. 22B). In the largest species of all genera the muscle has two separate bodies, the anterior arising from the medial surface of the mento-meckelian bones and the posterior from the anterior extremities of the dentaries. The mento-meckelian bones are not so prominent in the smaller species and no such division of the submentalis is detectable in them.

The intermandibularis is a thin sheet of fibres bearing a broad, elongate, median aponeurosis. The intermandibularis is differentiated by the presence of lateral elements. The site of origin of these elements on the medial surface of the mandibles varies from a site above the posterior margin of the intermandibularis (*C. darlingtoni*, *C. ornatus*, *C. oxyrhinus*) to a position somewhat more anterior and corresponding to the midsection of the mandible (in the remaining *Cophixalus* species and all *Genyophryne*, *Oreophryne* and *Sphenophryne* species). In each species, however, the anterior margin of the attachment of the muscle is always upon the lateral margins of the submentalis.

The interhyoideus anteriorly slightly underlies the posteromedial portion of the intermandibularis. Posteriorly the interhyoideus develops into a unilobular median lobe frequently bearing inverted transverse folds.

The vocal sac is confined to the area above the interhyoideus. The vocal sac apertures are slit-like or oval, and are located adjacent to the mandible near the posterior extremity of the intermandibularis. They are usually equivalent in length to about one-fifth of the length of the mandible.

FAMILY: PELODYTIDAE

Pelodytes of Europe is the only living pelodytid genus.

The submentalis of *Pelodytes* is small, elongate and araphic. The intermandibularis consists of a single sheet of thin, transversely-orientated fibres bearing a median raphe. The interhyoideus is poorly developed and does not extend beyond the postarticular extremities of the mandibles.

The vocal sac is situated above the entire interhyoideus and intermandibularis. The vocal sac apertures are elongate slits extending for a distance equivalent to approximately one-third of the total length of the mandibles.

FAMILY: RANIDAE

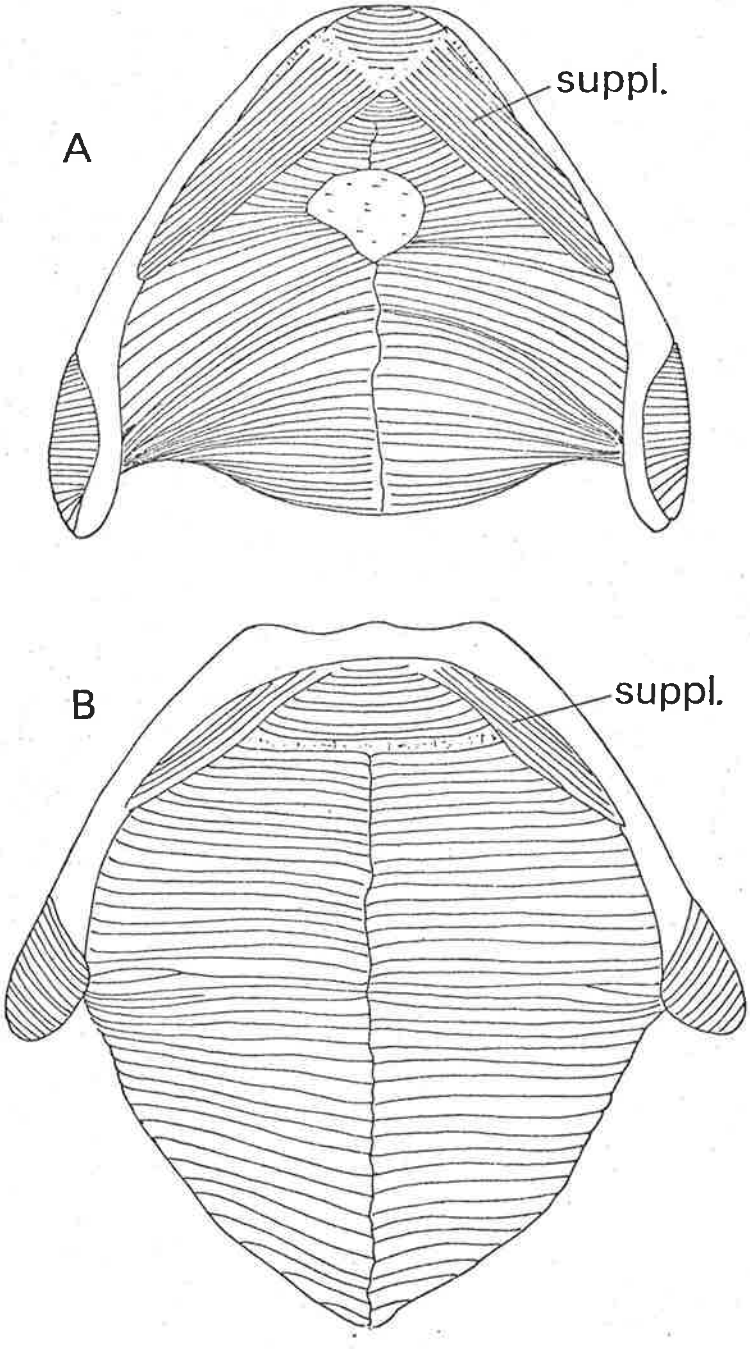
Delimiting this vast and widely distributed family constitutes one of the major unresolved, systematic problems. Several hundred species are currently recognised, of which *Rana* is the most diverse and widespread. I have been unable to find a reasonable sub-familial scheme. Previous contributions on musculature are confined to accounts of *Rana* species listed in the literature survey.

The submentalis of *Arthroleptis* (Fig. 23A) is extremely large, ovoid and araphic. The customary element of the intermandibularis is reduced posteriorly and bears a small, median aponeurosis. A supplementary element of the intermandibularis arises from the ventral surface of the mandible, passes forward and attaches upon the ventral surface of the submentalis.

The interhyoideus is slightly developed anteriorly and posteriorly. The three specimens examined are all females, so that no data are available about the vocal sac.

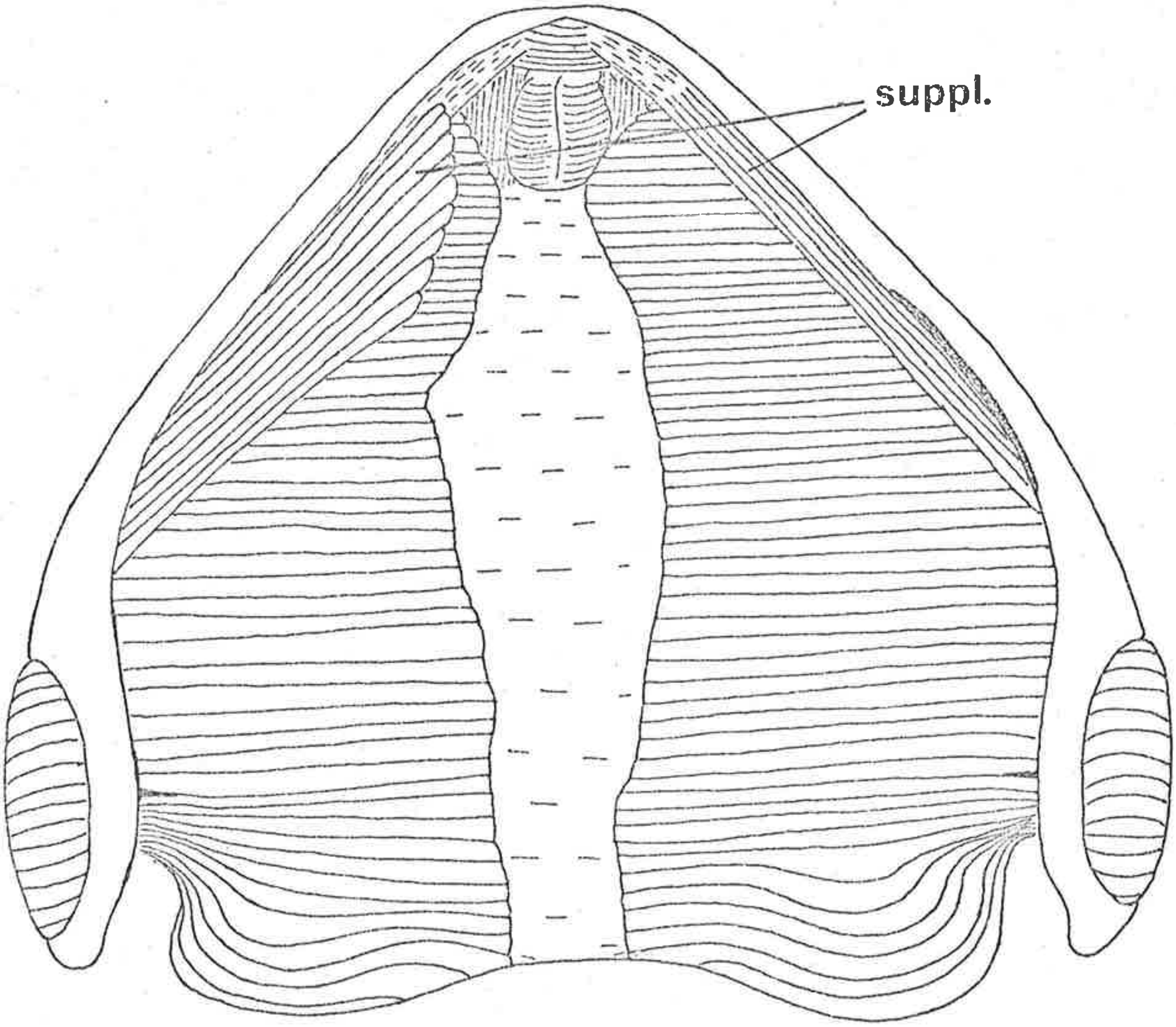
In *Ceratobatrachus* (Fig. 24), *Discodeles* and *Palmatorappia* the submentalis is small, elongate and araphic. The customary element of the intermandibularis is extremely thin and arrested anteriorly, so creating a broad gap between the posterior border of the submentalis and the

FIGURE 23: Superficial mandibular musculature.
A = *Arthroleptis stenodactylus*
B = *Hemisus marmoratum*



suppl. = supplementary elements of M. intermandibularis.

FIGURE 24: Superficial mandibular musculature of *Ceratobatrachus guentheri*.



suppl. = supplementary elements of M. intermandibularis.
Note most superficial element of left side removed.

anterior border of the intermandibularis. The medial portion of this gap is occupied by the ventral surface of the genioglossus. The intermandibularis bears a broad median aponeurosis extending for the entire length of the muscle in *Ceratobatrachus* and *Discodeles*, and for three-quarters of its length in *Palmatorappia*.

There are two supplementary elements of which the deep is a very narrow, elongate sheet arising from the medial surface of the mandible and passes anteromedially adjacent to the mandible. In *Ceratobatrachus* it attaches via a long slender tendon upon connective tissue on the ventral surface of the genioglossus, in *Discodeles* directly upon the ventral surface of the submentalis, and in *Palmatorappia* by a short tendon to the ventral surface of the submentalis. The superficial element arises at a similar site on the mandible, but is a broad, fan-shaped muscle which passes anteromedially and attaches upon the customary element of the intermandibularis.

The interhyoideus is slightly developed posteriorly with a bilobular posterior border. In *Ceratobatrachus* and *Discodeles* the interhyoideus medially bears a broad aponeurosis continuous with that of the intermandibularis, whereas *Palmatorappia* lacks an aponeurosis.

The vocal sac of *Ceratobatrachus* and *Discodeles* consists of two discrete, submandibular pouches which do not communicate and are medially separated by connective tissue. They extend above the interhyoideus and posterior one-quarter of the intermandibularis. *Palmatorappia* differs in having a single pouch. In all genera the vocal sac apertures are circular holes in the mouth floor located near the posterior limit of the intermandibularis. The diameter of the apertures in each species is equivalent to approximately one-tenth of the length of the mandible.

In *Phrynobatrachus* the submentalis is small, slender and araphic. The customary element of the intermandibularis medially is separated from the submentalis by the genioglossus and bears an elongate, anteromedial aponeurosis. A supplementary element of the intermandibularis arises from the medial surface of the mandible, passes anteromedially and attaches upon the genioglossus anteriorly, and the medial extremity of the customary element of the fibres of the intermandibularis. The interhyoideus is a simple sheet of transversely orientated fibres.

The single specimen examined is a female, hence no data are available for the vocal sac.

Platymantis and *Batrachylodes* have a very small, narrow and araphic submentalis. The customary sheet of the intermandibularis is very thin and bears a broad aponeurosis anteriorly. Two supplementary muscles lie ventral to the customary sheet. The deep supplementary muscle is slender, arises from the medial surface of the mandible, passes anteromedially and attaches upon the ventral surface of the genioglossus. The superficial element arises from the ventral surface of the mandible, passes anteromedially ventral to the deep element and attaches partly upon that element and partly upon the median aponeurosis of the customary sheet.

The interhyoideus is a small muscle extending only slightly beyond the postarticular extremities of the mandibles. The vocal sac lies above the posterior half of the customary element of the intermandibularis and above the entire interhyoideus. The vocal sac apertures are extremely short slits adjacent to the jaw articulation, their length equivalent to from one-seventh to one-tenth of the length of the mandible.

Ptychadena has a large and broadly oval, araphic submentalis. The customary sheet of the intermandibularis is a very thin sheet of perfectly transverse fibres bearing an elongate median aponeurosis. There is a supplementary element of the intermandibularis of the apical type arising from the medial surface of the mandible. It passes forwards anteromedially and attaches upon the ventral surface of the submentalis.

The interhyoideus is small and slender and does not extend posteriorly beyond the postarticular extremities of the mandibles. Although the only specimen studied is a female *P. anchietae*, Inger (1956) has described in detail the vocal sac of *P. porosissima*, noting the presence of bilobular, submandibular, dermal evaginations into which the separate lobes of the muscle protrude.

The submentalis of *Pyxicephalus* is extremely small and not visible in ventral view, being completely underlain by the intermandibularis. The intermandibularis lacks any supplementary elements and consists of very large fasciculi meeting at a median raphe.

The interhyoideus is extremely small and partly obscured by the postmandibular lymphatic septum which underlies the lateral segments.

The only specimen available for study is a female, hence no data are available for the vocal sac structure.

The only consistent characteristic of the superficial mandibular musculature of the genus *Rana* is that the submentalis is of moderate size, broadly oval and araphic. Insofar as the intermandibularis is concerned, there is certainly a distinct trend towards anteromedial orientation of the most superficial, ventral fibres attached upon the submentalis, but four variants may be recognised in the species examined:

Variant A: The superficial fibres pass anteromedially with the most lateral lying parallel to the mandible and the medial superficial fibres inclined more markedly anteromedially. Above this mass of fibres there is a slender sheet of fibres forming a separate body and passing anteromedially immediately medial to the mandible. Dorsally to these two components there is a third sheet of fibres directed posteromedially. The species representing this form are: *arfaki*, *grunniens*, *limnocharis*, *tigrina* and *verruculosa*.

Variant B: There is a more marked distinction between the anteromedially orientated fibres and those situated posterior to them in terms of separation from the customary mass. Nevertheless, they do not form a separate element. There is no separate muscle beneath them other than the remainder of the customary element which retains a transverse orientation. Of the species examined the following are representative of this form: *arvalis, catesbeiana, clamata, dalmatina, esculenta* (Fig. 25A), *palustris, temporaria* and *viridis*.

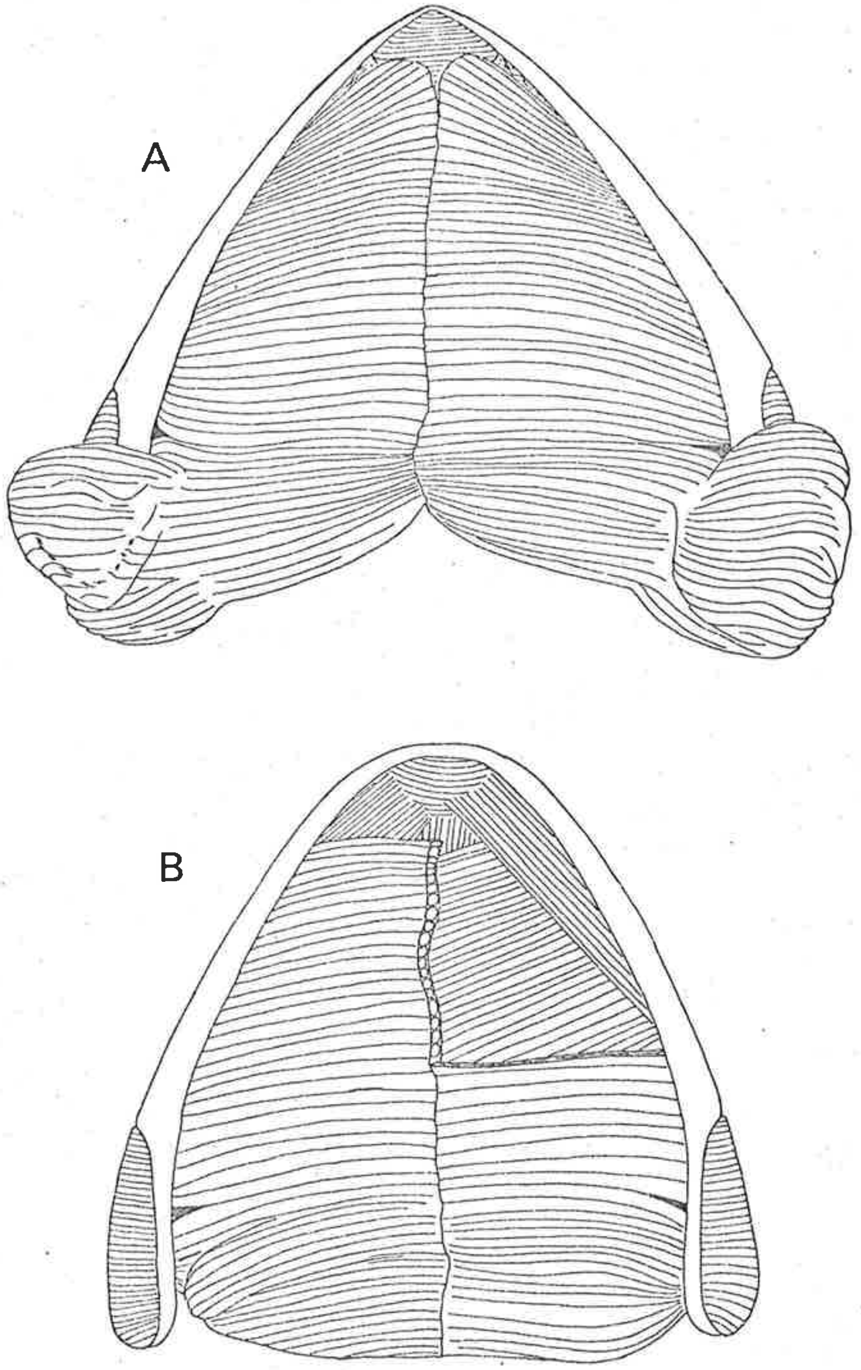
Variant C: The most superficially disposed fibres constitute a distinct, separate, fan-shaped element. The fibres arise from a narrow portion of the mandible. Beneath this element there is located an additional element similar in position to that of Variant A, but narrower. The customary sheet is composed entirely of transversely orientated fibres. The species examined representing Variant C are: *grisea, jimiensis* and *papua novabrittanae*.

Variant D: The most superficial fibres are transversely directed. They are separated from a sheet of posteromedially inclined fibres by a distinct element of anteromedially directed fibres. This variant is represented here by *vitigera* (Fig. 25B).

The interhyoideus is never a vast muscle, trends to increase in size invariably involve localised areas, and in no species does the interhyoideus extend medially much beyond the postarticular extremities of the mandibles. The development of discrete paired lobes is common to many species. These lobes may involve large portion of the muscle as in *vitigera*, or small discrete evaginations associated with evaginations of skin below them as in *esculenta* (Fig. 25A).

As indicated by the nature of the musculature, vocal sacs are largely

FIGURE 25: Superficial mandibular musculature.
A = *Rana esculenta*
B = *Rana vitigera*



Note that left anterior quadrant of M. intermandibularis of *R. vitigera* removed to expose supplementary elements situated dorsal to it.

confined to the area above the interhyoideus. They may be unilobular and submandibular, bilobular and submandibular, or bilobular and supramandibular. The apertures are usually rather small, varying from one-fifth to one-tenth of the length of the mandibles. The smaller apertures are usually quite circular.

The submentalis of *Staurois* is large, broadly oval and araphic. The most striking feature of the intermandibularis is an extremely large, median aponeurosis extending for the entire length of the muscle and narrowest at its anterior and posterior limits. The fibres of the customary element form two separate sheets. The anterior are inclined posteromedially, and the posterior anteromedially, progressively changing their orientation transversely in the latter portion of this component.

Two supplementary muscle sheets lie ventral to the customary sheet. The deepest of these arises via a short tendon from the medial surface of the mandible at the mid-section of the lower jaw. It is extremely slender and passes anteromedially, medial to the mandible and attaches upon the ventral surface of the posterolateral portion of the submentalis. The most ventral sheet is much broader and fan-shaped, underlying the slender muscle. It arises from a similar site on the mandible, passes anteromedially and attaches upon the medial border of the muscular portion of the customary muscle sheet.

The interhyoideus is extensively folded to form bilobular pouches medial to the postarticular portions of the mandibles.

The vocal sac is a bilobular submandibular structure lacking intercommunication between the left and right pouches. It is principally confined to the interhyoideus, extending only slightly above the muscular portions of the customary sheet of the intermandibularis. The vocal sac apertures are short slits located in positions near the posterolateral limit of the intermandibularis.

Hemisus (Fig. 23B) resembles some microhylids and constitutes perhaps the most aberrant 'ranid' genus. The submentalis is large and oval in shape. The customary sheet of the intermandibularis is a large sheet of transverse fibres meeting at a median raphe and separated from the submentalis anteriorly by a narrow, transverse gap. Supplementary elements of the intermandibularis arise from the ventral surface of the mandible at a position adjacent to the anterior one-third of the customary sheet, pass anteromedially parallel to the mandible and attach upon the ventral surface of the submentalis.

The interhyoideus is a vast, unilobular, postmandibular lobe. The vocal sac is entirely confined to the area above the interhyoideus, and the vocal sacs are short slits located at the posterolateral limit of the customary element of the intermandibularis.

FAMILY: RHINODERMATIDAE

The solitary member of this member is *Rhinoderma darwini* of Chile. Beddard (1908) has described the musculature in considerable detail but I am unable to locate one supplementary transverse sheet of the intermandibularis that he observed, and differ in interpretation of the identity of another.

The submentalis of *Rhinoderma* is small, ovoid and araphic. The customary sheet of the intermandibularis is large and bears a median raphe. Its anterior and posterior fibres are transversely orientated, whereas the median fibres pass slightly anteromedially. There is a supplementary muscle of the apical type of Tyler (1971a) lying ventral to the customary sheet. It arises from the medial surface of the mandible adjacent to the submentalis, passes posteromedially and attaches upon the median raphe of the customary element, resembling the condition in the hylids *Acris*, *Litoria* and *Nyctimystes*.

In the specimen illustrated the interhyoideus is exceptionally poorly developed, being represented by a very slender slip of fibres. However, in adult males retaining tadpoles within the vocal sacs the interhyoideus is known to be developed into a vast, median, unilobular pouch, extending posteriorly beneath the abdominal region (Gunther 1958), so being comparatively larger than in any other known anuran.

The vocal sac is situated above the entire interhyoideus and intermandibularis. The vocal sac apertures are slit-like and exceptionally long, extending for a distance equivalent to three-quarters of the length of the mandibles.

FAMILY: RHINOPHRYNIDAE

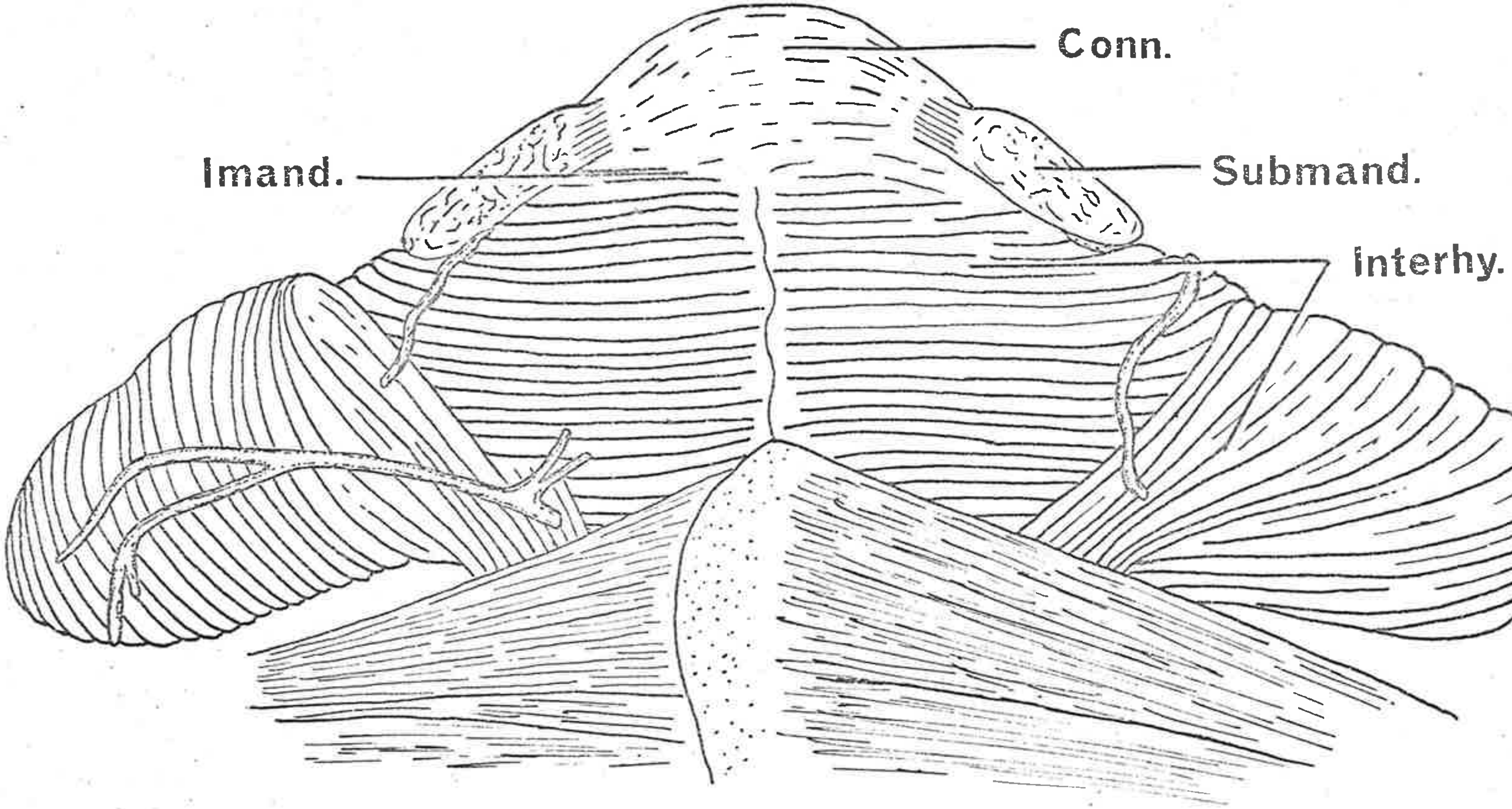
The sole living representative of this family is *Rhinophrynus dorsalis* of Mexico. Walker (1938) has briefly described the superficial mandibular musculature and vocal sac structure.

In the mandibular region the extremely thick ventral skin is intimately attached to the mandibles and the overlying muscles by a layer of very dense, white, fibrous connective tissue. This tissue has a greater tensile strength than the muscles, so making their exposure with minimal damage a difficult procedure. The nature of the myointegumental contact clearly precludes the existence of a submandibular lymphatic sac.

Following removal of the skin it was found that at the apex of the mandibles, the connective tissue had penetrated more deeply and had largely replaced the submentalis. Transverse incisions revealed few fibres within its mass. It was also not found possible to detect any definite separation of the submentalis from the most anterior fibres of the intermandibularis, at the position where the latter were anticipated to lie, similarly because of the presence of the connective tissue. Hence identification of the muscle fibres at the apex of the mandibles as representing the submentalis, followed customary nomenclature for such fibres, and was not based on evidence of the existence of a separate muscle.

The intermandibularis comprises an exceptionally thick muscle, the fibres of which meet medially at a distinct raphe (Fig. 26).

FIGURE 26: Superficial mandibular musculature of *Rhinophrynus dorsalis*.



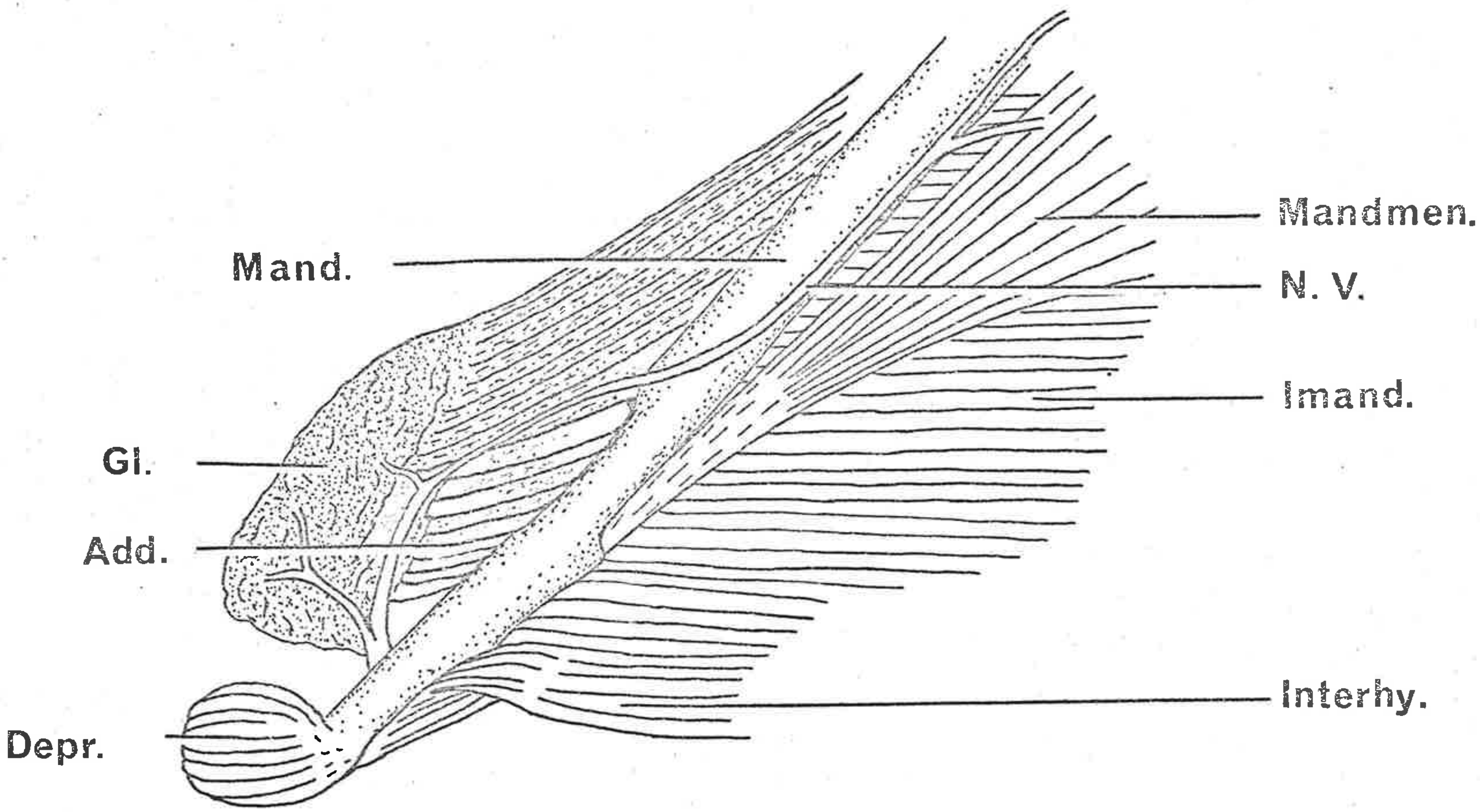
Conn. = connective tissue; imand. = M. intermandibularis; interhy. = M. interhyoideus; submand. = submandibular gland.

On the ventral surfaces of the mandible, at a site adjacent to the origin of the M. adductor mandibulae externus superficialis, is a rounded bony process, termed here the "submandibular process". From this process arises a muscle which I have termed the "M. mandibulomentalis". It arises via a slender, elongate tendon and, as it passes anteriorly, it diverges slightly from the mandible and broadens to form a triangular shape ultimately merging insensibly with the connective tissue at the apex of the mandibles. In superficial ventral view the mandibulomentalis is hidden by a large oval submandibular gland. This gland has been reflected to reveal the muscle in Figure 27.

The interhyoideus is a vast and complex muscle composed of very thick fibres arising from three distinct sites. The most superior fibres originate at the distal tip of the cranial portion of the anterior cornu and from the adjacent pro-otic bone. The second group of fibres arises from the squamosal, posterior to the attachment of the M. depressor mandibulae, and the third from fascia on the ventral surface of the eipcoracoid cartilages of the pectoral girdle. In consequence, the interhyoideus forms the customary transverse sheet attached posteriorly to the pectoral girdle by separately orientated sheets, and has bilateral expansions extending superiorly above the level of the mandibles to the position of the squamosals.

The vocal sacs are entirely separate, bilobular structures situated within the supramandibular lobes. They communicate to the floor of the

FIGURE 27: Articular region of mandible of *Rhinophrynus dorsalis*.



Submandibular gland reflected laterally. Add. = M. adductor mandibulae; depr. = M. depressor mandibulae; gl. = gland; imand. = M. intermandibularis; interhy. = M. interhyoideus; mand. = mandible; mandmen. = M. mandibulomentalis; n.v. = trigeminal nerve mouth via gaping holes, and each sac constitutes a distally expanding tubular outgrowth of the floor.

An additional noteworthy feature of the submandibular morphology is the presence of extremely large blood vessels on the surface of the intermandibularis and interhyoideus.

INNERVATION OF THE INTERMANDIBULARIS

Whereas the interhyoideus is innervated by a deep root of the facial nerve, the submentalis and intermandibularis are innervated by the superficial mandibular branch of the trigeminal which can be observed without difficulty in many species. De Watteville (1875), Hoffman (1878) and Strong (1895) have established the principal routes of these nerves in selected species. Here attention to the mandibular branch of the trigeminal is largely restricted to a more minor point of detail not previously investigated, namely establishing whether there is pronounced variation in the path or number of branches of the terminal portion of the mandibular branch and the disposition of supplementary muscle elements to the nerve.

The mandibular branch invariably passes medial to the major mandibular adductor muscle, and is exposed only in those species lacking a second and more superficially disposed adductor (the adductor mandibulae externus superficialis). The observations of Starrett (1960) on this variation have been confirmed, and it has been established that loss of the latter muscle has occurred in representatives of many genera (see Chapter 4). The mandibular branch traverses the mandible at a position superficial and ventral to the head of the deep adductor, or anteriorly to the site of the head of that muscle.

Three quite distinct variations in the mandibular branch of the nerve are recognisable (Fig. 28). The variants and the distribution of each in particular families are as follows:

A. The branch lacks major branches

Bufonidae
Centrolenidae
Dendrobatidae
Hylidae (part)
Leptodactylidae
Microhylidae (part)
Pelobatidae
Pelodytidae
Ranidae
Rhinodermatidae
Rhinophrynidae

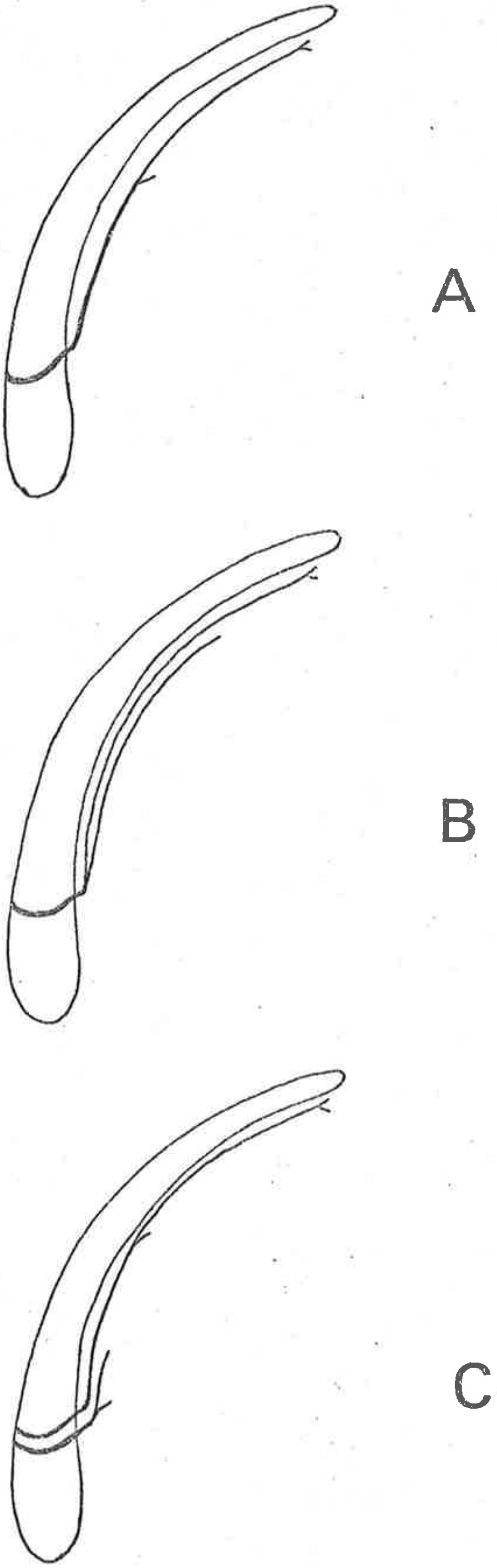
B. The branch divides into two major branches after traversing the mandible

Discoglossidae
Hylidae (part)
Leiopelmatidae
Microhylidae (part)

C. The branch divides into two major branches prior to traversing the mandible

Microhylidae (part)
Pipidae

FIGURE 28: Variation in mandibular branch of trigeminal nerve.



A Major branches absent

B Division after traversing mandible

C Division prior to traversing mandible

With the exception of the Hylidae and Microhylidae, each family exhibited a single condition. In the case of the Hylidae, variant B was observed only in the Phyllomedusinae. All other hylid representatives examined had an undivided branch (variant A). The majority of microhylids had a divided branch of the variant B form. However, *Cophixalus* had an undivided branch, and in *Xenobatrachus* and *Xenorhina* division of the branch occurred at a position prior to its traverse of the mandible (variant C).

The branch or branches of the mandibular pass anteriorly parallel to the medial surface of the mandible, extending to the origin of the submentalis. The path of the nerve and its relationship to the customary sheet of the intermandibularis above it vary only slightly. Where supplementary muscles arise from the medial surface of the mandible, the nerve passes ventral to them and simply provides, at the posterior border of any supplementary muscle, a small twig passing to the dorsal surface of that element. In anurans in which the muscle arises from the ventral surface of the mandible, the branch lies dorsal to the supplementary muscle.

Rhinophrynus dorsalis is exceptional to the extent that rather large twigs innervating the submandibular gland arise from the branch, whilst the twig entering the mandibulomentalis crosses the ventral surface of that muscle.

SYSTEMATIC SURVEY OF LYMPHATIC SEPTA AND ASSOCIATED MUSCLES

The data on the occurrence of the submandibular and pectoral lymphatic septa are summarised in Table 2. To provide complete representation of the Anura, these data include results gained from examination of representatives of several genera and families not included in the present systematic survey of musculature and vocal sacs.

With the exception of the Rhinophrynidae, in which the customary position of the submandibular lymphatic sac is occupied by dense connective tissue, there are only three variations from the generalised pattern. The first involves absence of the postmandibular septum in the families Discoglossidae and Pipidae (Fig. 29A), the second the absence of the pectoral septum in the Brachycephalidae (Fig. 29B), and the last the possession of a single dermal attachment of septa in the Leiopelmatidae (Fig. 29C).

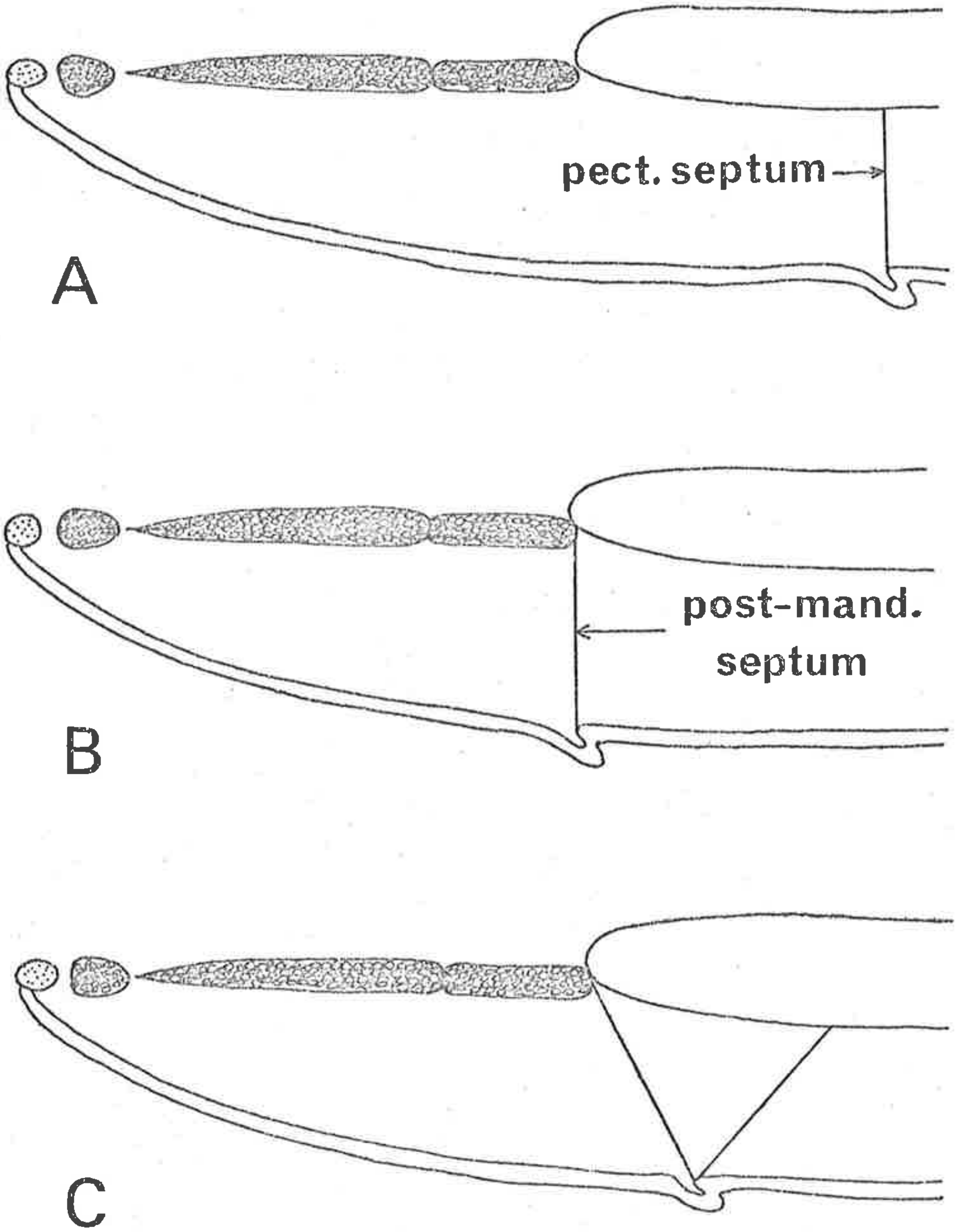
From the sub-order classification of families employed in Table 4, it is evident that four of the five aberrant families are members of the Archeobatrachia. Perhaps the most important aspect of these data is the presence of a unique septal form in *Ascaphus* and *Leiopelma* (Fig. 29C). Whether this constitutes simply a primitive feature common to all primitive frogs, and now persisting only in these genera, or represents an index of the closeness of their phylogenetic relationship is uncertain. It does, however, represent a previously unknown character shared by

TABLE 2

OCCURRENCE AND NATURE OF DERMAL ATTACHMENTS OF CERTAIN LYMPHATIC SEPTA IN THE ANURA

Family	Postmandibular Septum	Pectoral Septum	Dorsal Attachments of Septa
Leiopelmatidae	present	present	common site
Discoglossidae	absent	"	-
Rhinophrynidae	indistinguishable from dense connective tissue		
Pipidae	absent	present	-
Pelobatidae	present	"	separate sites
Pelodytidae	"	"	" "
Bufonidae	"	"	" "
Leptodactylidae	"	"	" "
Rhinodermatidae	"	"	" "
Dendrobatidae	"	"	" "
Brachycephalidae	"	absent	-
Hylidae	"	present	separate sites
Centrolenidae	"	"	" "
Pseudidae	"	"	" "
Ranidae	"	"	" "
Hyperoliidae	"	"	" "
Rhacophoridae	"	"	" "
Microhylidae	"	"	" "

FIGURE 29: Variation in occurrences and dermal attachments of lymphatic septa.



A = Discoglossidae and Pipidae
B = Brachycephalidae
C = Leiopelmatidae

and unique to these genera.

Variation in the depth of the septa was extensive throughout all polytypic genera adequately sampled. The only noteworthy exception was *Rana*, in which the pectoral septum was consistently short.

The cutaneous pectoris is the only muscle found to occur in association with the above lymphatic septa. Tyler (1971c) surveyed fourteen families, ninety-one genera and three-hundred and eighty-three species to demonstrate its restriction to the Ranidae (*sensu lato*). Of the material reported here the Pelodytidae and many genera and species of other families were not represented in that survey. The additional data now available confirm that conclusion.

The only ranid previously known to lack the cutaneous pectoris is *Arthroleptis* (Tyler, 1971c). Of the additional material it is also absent in the ranid *Hemisus*. However, *Hemisus* exhibits a curious combination of morphological characters that has led some authors to regard it as a member of the family Microhylidae. Hence the absence of a specifically ranid characteristic in that genus is not surprising and further emphasises the problems of its present family disposition.

CHAPTER 3 : ONTOGENY

MUSCLE ONTOGENY

(a) Ontogeny of Superficial Mandibular Muscles

In the larva the intermandibularis and interhyoideus constitute the branchial constrictors. It is only at metamorphic climax (the period of gross and rapid transformation from larva to juvenile frog) that the submentalis develops and the muscles assume their adult configuration. The vital stages extend from the eruption of the forelimbs through the loss of the superficial larval mouthparts and absorption of the tail, to the juvenile frog.

This sequence of events commonly occupies only two or three days, and the available material is often incomplete to the extent that relevant steps in the sequence are lacking. Because specific identification of juvenile frogs is frequently extremely difficult, few collections are retained in museum collections. Studies of New Guinea microhylids are rendered more difficult by the fact that they lack free-swimming tadpoles. The entire period of metamorphosis is passed within the egg membranes, and many species emerging from those membranes have snout to vent lengths of less than 5 mm. Examination of serial sections of one species (*Sphenophryne mehelyi*) did not reveal adequate detail of the mandibular region to permit any data to be obtained on the nature of the mandibular muscles in this family.

Adequate series of tadpoles of the following species were examined: *Cyclorana australis*, *Litoria aurea*, *L. ewingi*, *L. thesaurensis*, *L. wissellensis*, *Limnodynastes tasmaniensis*, *Neobatrachus pictus* and *Rana temporaria*. Incomplete series of the following species were also examined: *Litoria arfakiana*, *L. darlingtoni*, *Nyctimystes kubori* and *Ranidella signifera*.

Gosner (1960) proposed a numerical staging system based on standard features of external morphology to permit recognition of comparable stages in the development of species. This I employ here. During the early relevant stages of development there is a basic similarity in all species studied. Thus the description is a composite one and only the areas of divergence specifically mentioned.

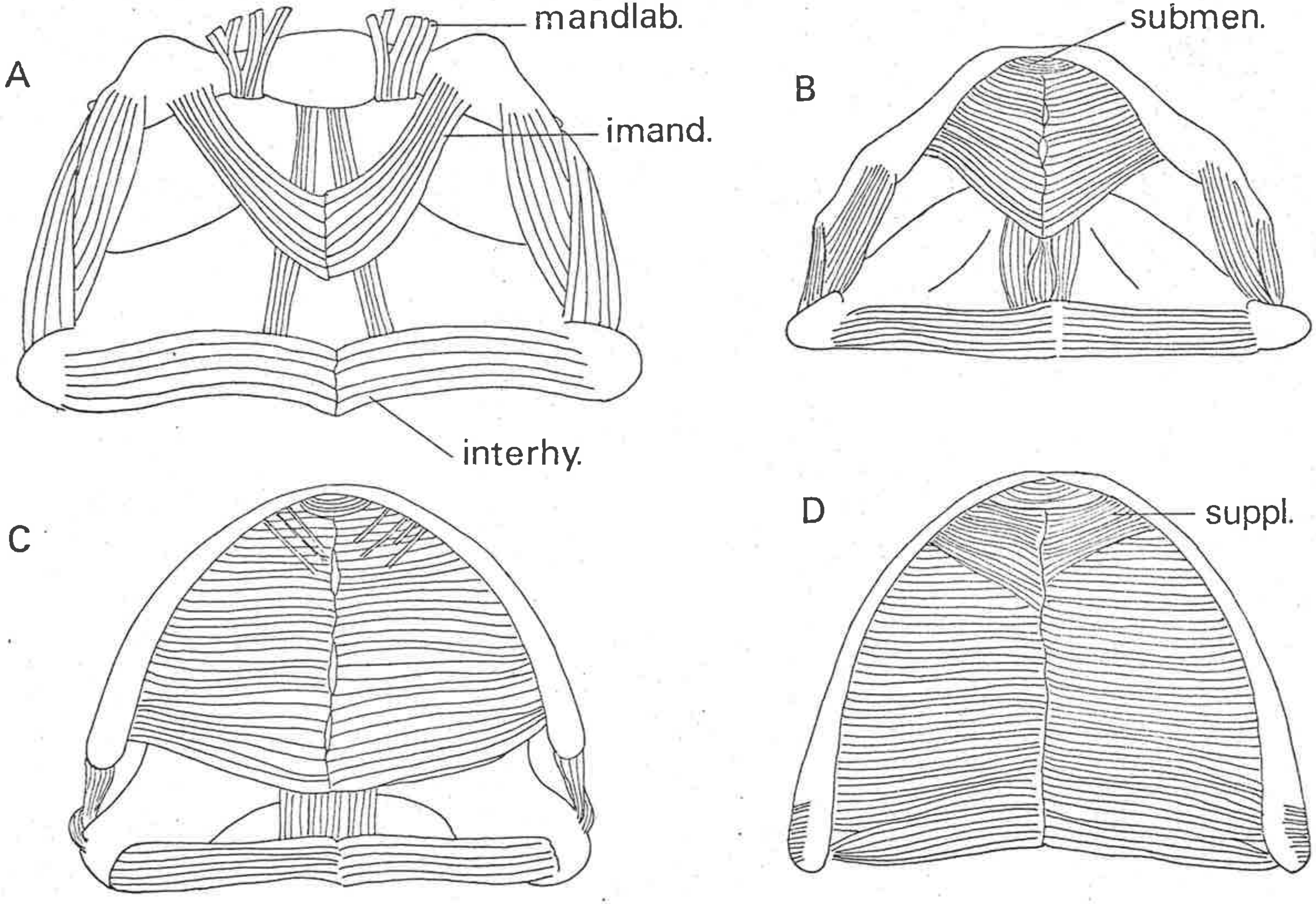
In the stage that immediately precedes the emergence of the forelimbs (Stage 41) the larva has attained its maximum total length. The hindlimbs are fully developed, the forelimbs are visible in outline through the skin and the larval mouthparts are retained. At that stage the mandibulolabialis arises from the base of the caudal side of the Meckel's cartilage and fans out into a series of diverging fasciculae to attach upon the skin beneath the lower labial border (Fig. 30A). This muscle is comparatively larger in the hylids than in the leptodactylids and ranids examined. The extent of its development appears to be associated with the degree of mobility of the labial border.

The submentalis does not exist at Stage 41. The intermandibularis

FIGURE 30: Ontogeny of superficial mandibular musculature in *Litoria*.

A = Stage 41; B = Stages 42-43; C = Stages 44-45; D = Post-metamorphic.

imand. = M. intermandibularis; interhy. = M. interhyoideus; mandlab. = M. mandibulolabialis; submen. = M. submentalis; suppl. = supplementary elements of M. intermandibularis.



is in the form of a crescentic, posteriorly directed loop arising from the ventral surface of Meckel's cartilage. The interhyoideus is a single, slender and rather slack muscle arising from the ventral surface of the ceratohyal and separated from the intermandibularis by a very broad gap.

This basic pattern of musculature is maintained throughout the entire preceding period of larval development. The first change occurs when development of the mandible is initiated. This step occurs simultaneously with the shedding of the larval mouthparts, histolysis of associated soft tissues, expansion of the mouth, and initiation of development (namely elongation) of the incipient mandibles. Externally it is associated with eruption of the forelimbs and the commencement of tail absorption. However, mandibular development and tail absorption are independent processes unlikely to be perfectly equated. Hence it is not surprising that there is no correlation between mandibular development, and particularly of muscle ontogeny, and the external feature employed by Gosner (1960). Thus the next recognisable step can occur at any point within Stages 42 and 43 (Fig. 30B).

In all species initiation of elongation and posterior inclination of the mandibles is associated with loss of the mandibulolabialis and concurrent appearance of the submentalis. Mandibular elongation is accompanied by rapid progressive development of the intermandibularis. In effect, the fibres take up additional sites available for occupation. Initially, development is most pronounced anteriorly, so that the fibres rapidly occupy the space separating the muscle from the submentalis. In *Neobatrachus* the fibres partially underlie the submentalis. In *Limnodynastes* there is a partial occupation of a position ventral to the submentalis, and in *Rana* there is an anteromedial orientation of the most anterior fibres. Posterior development is completely concurrent with the posterior migration of the mandible. However, the loop-like configuration is retained to the extent that posteromedially the muscle extends beyond the mandibular extremities. Rotation of the mandible transfers the site of origin from the ventral to the medial surface of the mandible.

The subsequent muscular ontogeny is a less dramatic and probably more prolonged process. As the mandible progresses posteriorly through Stages 44 to 45 (when the tail reduces to a mere black stump) so the intermandibularis develops further posteriorly, loses its posteromedial fibre inclination and approaches the intermandibularis. In the *Litoria* and *Nyctimystes* species the first fibres of the apical element of the intermandibularis appear at this step (Fig. 30C).

Ultimate proportional development of the mandibles is a post-metamorphic phenomenon in all species studied, as is the fusion of the posterior fibres of the intermandibularis with the anterior margin of the interhyoideus (Fig. 30D).

In female frogs the interhyoideus retains the size relationship to the intermandibularis throughout adult life. Development of postero-medially directed lobes of the interhyoideus in males is initiated in association with vocal activity and constitutes a secondary sexual characteristic.

(b) Ontogeny of the Mandibulolabialis

The mandibulolabialis is of particular interest because of current uncertainty about whether it is unique amongst the larval muscles in having no adult counterpart. In the larva it customarily represents a lower labial retractor, and it is certainly valid that there is no comparable adult function to be performed.

There are few published data on the fate of the mandibulolabialis, but Edgeworth (1911, 1935), de Jongh (1968) and Tyler (1971a) all state that the mandibulolabialis is lost concommitantly with the early development of the submentalis. The new data on *Neobatrachus pictus* and *Limnodynastes tasmaniensis* confirm these observations.

In his studies on *Bufo regularis* Sedra (1950) maintained that during metamorphic climax the mandibulolabialis migrates posteriorly to become contiguous with, and hence indistinguishable from, the most anterior fibres of the intermandibularis. The movement that he reports occurs after the loss of the larval mouthparts, and so requires replacement of fibres in a progressive posterior direction at a time when the muscle is performing no function. Certainly, there seem grounds for treating the assertion with caution.

More recently, Starrett (1973) has employed differences in the site of origin and attachment of the mandibulolabialis as one of a number of characters distinguishing various types of larvae represented amongst the Anura. She has further queried whether the infralabial constrictors of bufonids, hylids, leptodactylids, ranids, etc., are homologous with such muscles in microhylids and has stated, "there is evidence that the microhylid muscle is retained as an accessory slip running parallel to the mandible." From the data now available it is possible to contribute to each of these matters.

Firstly, insofar as difference in origin is concerned, Starrett's summarised data are at variance with all other workers, some of whom she cites. Hence the site of origin of the muscle in the Bufonidae, Hylidae, Leptodactylidae and Ranidae is Meckel's cartilage and not the infrarostral. The origin is quite uniform in all families known to possess the muscle and the homology that she queries is less likely to be suspect.

The concept that the mandibulolabialis could be represented in adult microhylids by the laterally disposed superficial mandibular muscle, here regarded a supplementary element of the intermandibularis, is an intriguing one. However, contrary to Starrett's statement, I know of no evidence in support of such an assumption, and she does not provide any. The situation is simply that there is a larval muscle without a proven adult equivalent and, in microhylids, an elongate muscle of uncertain origin.

Specimens of microhylids at metamorphic climax, which are so necessary to an effective evaluation of the hypothesis, are lacking and there are no published data on the ontogeny of the superficial adult muscle. However, on the basis of what is known about the migration of muscles at their origin and attachment during metamorphic climax, Starrett's intimation seems quite untenable. In microhylids the infralabial retractor (? mandibulolabialis) passes from the Meckel's cartilage to the infrarostral. The site on the Meckel's cartilage is the anterior extremity. As indicated here, in adult *Breviceps* the supplementary muscle extends from the posterior portion of the mandible to a site upon the submentalis. It follows that at metamorphic climax the caudal end of the muscle would be required to shift posteriorly almost the entire length of the elongating mandible. A migrationary feat of this magnitude would be little other than extraordinary.

Studies of the innervation of the microhylid infralabial constrictor have not been undertaken in larvae and no material has been available to me. However, in the adult the site of entry of the trigeminal root is adjacent to the posterior extremity of the muscle. Migration would require a more major change in the innervation than it seems reasonable to anticipate being possible. Hence it is likely that in microhylids the mandibulolabialis is lost at metamorphosis, as in most (if not all) anurans, and that the laterally disposed muscle arises from differentiation of the intermandibularis. That that muscle element has been suggested the adult representation of the mandibulolabialis is, perhaps, primarily because no other hypothesis has been proposed.

ONTOGENY OF VOCAL SACS

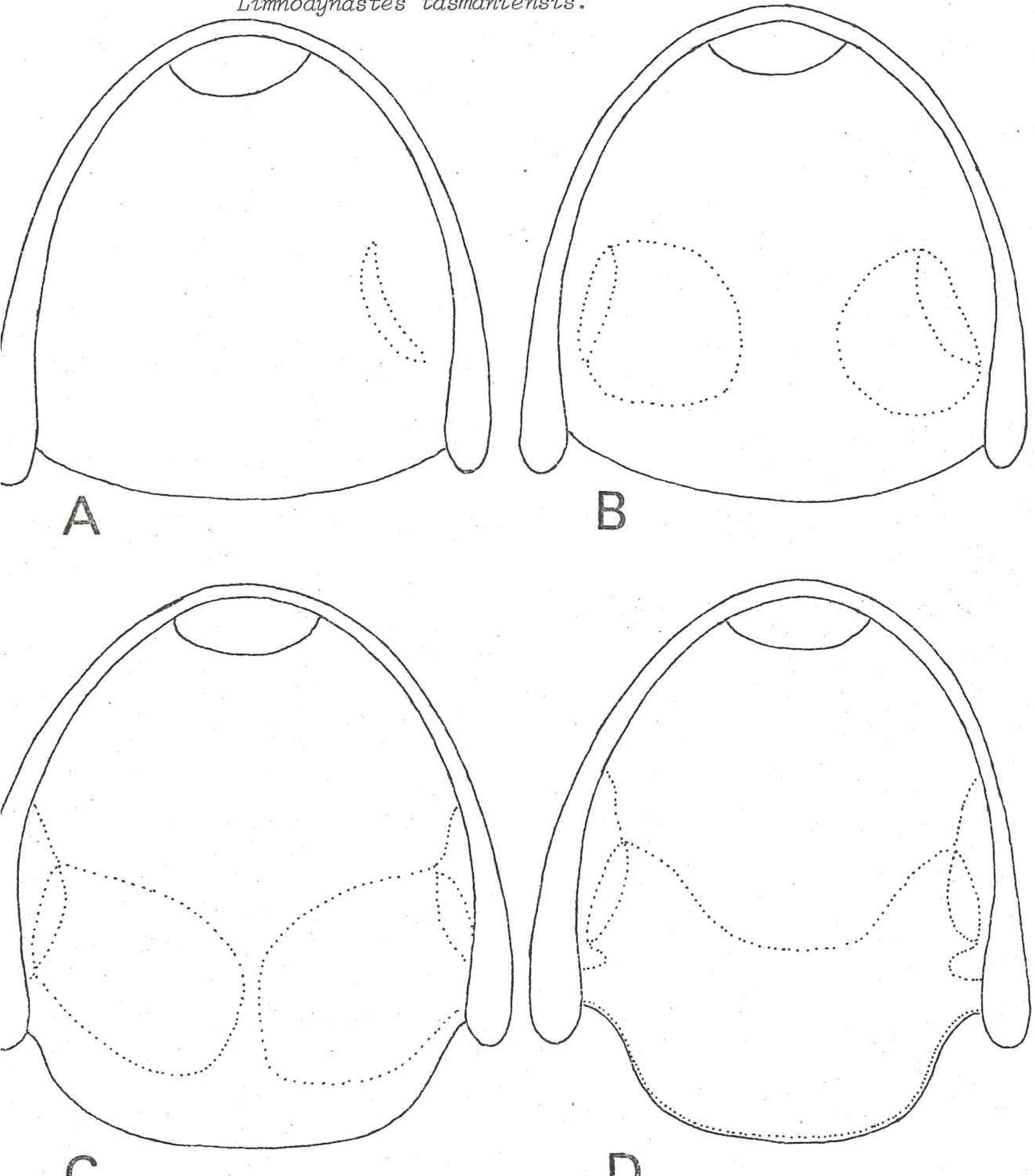
The vast majority of specimens collected are adults exhibiting secondary sexual characteristics. Subadult specimens are infrequently obtained, with the result that there is a dearth of material available for the study of the ontogeny of the vocal sac.

From the forty thousand specimens in the South Australian Museum, I was able to locate only three series of specimens from which the ontogeny of the vocal sac could be extrapolated for particular species. The most complete series consists of eighteen specimens from sixty-eight males of the leptodactylid *Limnodynastes tasmaniensis* collected at West Beach near Adelaide on 1 September, 1963. This series exhibited the complete developmental sequence, and from this sequence I have selected four steps depicted in Figure 31.

The first step involves development of a longitudinally orientated and slightly curved fold in the floor of mouth, bordered laterally by the lateral margin of the anterior cornu and medially by the medial border. It constitutes nothing more than an evagination of the mouth floor inclined mediad (Fig. 31A). In four out of five specimens, at this stage only the left evagination was developed; in the fifth similar development occurred on each side simultaneously.

From these folds the vocal sacs develop bilaterally and, as far as could be determined, quite concommitantly, into roughly circular sacs

FIGURE 31: Progressive stage in ontogeny of vocal sacs of *Limnodynastes tasmaniensis*.



intruding between the superficial and the deep intermandibular muscles (Fig. 31B). Mediad development is slightly more pronounced than anterior or posterior. Simultaneously, the portion of the mouth floor between the anterior cornu and the mandible become slightly depressed, rendering the aperture more conspicuous.

The bilateral sacs become progressively larger, extend further ventrally and approach one another near the midline (Fig. 31C). They finally meet, their contiguous wall ruptures and the tissues' common edges unite to form a single sac (Fig. 31D). This is followed by further development posteriorly associated with development of a posterior lobe to the interhyoideus.

An external index of the extent of the vocal sac development is provided by the presence of pigmentation of the skin of the submandibular regions. In specimens lacking the initial evaginations the skin was either completely unpigmented or bore a few scattered melanophores confined to the periphery of the mandibles. Development of the evaginations was accompanied by an increase in the density of pigmentation and of its medial limit. This pigmentation, and the appearance of the bright yellowish background colour of the throat, so characteristic of adult males of this species, progressed in an identical sequence until, at completion of vocal sac development, the skin covering the entire submandibular region was intensely pigmented.

The smallest individuals exhibiting the first and the last of the stages recognised here had snout to vent lengths of 23 mm and 32 mm, respectively.

The two other species studied are the hylids *Litoria caerulea* and *L. rubella*, which, like *Limnodynastes tasmanienses*, exhibit a unilobular, submandibular vocal sac. Although the series are not as complete as that of the species described above, the overall pattern appears basically similar. The only noteworthy feature involves *Litoria caerulea*, which is a particularly large species, with males ranging from 70 to 100 mm in snout to vent length. In that species the vocal sac aperture increases in length in conjunction with mediad development of the vocal sac. It originates at what constitutes its ultimate posterior limit adjacent to the position at which the anterior cornu passes above the mandible, and progressively lengthens in an anterior direction. Its ultimate anterior limit is reached when the vocal sac from each side fuses medially to form a confluent chamber.

THE ONTOGENY OF SKIN MODIFICATIONS ASSOCIATED WITH THE VOCAL SAC

Liu (1935) has reviewed the nature and extent of modifications to the skin covering the vocal sac and superficial mandibular muscles that are associated with, and apparently produced by, inflation of the vocal sac. The modifications range from a uniform increase of the surface area producing loose folds or pleats, to invaginations or evaginations of discrete areas of portions of the skin covering the interhyoideus. To date there are no published data on the ontogeny of skin modifications.

In the case of simple increase in skin surface area, it is reasonable to interpret it to be a consequence of distension exceeding the subsequent contractile potential of the skin. However, the localised evaginations or invaginations represent a more refined development of specific portions of skin.

Phrynohyas venulosa is a Central American hylid frog in which the adult males possess bilateral, supramandibular, evaginated skin pouches. A series of thirty-five specimens from Costa Rica has been examined, and although their requirement for other studies precluded dissection, it has been possible, from external examination and dissection of two additional specimens, to interpret the manner in which these pouches arise.

The first form of modification of the skin in *P. venulosa* involves an invagination adjacent to each postarticular extremity of the mandibles. It occurs prior to attainment of sexual maturity (as indicated by the size and lack of pigment of the nuptial pads) and during the onset of such maturity. As the nuptial pads enlarge and attain pigment, so the invagination deepens. Finally, the skin pouch everts and becomes heavily pigmented with melanin.

Dissection of an everted pouch demonstrates the lack of any contact with the lobe of the interhyoideus located at its orifice. It follows that it is likely that evagination occurs when the bilobular vocal sacs are inflated for the first time. Every specimen with evaginated pouches had enlarged, black nuptial pads customarily associated with the attainment of sexual maturity.

CHAPTER 4 : EVOLUTION

EVOLUTION OF VOCAL SACS

To assess the evolution of vocal sacs in modern anurans, it is necessary, firstly, to establish whether the ancestral stocks possessed vocal sacs or whether present structures could have evolved on more than one occasion.

The data presented here and that of Liu (1935) indicate that many species lack vocal sacs, so leading to the premise that ancestral stocks lacked them. However, closer examination of the incidence of absence indicates that although absence may be genuinely indicative of derivation from a stock that lacked them, it is equally likely to be an example of secondary loss. For example, in the hylid genus *Litoria* sacs are present in sixty species but absent in four species. Liu's data on the ranid genus *Rana* demonstrates a similar situation of the vast majority of species possessing vocal sacs and a few lacking them, whilst Inger (1954) noted presence or absence in *Rhacophorus leucomystax* associated with the geographic distribution of that species. Inger (1958) reported apparently random loss in *Bufo alvarius*. Because, at present, there is no justification for suggesting that species of genera such as *Rana* and *Litoria* lacking vocal sacs are the most primitive members of these genera, it follows that they can only be derived from stocks that possessed vocal sacs. Although the selective advantage of loss is unknown, the phenomenon has evidently occurred independently on numerous occasions. Data on the frequency of loss in the genera in which vocal sacs were found to be present or absent are presented in Table 3.

Three families are characterised by absence of vocal sacs: Leiopelmatidae, Pipidae and Discoglossidae. Whether they are derived from ancestral lines that possessed vocal sacs and subsequently lost them, or whether their ancestors simply had not evolved vocal sacs is debatable. In terms of seeking the least complex evolutionary path, the latter hypothesis is certainly simplest. The concept is an attractive one to the extent that these same families are universally regarded as exhibiting the greatest number of primitive osteological and myological characters, so that absence in these families may represent retention of the primitive character state.

The unique situation occurring in the discoglossid *Bombina bombina* can be interpreted as evidence in support of the above hypothesis ('primary' absence in the family). As reported here, incomplete lateral fusion of the normally contiguous margins of the intermandibularis and interhyoideus is characteristic of the Discoglossidae. Hence, if the customary vocal sac intruding above the interhyoideus could be envisaged in this family, the space between the interhyoideus and intermandibularis would constitute a non-muscular and inherently weak portion of the vocal sac structure when the sac is inflated. All that has occurred in *B. bombina* is that the geniohyoideus lateralis has been modified to permit

TABLE 3

GENERA STUDIED IN WHICH LOSS OF VOCAL SACS OBSERVED

Family	Genus	Sacs Absent	Sacs Present
Hylidae	*Anotheca*	1	0
"	*Cryptobatrachus*	1	0
"	*Gastrotheca*	1	2
"	*Hemiphractus*	2	0
"	*Hyla*	3	81
"	*Litoria*	4	60
"	*Nyctimystes*	2	9
"	*Phyllomedusa*	1	8
"	*Plectrohyla*	1	1
Leptodactylidae	*Lechriodus*	1	2
"	*Taudactylus*	1	2

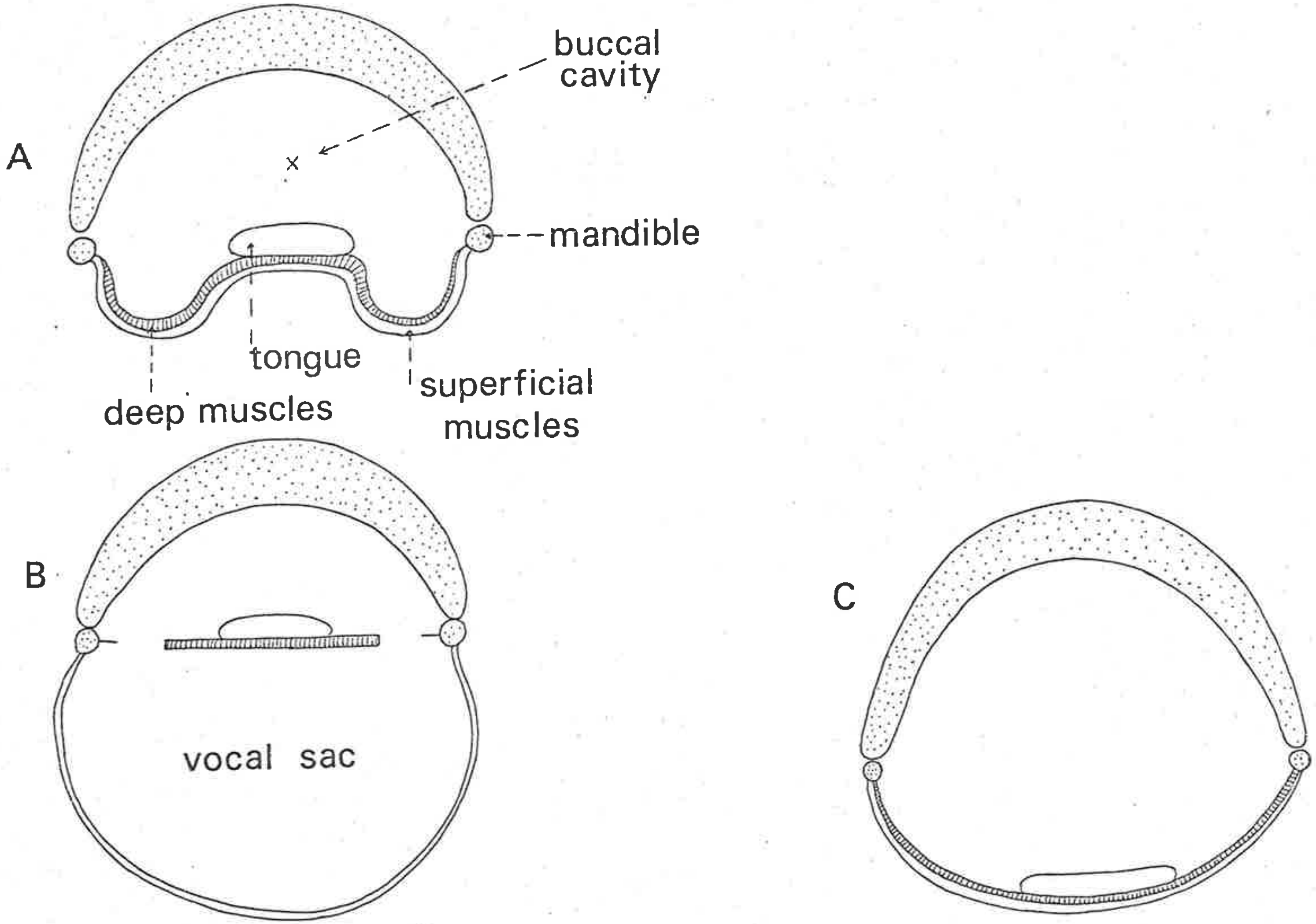
it to distend ventrally and occupy that gap. This modification and the associated changes in the mouth floor can therefore be interpreted to be a reflection of the predetermined limitations imposed by a musculature comparable to that existing in the modern species of discoglossids. Hence it constitutes an independent solution to increasing the capacity of the buccal chamber as the primary resonance chamber. It follows that the modifications are not 'primitive' to the extent that they are not precursors of customary vocal sacs exhibited by other anurans (conflicting with the suggestion of Liu, 1935).

The only other anomalous condition is that of the closely allied Australian leptodactylid genera *Neobatrachus* and *Heleioporus*. In these genera there is no vocal sac, but the floor of the mouth can be depressed, so enlarging the capacity of the buccal cavity which functions as the resonance chamber. The morphological adaptations that have resulted in the evolution of this structure represent the end product of an entirely independent evolutionary line. This adaptation is not a primitive structure but reflects simply a different method of achieving a similar objective.

The adaptations of *Bombina bombina, Neobatrachus* and *Heleioporus* and the common features of vocal sacs are represented digrammatically in Figure 32. The principal differences are that *B. bombina* (Fig. 32A), *Neobatrachus* and *Heleioporus* (Fig. 32C) involve distending the floor of the buccal cavity or a portion of it, whereas a vocal sac is a vast

FIGURE 32: Forms of resonance chambers.

A = Bilateral distension of mouth floor *(Bombina)*
B = Customary vocal sac
C = Complete distension of mouth floor *(Neobatrachus and Heleioporus)*



intrusion of the mouth floor between the superficial muscles and the deep mandibular muscles (Fig. 32B).

The vocal sac requires an initial evagination of the mouth floor, and an understanding of the process by which this has arisen requires focussing attention upon the nature of the vocal sac aperture. As reported in the ontogenetic studies on *Limnodynastes tasmaniensis* and two *Litoria* species, the initial stage involves an evagination beneath the anterior cornu. This evagination progressively extends through a bilobular stage, and resulting ultimately in fusion and intercommunication of the paired sacs to form a single structure.

The extent of morphological diversity of vocal sacs in the Anura is considerable. The location of the sac in relation to the muscles above it is highly variable, and in many cases the muscles themselves are highly modified. The evolutionary paths by which they may have formed their present structures are obscure, but it is apparent that there are a number of physical factors which have probably contributed to the existing diversity. For example, the position that the sac occupies, and its overall shape and inflated size will be influenced by a number of factors, of which the following are probably important:

(a) Median Length of Mandibular Region

As the angle of inclination of the mandibles to the mandibular symphysis increases, so the median length of the mandibular region shortens. Hence, in animals with particularly obtusely angled mandibles, this effectively reduces the surface area that can be occupied by muscle fibres transversely orientated to the median plane. Thus in such animals the submandibular length for the vocal sac is similarly reduced. In practice, the interhyoideus is frequently developed posteriorly when the mandibles are obtuse, so transferring the greater part of the vocal sac posteriorly. This can be regarded a consequential compensation.

(b) Elasticity of Skin

From subjective observations it would appear that the elasticity of submandibular skin is not similar in all anurans. For example, areas which are thick and contain complex glands and ducts lack the ability to stretch to the extent of those lacking them. In such a situation the submandibular vocal sac is simply unable to distend.

Even in many *Rana* species which do not have particularly thick submandibular skin there is evidently difficulty in achieving distension. It has been overcome by developing localised areas of thinner skin through which the muscles and vocal sac can protrude.

(c) Lymphatic Septa

The initial inflation of the vocal sac involves occupation of the submandibular and pectoral lymphatic sac (Tyler, 1971b, 1972). Hence the depth of the pectoral septum constitutes the extent to which the skin can be forced away from the underlying structures, before the elasticity of the skin imposes a restraining influence to further distension.

(d) Elasticity of the Lining of the Mouth Cavity

Because the vocal sac is derived from the lining of the floor of the mouth, its intrinsic elasticity may vary. Certainly, in *Bufo* species, which frequently retain bilobular, submandibular sacs, and quite frequently unilateral structures, the lining is exceptionally thick.

(e) Distensibility of Mandibular Muscles

The data presented here on *Triprion* demonstrated a three-fold difference in the thickness of the intermandibularis against the interhyoideus, and restriction of the vocal sac to the latter muscle in that genus. Gross distension of muscles in preserved specimens of other species only occurred in situations where the muscles were exceptionally thin (determined from representatives of the same species with undistended muscles).

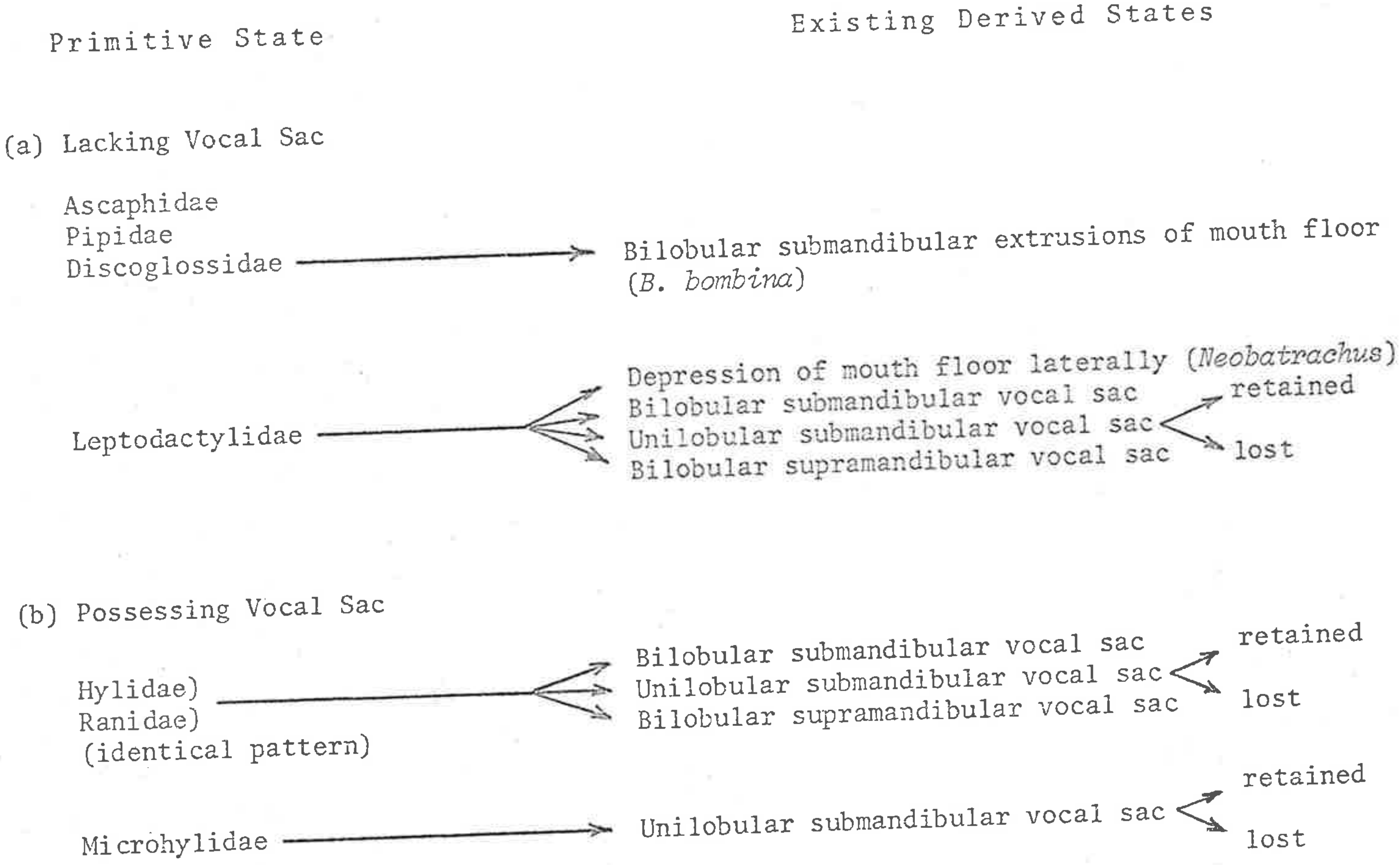
It is therefore apparent that any one of a number of adaptive shifts in gross morphology, such as broadening of the jaws, development of skin glands, etc., is likely to have a profound effect upon the vocal sac. This being so, Liu's (1935) tentative attempts to assess existing vocal sacs as primitive or variously derived without reference to these considerations are of dubious value. An additional important consideration is the disposition of the anterior cornu of the hyoid within the submandibular region, for, as demonstrated here, this is what determines the location of the initial evaginations that give rise to the vocal sac.

Whether it is realistic to attempt to trace an evolutionary sequence from a submandibular site, through postmandibular bilobularity of the interhyoideus to discrete, paired supramandibular structures is dubious. Trueb (1970) has used the presence of bilobular vocal sacs in support of her concept of the phylogeny of the casque-headed hylid tree frogs, in particular for the *Phrynohyas/Osteocephalus/Trachycephalus* lineage. Certainly, in these three genera the sacs are basically similar and the associated muscular modifications comparable. Nevertheless, the utilisation of submandibular and supramandibular sites involve modification of different portions of muscles, and each of the existing species exhibiting these variants is the ultimate or intermediary step of different evolutionary processes.

What makes the problem of interpretation of direction of change additionally difficult is the clear indication of parallel evolution in several families (Fig. 33). From the evidence summarised there it becomes apparent that loss of the vocal sac (as opposed to absence in the families that may never have evolved these structures) occurs only in genera that have submandibular vocal sacs. It suggests that regression is most likely to occur in stocks that have been structurally minimally modified to accommodate their presence; it implies a progressive loss of potential adaptive plasticity as the vocal sac evolves along a particular path.

FIGURE 33

PATTERNS OF EVOLUTION OF VOCAL SACS IN VARIOUS FAMILIES



EVOLUTION OF MANDIBULAR MUSCLES IN ANURANS

The Primitive State of Superficial Mandibular Musculature

To permit investigation of the possible nature and directions of evolutionary change in the superficial mandibular musculature, it is necessary to establish what constitutes the most primitive character states of these muscles.

Previously Jarvik (1963) has drawn attention to the similarity in the disposition of supplementary elements of the intermandibularis of certain anurans with the ventral, dermal, bony plates of osteolepiform fishes. Although his reference to these muscles is brief, it is clearly cited in support of his hypothesis of a diphyletic origin for the Amphibia and, particularly, of the osteolepiform ancestry of the Anura. The implication of his comparison is that such supplementary anuran muscles are derived from the retrogression of ancestral features, and that their presence in some anurans represents the persistence of a primitive feature in a radically changed tissue form. Clearly, by Jarvik's deduction, it would not be possible to envisage the absence of such supplementary muscles as anything than a derived state in terms of the evolution of intermandibular muscles.

Jarvik's comments appear to emanate from the observations of Trewavas (1933), and the only attempt to review the occurrence of these supplementary muscles at a generic and family level is that of Tyler

(1971a). Here these same data have been supplemented to include all anuran families (Table 4). In assessing those data in relation to Jarvik's hypothesis three possibilities need to be considered. The first is to assume that supplementary muscles (if genuinely primitive) will occur in association with other primitive characters. The second is that the muscle characters could be primitive, but that they have been retained independently of other primitive characters, whilst the third is that they represent derived character states.

Applying Jarvik's hypothesis to the first concept is totally inconsistent with the summation of current views as summarised by Duellman (in press), namely, because all primitive families (Archeobatrachia) lack supplementary muscles. The second concept is less readily dismissed, but for it to be tenable, it requires all Archeobatrachian families to be derived from a common stock that had lost the muscles; all such families to independently lose the supplementary muscles, or to assume a diphyletic origin for the Archeobatrachia and the Neobatrachia from a common ancestral stock. There is no evidence to support such proposals.

By far the simplest explanation is to assume that supplementary muscles have evolved within the Anura and, particularly, within the more recent families of the Neobatrachia. Although my data suggest that they have evolved on more than one occasion (principally because the only thing common to all except the ranids is that they lie ventral to the customary muscle sheet), this detail is immaterial to the concept that

TABLE 4

OCCURRENCE OF SUPPLEMENTARY ELEMENTS OF THE INTERMANDIBULARIS

Suborder	Family	Number of Genera Present	Number of Genera Absent
Archeobatrachia	Leiopelmatidae	0	2
"	Discoglossidae	0	3
"	Rhinophrynidae	0	1
"	Pipidae	0	2
"	Pelobatidae	0	1
"	Pelodytidae	0	1
Neobatrachia	Bufonidae	0	1
"	Leptodactylidae	3	28
"	Rhinodermatidae	1	0
"	Dendrobatidae	3	0
"	Brachycephalidae	1	0
"	Hylidae	7	25
"	Centrolenidae	0	3
"	Pseudidae	0	1
"	Ranidae	12	0
"	Hyperoliidae	1	0
"	Rhacophoridae	2	0
"	Microhylidae	14	0

This sequence in the presentation of families follows the concept of 'primary adaptive shift' of Duellman (in press). Data for families not included in the thesis are derived from Tyler (1971a) and unpublished data, and Beddard (1895a, 1895b). No data are available for the Sooglossidae.

they are 'derived' structures.

Tyler (1971a) suggested that the origin of supplementary muscles should be viewed from the functional implications of the stresses placed upon the customary sheet by the evolution of vocal sacs.

The pitfalls of attempting to deduce function solely from observed morphology have been emphasised by Duellemeijer (1968) and by Gans and Bock (1965). With awareness of their expressed concern, the assumption that demand can be regarded the cause of structure is at least more reasonable than assuming retrogradation, as Jarvik has done, a tenet so severely criticised by Gans (1966).

Excluding the submentalis, which is principally concerned with permitting limited independent movement of the mandibles at their symphysis, the customary sheets of the intermandibular muscles can only raise the floor of the mouth. The actions of these muscles in *Rana catesbeiana* have been examined by de Jongh and Gans (1969) using electromyographic techniques. They found that maximal buccal pressure within a respiratory cycle is associated with the contraction of these muscles.

The simplest theoretical structural arrangement for the intermandibular muscles to perform their primary function of raising the floor of the mouth is one in which there is a transverse orientation of muscle fibres and a median raphe. Supplementary muscles are not required; there is no need for the interhyoideus to extend anteromedially into the area occupied by the intermandibularis, or for the interhyoideus to develop posteriorly into a lobe or lobes beyond the postarticular extremities of the mandibles.

It is realistic to assume that constraints on the achievement of the model of simplicity could be placed upon any adult by the nature of the larval structure. Hence certain apparent modifications (discussed in the following section) may need to be viewed in this light. Nevertheless, this does not influence the premise that any divergence from the theoretical form is derived when viewing the Anura as a whole.

An example of the theoretical model of simplicity is exhibited by the pattern of muscle architecture of the existing members of the Leiopelmatidae. Because this family is considered to retain the greatest number of other primitive characters, this lends tenuous support to the assumption that the above theoretical structure is genuinely primitive. Hence any modification of that pattern, particularly the presence of supplementary sheets, can only represent derived features.

The Extent of Divergence and the Possible Paths of Evolution

Despite the diversity in the form, shape and size of submandibular muscles and the nature and extent of their contact with one another, the variation can be distinguished and a number of clear categories recognised.

For example, there are six forms of association between the customary sheet of the intermandibularis and the submentalis, falling into three

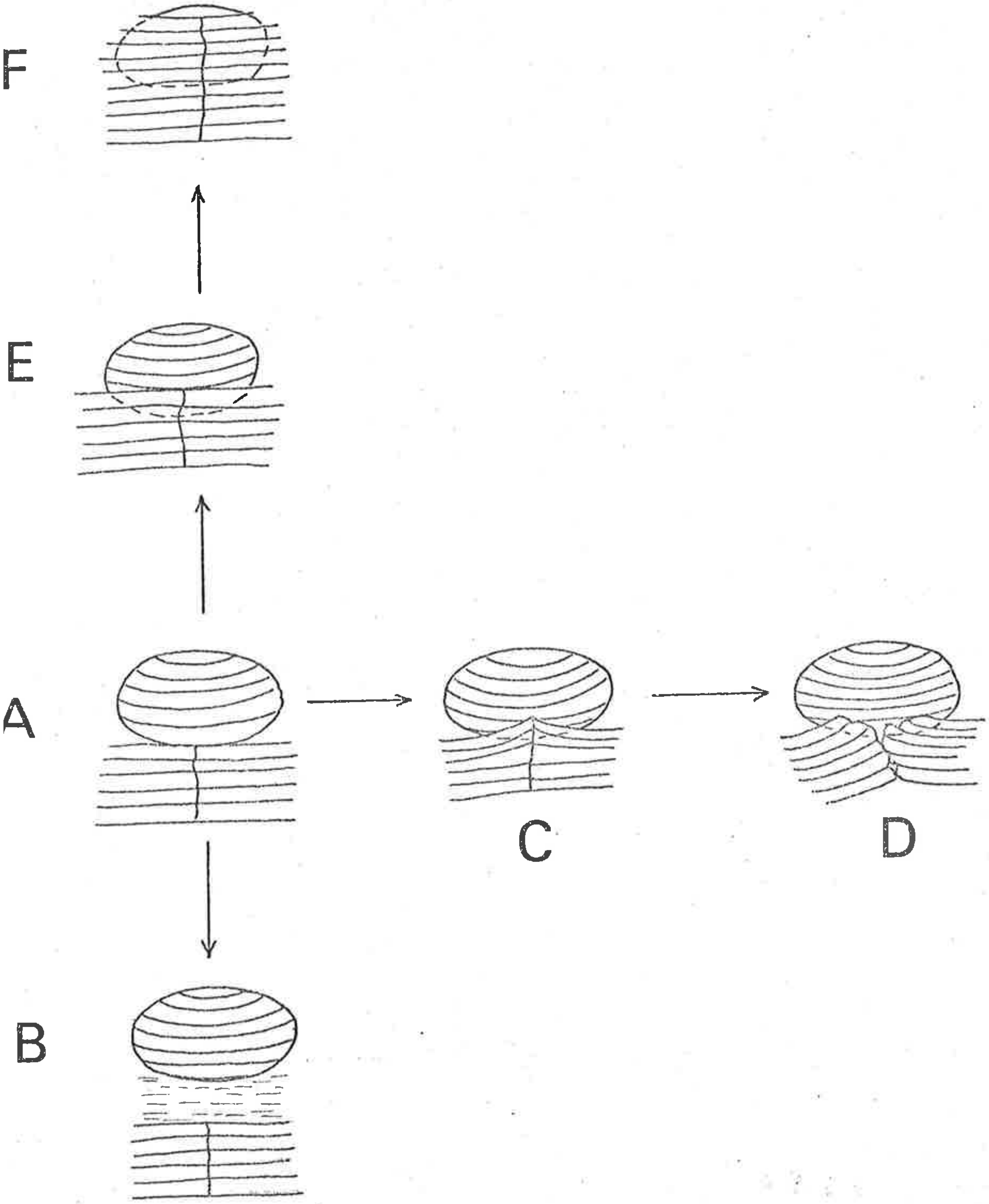


FIGURE 34: Differences in associations between M. submentalis and M. intermandibularis, and their possible evolutionary paths.

supercategories. Hence the most anterior fibres of the intermandibularis may be contiguous with the posterior fibres of the submentalis (Fig. 34A), or the two muscles may be separated from one another (Fig. 34B). The medial tips of the anterior fibres may attach upon the medial portion of the posterior fibres of the ventral surface of the submentalis (Fig. 34C), or upon the entire posterior border (Fig. 34D). The anterior fibres may traverse the posterior border (Fig. 34E), or even cover the entire ventral surface (Fig. 34F).

For the purpose of evaluating the possible directions of evolutionary change (indicated by arrows in the figure), it is assumed that each of the forms either has arisen directly from the one most readily equated with the theoretically primitive model, or from it via an intermediate step in the same evolutionary direction.

The morphological divergence in the anterior division of the intermandibularis can be assessed, but perhaps with less assurance. Basically, there is a single sheet of fibres (Fig. 35A), of which the most anterolateral may change their orientation uniformly (Fig. 35B). Alternatively, the superficial fibres may change their orientation, but the deep fibres dorsal to them may remain unchanged, so producing a separate sheet of the muscle (Fig. 35C). Further evolutionary opportunities are available to the newly evolved sheet. Hence it may migrate laterally on to the ventral surface of the mandible (Fig. 35D), or shift anterolaterally until it lies adjacent to the mandible (Fig. 35E). From the form in

FIGURE 35: Morphological divergence in anterior division of M. intermandibularis and possible paths of evolution.

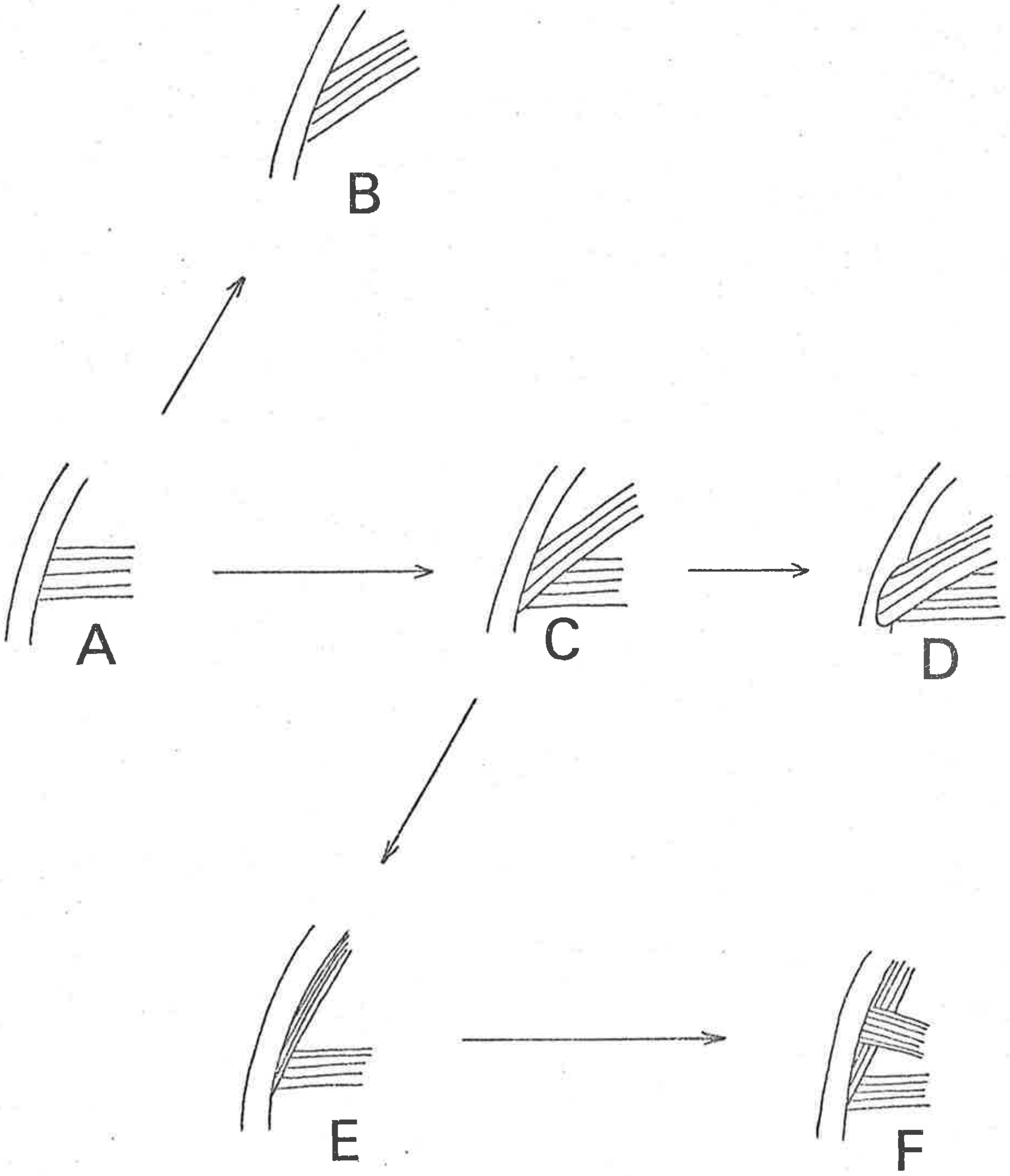
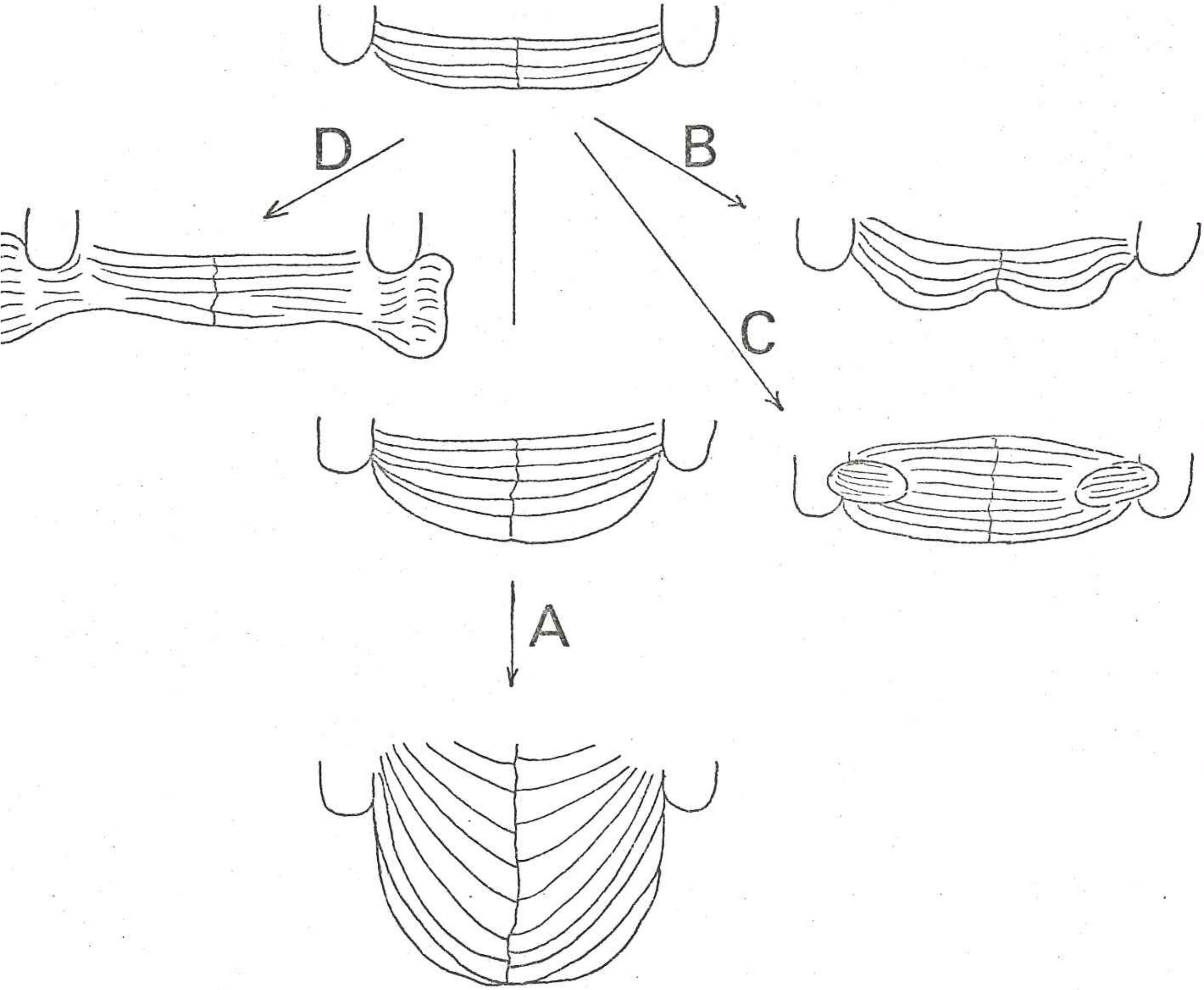


Fig. 35E the condition represented in Fig. 35F may arise, namely evolution of a further supplementary muscle sheet. To achieve that end all that is required is for the fibres of the customary sheet to extend to and occupy a more ventral position on the mandible, so enveloping the sheet lying adjacent to the mandible.

Insofar as the posterior border of the intermandibularis is concerned (and hence its position in relation to the interhyoideus), only two clear variants from the basic pattern have been observed. Hence the interhyoideus may extend anteromedially and so occupy a portion of the submandibular area either with a compensatory reduction of the intermandibularis as in *Arthroleptis* (Fig. 23), or without such a reduction as in many microhylids. These are independent evolutionary paths reflected by comparably major differences in larval muscle relationships (Starrett, 1973). Whether median aponeuroses, so frequently observed in the intermandibularis and less frequently in the interhyoideus, similarly reflect larval divergence is not known. Because the existence of a broad aponeurosis indicates a reduction in the functional powers of the muscle possessing it, it is interpreted to be a derived state.

Several evolutionary paths are represented in the observed extent of divergence of the interhyoideus. The first path involves posterior development (Fig. 36A). The second is represented by the evolution of either bilateral lobes in a ventral position, which can be either broad

FIGURE 36: Morphological divergence in M. interhyoideus and possible paths of evolution.



involutions (Fig. 36B) or discrete evaginations (Fig. 36C). The third involves supramandibular dilatations of muscles to form discrete pouches (Fig. 36D).

The Processes of Evolution

The morphological variation of mandibular muscles reported here can be assessed in terms of the likely processes by which the variation has arisen. Basically there are two major areas: paedomorphosis, being the perpetuation in the adult of a stage normally occurring in the larval or juvenile animal, or gerontomorphosis, which represents modifications only occurring in the adult.

Paedomorphosis is an attractive evolutionary outlet to the extent emphasised by Huxley (1954) of it providing the "possibility of escaping from the blind alleys of specialization". For the anuran mandibular muscles, paedomorphosis is probably exhibited in two distinct modes. Firstly, there is simply the premature arrest of development during ontogeny, without any obvious causative factors, and, secondly, arrest as a consequence of heterochrony in the ontogeny of adjacent muscles.

An example of 'paedomorphic arrest' is exhibited by *Hemiphractus* (Tyler, 1971a, Fig. 8). In that genus anterior development of the intermandibularis has been arrested, so creating a broad gap between the intermandibularis and the submentalis. Similarly, the customary juxtaposition of the intermandibularis and interhyoideus is lacking in that genus. Because all larvae of anuran species studied and reported in the literature exhibit such a stage in the course of their ontogeny, the definition of the adult condition of *Hemiphractus* as paedomorphic is considered justified.

Paedomorphosis as a consequence of a positive competitive situation involving heterochrony during ontogeny has been proposed by Tyler (1972a) to explain his observations on *Glauertia*. In that genus the intermandibularis is arrested anteriorly, but in association with a more superficial origin of the geniohyoideus lateralis. Thus the geniohyoideus occupies a portion of the mandible customarily providing a site for the most anterior fibres of the intermandibularis. It follows that such a condition precludes normal anterior development of the interhyoideus and is not an example of the muscle simply arresting.

In the case of the supplementary muscles, data available at the present time indicate that they arise immediately following metamorphosis (data from Tyler, 1971a, for *Litoria*). These therefore constitute subgerontomorphic changes which, if the present interpretation is correct, are of functional significance only to adult males.

Evolutionary Trends and Phylogenetic Implications

Numerous studies have been undertaken with the object of establishing the most reasonable phylogeny of the Anuran families, of genera within those families, and species within genera. The current trend is to question the reliance placed upon certain characters by early workers such as Boulenger and Cope, in particular the vertebral column and the pectoral girdle. We now see the amassing of considerable data and attempts to establish the direction of change of each character from 'primitive' to 'derived' states, with 'primitiveness' being assessed for species, genera or families retaining the greatest number of primitive characters. The contributions of Lynch (1970, 1973) illustrate this form of approach.

Certainly, I have argued previously that certain myological conditions exhibited by existing species are primitive, but only in the sense that they have in no way been modified from the musculature possessed by ancestral forms. It is the derived and highly modified forms of musculature which are of the greatest interest, for their diversity should be compatible with current phylogenetic concepts if the evolutionary sequences presented here have any merit.

At the outset it is necessary to establish my attitude to the treatment of the data that I consider. The most important issue is that I do not regard the muscular tissues of the mandibular region and the vocal sac as a single character, but as an array of characters subject to change. An analogy can be drawn with the skull, to the extent of there being numerous components which in certain respects are independent and in other respects interdependent. Enlargement of any one is usually only accomplished by reduction in the size of another. In certain circumstances roles may alter and, in the case of the muscles, additional sheets may evolve.

Mandibular muscles tend to be conservative in the evolutionary sense (Tyler, 1971a). Certainly, it has been demonstrated that the differences between genera established by other workers using other criteria are of a greater order of magnitude than the differences between congeneric species.

My object in this section of this chapter is to establish the evolutionary trends of the superficial mandibular musculature of the anurans studied, and to determine whether these are compatible with recently published contributions on the phylogenetic relationships and evolutionary history of those same anurans.

(a) Microhylidae

This family occurs in the southern half of the African continent, south-east Asia, New Guinea, the extreme north and north-east of Australia, the southern portion of North America, in Central America, and north-western South America. Savage (1973) regards the family "probably the most difficult and diverse of frog groups". My survey has included all genera occurring in New Guinea and Australia, but few from outside this region. It does, however, permit examination of Savage's action of combining the two subfamilies occurring in New Guinea. Such subfamilial units (the Asterophryinae and Sphenophryninae) were proposed by Parker (1934), and have been recognised by all subsequent contributors prior to Savage (1973). Savage maintained that the subfamilies differ only in that the vertebrae of the Asterophryinae are diplasiocoelous, whereas those of the Sphenophryninae are procoelous. He drew attention to several features shared by both subfamilies and claimed that Parker's (1934) inclusion of the procoelous *Genyophryne* in the Asterophryinae supported his own action of lumping the two subfamilies together (an action that Parker had indicated might prove necessary).

Savage did not cite Zweifel (1971) who referred *Genyophryne* to the Sphenophryninae, and, whilst Savage's paper was in press, Zweifel (1972) completely reassessed the generic content and relationships of the reconstituted Asterophryinae.

As demonstrated here, *Genyophryne* and the other members of the Sphenophryninae share a comparatively simple form of superficial mandibular musculature as far as microhylids are concerned. The presence of a comparable form of musculature in the Asterophryine *Hylophorbus* means that there is no unique myological character supporting the recognition of the Sphenophryninae. However, the complexity of the Asterophryinae can be interpreted as follows.

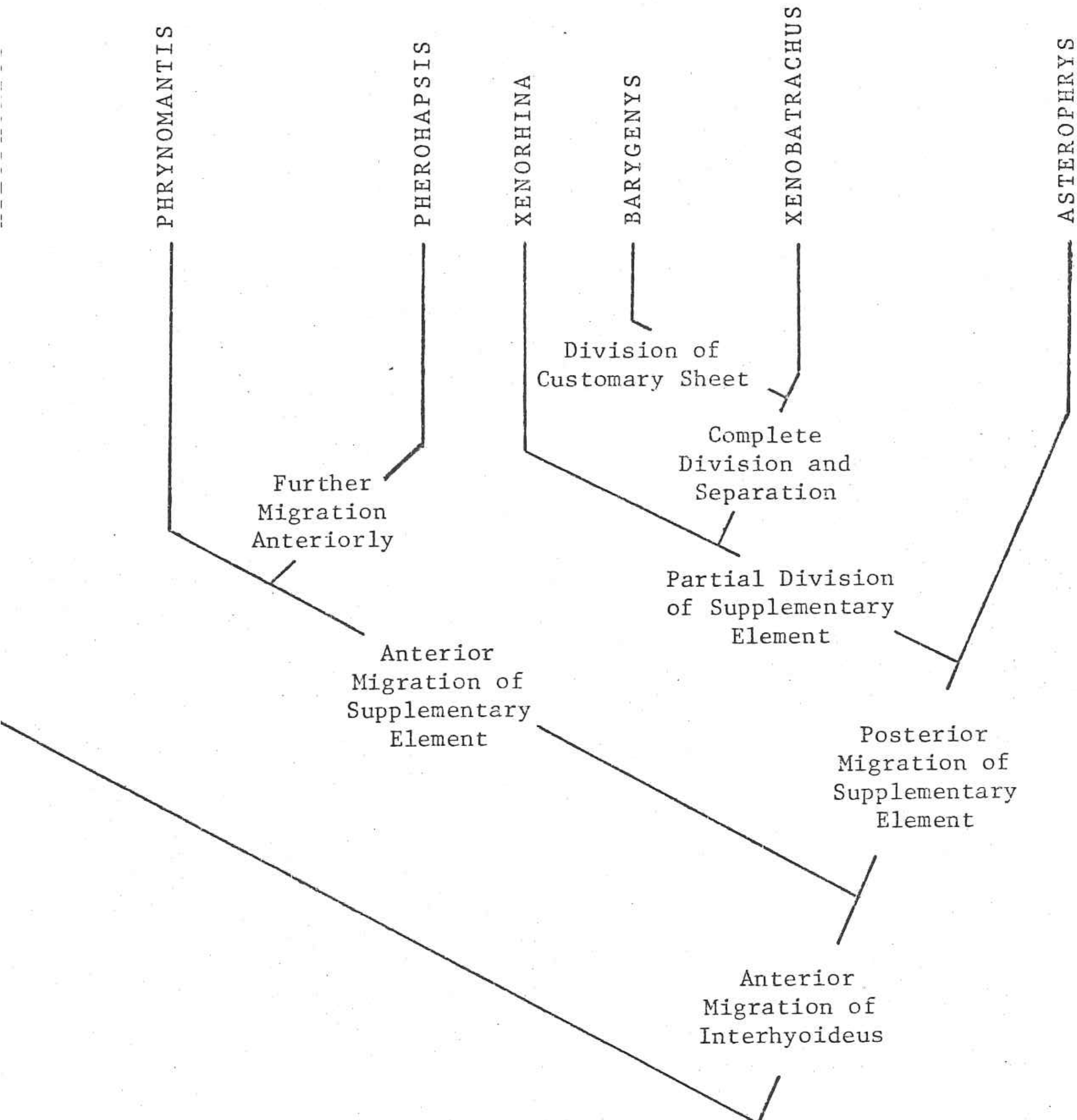
Although there is considerable morphological diversity in the genera of the Asterophryinae, all have an intermandibularis bearing a median aponeurosis; all exhibit at least one additional element of the intermandibularis, and there is a trend towards the division of the element. In addition, in the majority of genera the interhyoideus partly underlies and attaches upon the customary sheet of the intermandibularis.

Of the seven genera I regard the superficial mandibular musculature of *Hylophorbus* the most primitive, principally because the supplementary element of the intermandibularis is the simplest form in the subfamily. The site of origin, shape and the discrete nature of this muscle are features shared by the members of several families. In contrast, the vast posterior lobe of the interhyoideus in *Hylophorbus* is a quite independent feature and clearly represents a derived state.

From the basic form of the supplementary element in *Hylophorbus* it is possible to trace two major paths (Fig. 37). The first of these involves anterior migration of the site of origin and reduction of the width of the muscle exhibited in an anagenetic sequence through *Phrynomantis* to *Pherohapsis*. In fact, the evolution of the type of musculature exhibited by *Pherohapsis* from a *Hylophorbus* type is only possible via a form of musculature comparable to that now exhibited by *Phrynomantis*.

The second, and diverging, evolutionary path involves posterior migration of the site of origin accompanied by division of the body of the muscle. From a *Hylophorbus* form this could be accomplished via an intermediate stage of incipient division (as exhibited by *Xenorhina*, where three heads and two insertion sites occur) leading to two separate muscles in *Xenobatrachus* and *Barygenys*. Thus, although there is a considerable morphological gap between *Hylophorbus* and *Barygenys*, the presence of potentially intermediate conditions in the other living genera indicate the path by which the current complexity of *Barygenys* may

FIGURE 37: Dendrogram of phylogenetic relationships of the Asterophryine microhylid genera.



have evolved. Zweifel (1972) presented alternative phylogenies derived from cranial characters which, with one exception, were osteological features. In each phylogeny *Hylophorbus* is represented as the genus retaining the largest number of primitive character states, and *Pherohapsis/Asterophrys* and *Xenorhina/Xenobatrachus* are considered very closely related pairs of genera. Hence Zweifel's phylogenies and the one presented here differ principally in that the myological data do not support the concept of a close relationship existing between *Pherohapsis* and *Asterophrys*.

(b) Ranidae

The Ranidae are virtually cosmopolitan and the only continent upon which their distribution is sparse is Australia, where they are confined to the Cape York Peninsula. Liem (1970) has proposed the resurrection of the Hyperoliidae and Rhacophoridae for the Old World (ranid) tree frogs, but Savage (1973) accords them only their former sub-familial status. The systematics of the Ranidae remains chaotic, and so it is of interest to establish the morphological diversity of the species described here and the systematic implications of that variation.

The superficial mandibular musculature was examined by Liem (1970), who identified the supplementary muscles according to their shape rather than their relationship to one another. Hence he erected the name dentomentalis for the slender slip and submaxillaris ventralis for the clearly separated, broader ventral muscle sheet.

Unfortunately, I find up to four separate layers of muscle fibres and not three, and I have been unable to apply Liem's terminology. I certainly admit the desirability of a muscle nomenclature in such a morphologically complex situation, but at present it is not possible to use Liem's names (when comparing genera) with any certainty that the structures are homologous.

The data presented here demonstrate a fairly common trend towards anteromedial inclination of the anterior fibres of the intermandibularis, of attachment of some of the fibres upon the ventral surface of the submentalis, and of separation of the intermandibularis into two or more sheets. The only conspicuous exception is the African *Pyxicephalus*, where the transverse orientation of the intermandibularis fibres is maintained and the single sheet completely underlies the ventral surface of the submentalis.

The most striking example of morphological divergence in the Ranidae is exhibited by the African *Hemisus*. The very large posterior lobe of the interhyoideus was not observed in any other ranid genus but is common to many microhylids. In fact, the shape and size of the interhyoideus was not observed in any other ranid genus but is common to many microhylids; the features of the interhyoideus and the form of the supplementary elements of the intermandibularis of *Hemisus* are strikingly like the muscle architecture of the microhylid genus *Breviceps*.

Hemisus was regarded a microhylid until de Villiers (1933) considered such a relationship untenable and referred the genus to the Ranidae. Although Parker (1934) and subsequent contributors have supported de Villiers and adopted his proposal, the data on superficial mandibular musculature, complemented by the absence of the cutaneous pectoris, indicate that *Hemisus* would be more appropriately placed in the Microhylidae.

Also worthy of particular note are the numerous features common to all genera confined to the Solomon Islands (*Ceratobatrachus, Palmatorappia* and *Batrachylodes*), and to *Discodeles*, which occurs in the Solomon Islands and New Britain. The concept of the monophyletic origin of this group of genera is strongly supported by the new data on superficial mandibular musculature.

The morphological divergence observed in *Rana* is correlated with the geographic distribution of the species examined. Hence variant A is confined to New Guinea and the Oriental Region; variant B to the Holarctic Region; variant C to New Guinea and islands to the east and variant D to the Philippines. The sample is small in terms of the number of species now retained in the genus, but it is quite conceivable that this geographic association could ultimately contribute to any future review of the genus.

(c) Hylidae

There are so many species and genera of hylid frogs that the major problem facing present zoologists is to establish whether the family is genuinely monophyletic. With a few notable exceptions, there is scant variation in the basic architecture of superficial mandibular muscles and the extent to which they can contribute to the problem is limited. This contribution is discussed by Tyler (1971a) and is summarised as follows.

Basically, hylids exhibit four quite distinct types of musculature: (1) absence of supplementary muscles; (2) presence of an anterolaterally disposed supplementary element; (3) presence of an apical element and (4) presence of a posterolaterally disposed element. These are clear-cut morphological types, highly suited as criteria of value in anuran systematics. However, the contrast with the Ranidae and Microhylidae is the absence of any existence of "intermediate" steps in the living genera, and there is little that the muscles can contribute to an overall understanding of the phylogeny of the family. It is certainly possible to arrive at the assumption that each of the three forms of supplementary muscles has resulted independently.

Savage (1973) has resurrected the family name Pelodryadidae for the Australian and New Guinea hylids and only quotes my studies on superficial mandibular musculature as a means of support for this proposal. The reference that he cites is the manuscript of my 1971a paper. I believe his information is based on a lecture on this topic that I presented at the University of California in 1971. Although I do indeed doubt that the hylids of Australia are genuine hylids, my data do not, as he states, "refute" their familial disposition. All that they have demonstrated are: (1) that these species are not congeneric with *Hyla*, hence my proposal for the resurrection of *Litoria* for them; (2) that all hylids from Australia and New Guinea exhibit a similar supplementary element of the intermandibularis.

(d) Leptodactylidae

The overall nature of morphological divergence observed in the Leptodactylidae is similar to that reported above for the Hylidae, with the exception that the condition of the anterior portion of the customary element of the intermandibularis in the Cycloraninae is not exhibited by any hylid. The only subfamilies that have been completely sampled by me are the Cycloraninae, Myobatrachinae and Heleophryninae. I shall confine my attention here to them.

The superficial mandibular musculature provides evidence in support of the recognition of subfamilial separation for the genera currently referred to the Cycloraninae and Myobatrachinae. The musculature of the Myobatrachinae is of a simple and largely primitive pattern. In contrast, all Cycloranine genera exhibit derived conditions. If *Cyclorana* is initially excluded from consideration, the subfamily can be defined as a group of Australo-Papuan genera in which the anterior fibres of the intermandibularis underlie at least a portion of the submentalis. *Cyclorana* does not exhibit this condition, and is further distinguished from all other Cycloranine genera by its possession of a supplementary element of the intermandibularis of the apical type. It is because of the extent of homogeneity of all other Cycloranine genera that the divergence of *Cyclorana* has assumed importance (Tyler, 1972a). Substantiation for the hylid affinities that the musculature indicates has been provided by Watson and Martin (1973), who found comparable affinities to hylids and divergence from leptodactylids when they undertook a study of external larval morphology.

The monogeneric Heleophryninae has musculature comparable to that exhibited by the Myobatrachinae, which conflicts with Lynch's (1973) contention of there being a closer association between the Heleophryninae and Cycloraninae than between the Heleophryninae and Myobatrachinae. Nevertheless, Lynch's means of separation is tenuous and is at least partly derived from false data (for example, the statement that no member of the Cycloraninae is known to exhibit inguinal amplexus; in reality, all genera examined by me exhibit it).

(e) Supra-familial Relationships

It has been demonstrated that there are some basic similarities between the musculature of most ranids and microhylids and between hylids and leptodactylids. The former pair of families exhibit a trend towards the evolution of supplementary muscle elements occupying the anterior segment. The Hylidae and Leptodactylidae exhibit a variety of elements common to both families, and one, the 'apical' element, is not exhibited by any ranid or microhylid. Thus the muscle data do not conflict with current concepts of the Hylidae and Leptodactylidae being phylogenetically closely related to one another.

Of the other families studied but not discussed above, two require individual attention: the Rhinodermatidae and Rhinophrynidae, both of which are monogeneric. The Rhinodermatidae was erected for *Rhinoderma* by Lynch (1973) and had formerly been placed in the Leptodactylidae. Lynch makes it clear that he recognises a close association between the two families. The presence of an apical element of the intermandibularis in *Rhinoderma* attests to it.

It has frequently been suggested that the Rhinophrynidae is closely related to the Pipidae. Unfortunately, the superficial mandibular musculature does not provide support for the existence of such a relationship. Whereas *Rhinophrynus* has an incredibly complex musculature, with supramandibular lobes to the interhyoideus, an interhyoideus component proceeding from the dorsal surface of the pectoral girdle, and the presence of the mandibulo-mentalis, the pipids *Pipa* and *Xenopus* have an incompletely developed intermandibularis, a poorly developed interhyoideus of simple form and no additional muscles (Beddard, 1895a, 1895b).

EVOLUTION OF MANDIBULAR MUSCLES IN VERTEBRATES

The problems of attempting to employ cranial muscles in broad interpretations of evolution within the Vertebrata have been well summarised by Brock (1938) as follows:

"Muscles are notoriously difficult to reduce to a coherent, comparative scheme, since they are the most adaptable and changeable of morphologic structures, responding to new functional demands upon them with a readiness to migrate, to subdivide, or not to 'divide'."

Of the cranial, by far the greatest attention has been devoted previously to the maxillo-mandibular muscle complex, but knowledge of the path of the trigeminal in the Anura, important to deduction, has been confined to studies on very few species. This deficiency has led to false conclusions. Hence Lubosch (1933) reached the conclusion that the adductors mandibulae of the Selachian fishes was independently derived from the general superficial constrictor sheet, claiming that in that group the trigeminal is unique amongst vertebrates in lying lateral to the constrictor muscles. Brock (1938) is in agreement with the anatomical data but not with the deduction. She states, however, that in all tetrapods the trigeminal nerve is embedded in the muscle mass. That statement is erroneous, for in the Anura the trigeminal is within or lateral to the mandibular adductors, but admittedly as a loss of superficial muscles on several occasions. For example, in the hylid genera *Acris, Hyla, Hylella, Plectrohyla, Ptychohyla, Sphaenorhynchus* (Starrett, 1960), and twenty-eight species of *Litoria* and in the leptodactylid genera *Cyclorana, Lechriodus, Limnodynastes* and *Notaden* (Tyler, unpublished observations), the trigeminal occupies a superficial position. The nerve has remained absolutely unchanged, but the muscles lying lateral to it have been variously lost.

Tracing homologies is a hazardous occupation. However, it is clear that the superficial intermandibularis and interhyoideus persist throughout the fishes and reptiles. The submentalis is the muscle which is of variable occurrence. It is present in some members of the Urodela and Lacertilia, but absent in others (Lightoller, 1939; Piatt, 1940; Kesteven, 1944; Tanner, 1952; Ozeti and Wake, 1969). It is absent in the Dipnoi and Rhyncocephalia, and recognisable as distinct from the intermandibularis mass in only some birds (Kesteven, 1944). The variation in the urodeles needs to be qualified by noting that it is present in all larvae and is lost at metamorphosis in several families.

Within the Class Amphibia the interhyoideus is of particular interest. In all urodeles this muscle forms two distinct portions: the interhyoideus and the interhyoideus posterior in both larvae and adults. In larval anurans the interhyoideus posterior is present in only a few species, whilst in adults the separate slip described here in *Rhinophrynus dorsalis* may constitute the sole occurrence in the entire order.

Extending interpretation of homologies to higher vertebrates appears to hinge upon the peculiar condition exhibited by the monotremes. The most major change in comparison with the lower vertebrates involves the radical alteration of the jaw suspension, resulting in loss of the depressor mandibulae. Whereas the monotremes have developed the detrahens mandibulae to undertake the new function, and innervated entirely by the trigeminal, the marsupials and placental mammals have evolved a digastric muscle, of which the anterior belly is innervated by the trigeminal nerve and the posterior by the facial. Despite the magnitude of this evolutionary step and the gross intergeneric variation (Adams, 1919; DuBrul, 1958), the derivation of these bellies are from a superficial division of the customary vertebrate intermandibularis and a portion of the interhyoideus (Huber, 1930; Edgeworth, 1935).

Throughout each vertebrate group the intermandibular muscles have undergone major adaptive changes associated with various cranial mechanics. For example, in the urodele families Plethodontidae (Tanner, 1952) and Salamandridae (Ozeti and Wake, 1969) divergence, particularly in the position of sheets of the intermandibularis, can be attributed to the functional demands of feeding techniques involving depression of the mouth floor.

When the divergence in the Anura reported here is compared with the corresponding extent of divergence amongst other vertebrates, it can be viewed in its proper perspective. It seems reasonable to interpret the morphological changes as a reflection of major adaptive shifts, and to recognise that these changes are sufficiently profound to partly obscure the evolutionary progression that is detectable throughout the vertebrate kingdom. It follows that to attempt to homologise particular anuran muscle elements with similarly disposed sheets in other vertebrates would constitute an unjustified and extremely hazardous extrapolation.

APPENDIX I

LIST OF SPECIES EXAMINED

FAMILY: DISCOGLOSSIDAE

Alytes obstetricans

Barbouroula busuangensis

Bombina bombina, B. variegata

FAMILY: HYLIDAE

Sub-Family: Amphignathodontinae

Amphignathodon guntheri

Anotheca spinosa

Cryptobatrachus fuhrmanni

Flectonotus fissilis

Fritziana goeldi, F. ohausi

Gastrotheca ceratophrys, G. marsupiatum, G. nicefori.

Nyctimantis rugiceps

Sub-Family: Hemiphractinae

Hemiphractus proboscideus, H. scutatus

Sub-Family: Hylinae

Acris crepitans, A. gryllus

Allophryne ruthveni

Aparasphenodon brunoi

Aplastodiscus perviridis

Argenteohyla siemersi

Calyptahyla lichenata

Corythomantis greeningi

Hyla albofrenata, H. alboguttata, H. albomarginata,
H. albopunctata, H. albosignata, H. arborea, H. bifurca,
H. bipunctata, H. boans, H. boulengeri, H. brieni,
H. calcarata, H. catharinae, H. circumdata,
H. columbiana, H. colymba, H. crepitans, H. crospedospila,
H. crucifer, H. cuspidata, H. decipiens, H. depressiceps,
H. ebracatta, H. egleri, H. elongata, H. euphorbiacea,
H. faber, H. fasciata, H. femoralis, H. fuscomarginata,
H. fuscovaria, H. garbei, H. geographica,
H. goughi, H. granosa, H. granulata, H. gratiosa,
H. hayi, H. heilprini, H. lancasteri, H. lanciformis,
H. leucophyllata, H. lindneri, H. loquax, H. marianae,
H. marmorata, H. megapodia, H. microcephala,
H. microps, H. miliaris, H. minuta, H. misera,
H. nana, H. nasica, H. pardalis, H. parviceps,
H. pellucens, H. pentheter, H. phrynoderma, H. pickeli,
H. polytaenia, H. pulchella, H. pulchrilineata,
H. punctata, H. raddiana, H. regilla, H. reticulata
H. rivularis, H. robertsorum, H. rondoniae,

H. rosenbergi, H. rubra, H. sanborni, H. senicula,
H. simplex, H. smaragdina, H. spegazzini,
H. squirella, H. subocularis, H. truncata, H. vasta,
H. versicolor, H. werneri, H. wilderi

Limnoedus ocularis

Litoria adelaidensis, L. alboguttata, L. amboinensis,
L. angiana, L. arfakiana, L. aurea, L. bicolor,
L. booroolongensis, L. brevipalmata, L. burrowsi,
L. caerulea, L. chloris, L. citropa, L. congenita, L. contrastens,
L. coplandi, L. cyclorhynchus, L. darlingtoni, L. dayi, L. dentata,
L. dorsalis, L. dorsivena, L. eucnemis,
L. everetti, L. ewingi, L. freycinetti, L. genimaculata, L. glauerti,
L. gracilenta, L. impura, L. inermis, L. infrafrenata, L. iris,
L. jervisiensis, L. latopalmata, L. lesueuri, L. longicrus, L. lutea,
L. maculata, L. meiriana, L. microbelos, L. micromembrana,
L. modica, L. moorei, L. multiplica, L. nannotis,
L. nasuta, L. nigrofrenata, L. nigropunctata,
L. pearsoni, L. peroni, L. phyllochroa, L. prora, L. pygmaea,
L. rothi, L. rubella, L. sanguinolenta, L. spinifera,
L. thesaurensis, L. timida, L. verreauxi, L. vincivocens,
L. wisselensis, L. wotjulumensis.

Nyctimystes cheesmanae, N. daymani, N. foricula, N. kubori,
N. narinosa, N. papua, N. pulchra, N. rueppelli

N. tympanocryptis, N. vestigea, N. zweifeli.

Osteocephalus buckleyi, O. leprieuri, O. pearsoni, O. taurinus, O. verrucigerus

Osteopilus brunneus, O. dominicensis, O. septentrionalis

Phrynohyas coriacea, P. mesophaea, P. venulosa

Phyllodytes wuckereri

Plectrohyla guatamalensis, P. ixil

Pseudacris nigrita, P. ornata, P. triserrata

Pternohyla fodiens

Ptychohyla leonhardschultzei, P. spinipollex

Smilisca baudina, S. phaeota, S. puma

Sphaenorhynchus aurantiacus, S. eurhotus, S. orophilus

Trachycephalus jordani, T. nigromaculatus

Triprion petasatus, T. spatulatus

Sub-Family: Phyllomedusinae

Agalychnis callidryas, A. saltator

Pachymedusa dacnicolor

Phyllomedusa appendiculata, P. bicolor, P. burmeisteri, P. edentula, P. fimbriata, P. guttata, P. hypochondrialis, P. lemur, P. rohdei

FAMILY: LEIOPELMATIDAE

Ascaphus truei

Leiopelma archeyi, L. hamiltoni, L. hochstetteri

FAMILY: LEPTODACTYLIDAE

Sub-Family: Cycloraninae

Adelotus brevis

Cyclorana australis, C. brevipes, C. cultripes, C. dahli, C. platycephalus

Heleioporus albopunctatus, H. australis, H. barycragus, H. eyrei, H. inornatus, H. psammophilus

Kyarranus loveridgei, K. sphagnicolus

Lechriodus fletcheri, L. papuanus, L. platyceps

Limnodynastes convexiusculus, L. dorsalis, L. dumerili, L. fletcheri, L. insularis, L. ornatus, L. peroni, L. salmini, L. spenceri, L. tasmaniensis, L. terraereginae

Mixophyes balbus, M. fasciolatus, M. iteratus

Neobatrachus centralis, N. pelobatoides, N. pictus, N. sutor, N. wilsmorei

Notaden bennetti, N. melanoscaphus, N. nichollsi

Philoria frosti

Sub-Family: Ceratophryinae

Ceratophrys appendiculata

Sub-Family: Elosiinae

Hylodes aspera

Sub-Family: Heleophryninae

Heleophryne natalensis, H. purcelli

Sub-Family: Leptodactylinae

Leptodactylus nanus

Pseudopaludicola falcipes

Sub-Family: Myobatrachinae

Assa darlingtoni

Crinia georgiana, C. haswelli

Geocrinia laevis, G. leai, G. victoriana

Glauertia orientalis, G. russelli

Myobatrachus gouldi

Pseudophryne bibroni, P. corroboree, P. dendyi, P. guentheri, P. nichollsi, P. occidentalis, P. semimarmorata

Ranidella glauerti, R. parinsignifera, R. riparia, R. signifera, R. tinnula

Rheobatrachus silus

Taudactylus acutirostris, T. diurnus, T. rheophilus

Uperoleia marmorata, U. rugosa

Sub-Family: Telmatobiinae

Cycloramphus asper, C. dubius

Eleutherodactylus guntheri

Hylactophryne augusti

Ischnocnema quixensis

Thoropa miliaris

FAMILY: MICROHYLIDAE

Sub-Family: Asterophryinae

Asterophrys turpicula

Barygenys atra, B. cheesmanae

Hylophorbus rufescens

Pherohapsis menziesi

Phrynomantis humicola, P. lateralis, P. personata, P. robusta, P. stictogaster, P. wilhelmana

Xenobatrachus mehelyi, X. obesus, X. rostratus

Xenorhina dubia

Sub-Family: Brevicipitinae

Breviceps poweri, B. mossambica

Sub-Family: Cophylinae

Rhombophryne testudo

Sub-Family: Microhylinae

Kaloula conjuncta, K. picta, K. pulchra

Sub-Family: Sphenophryninae

Cophixalus cheesmanae, C. darlingtoni, C. ornatus, C. oxyrhinus, C. parkeri, C. riparius, C. shellyi, C. verrucosus

Genyophryne thomsoni

Oreophryne biroi, O. brachypus, O. flava

Sphenophryne brevicrus, S. cornuta, S. fryi, S. mehelyi S. robusta

FAMILY: PELODYTIDAE

Pelodytes punctatus

FAMILY: RANIDAE

Arthroleptis stenodactylus

Batrachylodes elegans, B. mediodiscus, B. trossulus, B. vertebralis, B. wolfi

Discodeles bufoniformis, D. guppyi

Hemisus marmoratum

Palmatorappia solomonis

Phrynobatrachus natalensis

Platymantis boulengeri, P. corrugatus, P. dorsalis, P. hazelae, P. meyeri, P. papuensis

Ptychadena anchietae

Pyxicephalus adspersus

Rana arfaki, R. arvalis, R. catesbeiana, R. clamata, R. dalmatina, R. esculenta, R. grisea, R. grunniens, R. jimiensis, R. limnocharis, R. palustris, R. papua, R. ridibunda, R. temporaria, R. tigrina, R. verruculosa, R. viridis, R. vitigera

Staurois natator

FAMILY: RHINODERMATIDAE

Rhinoderma darwini

FAMILY: RHINOPHRYNIDAE

Rhinophrynus dorsalis

APPENDIX II

SOURCES OF MATERIAL EXAMINED

FROM INSTITUTIONS

American Museum of Natural History (Dr R. G. Zweifel, Dr C. W. Myers)

Australian Museum (Dr H. G. Cogger)

British Museum, Natural History (Miss A. G. C. Grandison)

California Academy of Sciences (Dr A. E. Leviton)

Dominion Museum (Mr J. Moreland)

Museum of Comparative Zoology (Professor E. E. Williams)

National Museum of Victoria (Mr J. Coventry)

Naturhistorisches Museum, Vienna (Dr J. Eiselt)

Queensland Museum (Miss J. Covacevich)

South Australian Museum (late Mr F. J. Mitchell, Dr T. Houston)

United States National Museum (late Dr J. A. Peters)

University of Florida (Dr W. Auffenbeck)

University of Kansas (Professor W. E. Duellman)

University of Zambia (Professor P. M. Miles)

University of Melbourne (Dr M. J. Littlejohn, Dr A. A. Martin)

University of New England (Mr J. de Bavay)

University of Papua and New Guinea (Mr J. I. Menzies)

Western Australian Museum (Dr G. M. Storr)

Zoologisches Forschungsinstitut und Museum Alexander Koenig (Dr W. Böhme)

FROM INDIVIDUALS

Miss M. Anstis, Mr D. Bloodworth, Mr B. Brock, Mr K. Cole, Mr H. Ehmann, Mr A. Fischer, Mr F. Parker, Dr L. A. B. Richardson, Mr A. D. Roberts

PUBLISHED PAPERS RELEVANT TO TOPIC OF THESIS

1. The phylogenetic significance of vocal sac structure in hylid frogs.
   Univ. Kansas Publ. Mus. Nat. Hist. (1971) 19 (4): 319-360.
2. Observations on anuran myo-integumental attachments associated with the vocal sac apparatus.
   J. Nat. Hist. (1971) 5: 225-331.
3. The occurrence of the Musculus cutaneous pectoris in the Anura.
   Herpetologica (1971) 27 (2): 150-152.
4. Voluntary control of the shape of the inflated vocal sac by the Australian leptodactylid frog *Limnodynastes tasmaniensis*.
   Trans. R. Soc. S. Aust. (1971) 95 (1): 49-52.
5. Superficial mandibular musculature, vocal sacs and the phylogeny of Australo-Papuan leptodactylid frogs.
   Rec. S. Aust. Mus. (1972) 16 (9): 1-20.
6. Endochondral ossification of the hyoid plate in Australo-Papuan hylid frogs.
   Zool. Anz. (1972) 189 (5-6): 331-336.
7. (With L. Trueb)
   Systematics and evolution of the greater Antillean hylid frogs.
   (In press)

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Endochondral Ossification of the Hyoid Plate in Australo-Papuan Hylid Frogs

By

Michael J. Tyler[1]

With 1 Figure and 1 Table

(Eingegangen am 10. Januar 1972)

Introduction

The principal component of the adult anuran hyoid is a thin, flat and lly entirely cartilaginous plate situated beneath the tongue. It is derived netamorphic climax usually from the fusion of paired, lateral branchial ctures to the single, median, basibranchial plate. From the lateral borders he resultant adult hyoid plate processes communicate to other skeletal ctures, whilst muscles attached to the dorsal, ventral and lateral surfaces he hyoid plate pass to the mandibles, tongue, larynx, cranium and ster- . The plate is thus a morphologically complex structure functionally in- ed in buccal respiratory movements, feeding and vocal activity.

Partial endochondral ossification of the hyoid plate has been reported many anuran species (Parker 1881, Trewavas 1933, Stephenson 1960).

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Although such ossification may constitute a means of strengthening a portio of the plate, there have been no attempts to correllate the presence of suc ossification with the presence or absence of associated structures, nor to asses its possible functional significance.

Of forty-two species of Australo-Papuan hylid frogs that I have examine endochondral ossification of the hyoid plate occurs in four species. In thi paper I briefly review and compare the various forms of hyoid ossificatio occurring in the Anura reported in the literature, describe the form and ex tent of the ossification in those Australo-Papuan hylids, and discuss the pos sible functional implications of such ossification. Variation in structural feat ures of the hyoid is also reported.

Species Examined

Adult specimens of the following species of Australo-Papuan hylid frog were examined: *Litoria adelaidensis, L. amboinensis, L. angiana, L. arfakian L. aurea, L. bicolor, L. booroolongensis, L. burrowsi, L. caerulea, L. chlori L. citropa, L. cyclorhynchus, L. darlingtoni, L. dorsalis, L. eucnemis, L. eve retti, L. freycineti, L. genimaculata, L. glauerti, L. inermis, L. infrafrenat L. iris, L. latopalmata, L. lesueuri, L. lutea, L. meiriana, L. micromembran L. moorei, L. multiplica, L. nasuta, L. nigrofrenata, L. peroni, L. phyllochro L. rothi, L. rubella, L. thesaurensis, L. wotjulumensis, Nyctimystes foricul N. kubori, N. narinosa, N. papua, N. tympanocryptis, N. zweifeli.*

Morphology

Of the species listed above endochondral ossification of the hyoid plat occurs in all specimens examined of four species: *Litoria eucnemis, L. geni maculata, L. lesueuri* and *Nyctimystes tympanocryptis,* in each of which suc ossification is confluent with the ossified postero-medial processes of the plat Inter-specific variation between the four species involves the extent to whic the endochondral ossification extends anteriorly from the customary bound ries of these postero-medial processes.

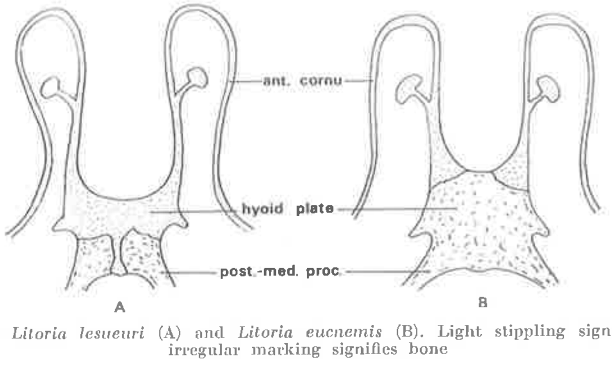

Fig. 1. Hyoids of *Litoria lesueuri* (A) and *Litoria eucnemis* (B). Light stippling signifies cartilage a irregular marking signifies bone

Ossification of the hyoid plate is least extensive in *L. genimaculata* and *lesueuri,* in which species it is confined to the immediate vicinity of the tero-medial processes so that these processes present the appearance of ing irregular anterior extremities (Fig. 1 A). In *N. tympanocryptis* the terior half of the plate is ossified and in *L. eucnemis* ossification extends lially to the anterior border of the plate in some individuals (Fig. 1 B) and roaches it in others. In transverse section of the hyoid plate of adult *L. nemis* the replacement of cartilage by bone was found to be complete.

The only observed clear-cut variation in the structure of the hyoid in the cies examined is the presence or absence of the alary processes, which e present in twenty-four species and absent in eighteen (Tab. 1).

Previous Reports of Hyoid Ossification in Australian Hylids

Parker's (1881) illustration of the hyoid of "*L. marmorata*" indicates the stence of ossification comparable in area to that reported here in *N. tym- ocryptis.* He also reported the existence of an isolated area of ossification the hyoid of *L. caerulea.* Unfortunately the specific identity of the speci- is examined by Parker is uncertain; errors in the identification and il- rations of other species in the same paper have been reported (see Ride- D 1897, p. 578 footnote, and p. 580). *Litoria marmorata* was originally cribed from specimens purported to have been collected in eastern Aus- ia, but was considered by Moore (1961) to be a synonym of *L. cyclorhyn- s,* a species confined to Western Australia. I have not observed ossifica- of the hyoid in *L. cyclorhynchus,* and neither Trewavas (1933) nor I e observed ossification in *L. caerulea.*

Discussion

On the basis of superficial similarities in the portions of the hyoid plate are ossified, the various examples of ossification that I have observed in Hylidae and other families, and those reported in the literature, may be veniently considered under the following three categories:

(a) Parahyoid bones: Distinct bones, usually with contoured irregular surfaces, lying upon the surface of the hyoid plate or replacing t of it, have been described in representatives of several families, and are tomarily termed "parahyoid bones".

A single, median parahyoid bone occurs on the ventral surface in all cies of the ascaphid genus *Leiopelma* (Trewavas 1933, Stephenson 1960), paired bones in the discoglossid genera *Alytes, Bombina* and *Discoglos-* In *Discoglossus* the two bones are united by a transverse bar. Trewavas 33) considered that despite variation in number and position the parahyoid es of the above four genera are homologous structures.

Table 1

Species	Vocal sac	Alary Processes	Hyoid Ossification
L. adelaidensis	present	absent	absent
L. amboinensis	„	„	„
L. angiana	„	„	„
L. arfakiana	„	„	„
L. aurea	„	present	„
L. bicolor	„	absent	„
L. booroolongensis	absent	present	„
L. burrowsi	present	„	„
L. caerulea	„	absent	„
L. chloris	„	„	„
L. citropa	„	present	„
L. cyclorhynchus	„	„	„
L. darlingtoni	„	absent	„
L. dorsalis	„	present	„
L. eucnemis	absent	„	present
L. everetti	present	absent	absent
L. freycineti	„	present	„
L. genimaculata	absent	„	present
L. glauerti	present	„	absent
L. inermis	„	„	„
L. infrafrenata	„	„	„
L. iris	„	absent	„
L. latopalmata	„	present	„
L. lesueuri	absent	„	present
L. lutea	present	„	absent
L. meiriana	present	present	absent
L. micromembrana	„	absent	„
L. moorei	„	present	„
L. multiplica	„	absent	„
L. nasuta	„	present	„
L. nigrofrenata	„	„	„
L. peroni	„	absent	„
L. phyllochroa	„	present	„
L. rothi	„	absent	„
L. thesaurensis	„	present	„
L. wotjulumensis	„	„	„
N. foricula	„	absent	„
N. kubori	„	„	„
N. narinosa	„	„	„
N. papua	absent	„	„
N. tympanocryptis	„	present	present
N. zweifeli	present	absent	absent

A narrow and slightly angular, transverse parahyoid ossification extend ing completely across the ventral surface of the plate occurs in the rhinophry nid *Rhinophrynus dorsalis* (Walker 1938), and an equally slender but dif ferently shaped structure is found in the pelobatid *Pelodytes.* In the latte genus it consists of a transverse bar of bone, from each end of which extenc

antero-lateral bars and short postero-lateral bars. Ridewood (1897) re-
ed to this structure as a "splint-bone" and noted that it is attached to the
id plate only at its extremities: he reported that some of the fibres of the
culus hyoglossus pass between the bone and the hyoid plate.

The only parahyoid bone situated dorsal to the hyoid plate which I have
d in the literature is that described in the fossorial African ranid, *Hemi-
guttatum*, by Beddard (1908). This bone does not adhere to the hyoid
e but is apparatenly adpressed to it, and loosely attached to the ventral
ace of the pharynx.

(b) Ossification of isolated portions of the hyoid
te: On the Hyoid of *Hyla albomarginata* there are four small, discrete
s of ossification (Parker 1881).

(c) Ossification confluent with the postero-me-
l processes: The condition in Australian hylids reported here re-
ents this category.

It is therefore apparent that there is no common structural pattern to the
ous forms of ossification listed above. Parahyoid bones include a variety
ructures differing in shape and in the position that they occupy upon the
id. They are therefore probably derived from different portions of the
al hyoid skeleton. In contrast the ossification in Australo-Papuan hylid
ies is basically similar in that in each species it emanates from the pos-
-medial processes. This is quite certain in *L. genimaculata* and *L. lesueuri*,
is assumed to be so in the other species because ossification progressing
any site upon the hyoid plate towards the postero-lateral processes,
ld not be excepted to produce the observed obliteration of the anterior
gins of these processes.

The anuran hyoid plate is normally a thin structure and extremely pli-
in living animals. It can be argued that because parahyoid bones do not
pletely replace the cartilage of the plate, and usually are not intimately
hed to it, their presence is unlikely to affect its flexibility. The nature of
ossification in Australo-Papuan hylids, in contrast, clearly does reduce the
bility of the hyoid plate, indicating a loss of or an alteration to any ac-
y requiring flexion. Accordingly in seeking an explanation for the pre-
e of ossification in such species, I first sought evidence of an association
he presence or absence of ossification, with the presence or absence of
r mandibular structures. The only variable structures in the species ex-
ned proved to be alary processes and the male vocal sac which, in Australo-
uan hylids, is situated ventral to the hyoid (Tab. 1). Each of the four spe-
lacking a vocal sac has an ossified hyoid; conversely no species possessing
cal sac has an ossified hyoid (Tab. 1).

However, two other Australo-Papuan hylids which lack vocal sacs (*Lito-
booroolongensis* and *Nyctimystes papua*: Tyler 1971) also lack ossifica-
One of them, *Nystimystes papua*, has thickened hyoid plate with evi-

dence of calcification which can be an incipient stage in the process of oss fication.

The vocal sac is an inflatable struture functioning as a resonance char ber, so that species lacking a vocal sac produce calls lacking the resonance those species possessing them. Because the mating call emitted by the male the breeding site customarily attracts the female to it, loss of the vocal s reduces the distance at which sound alone can bring about the juxtapositi of the sexes. In the absence of detailed studies of the pre-mating behaviour species lacking vocal sacs, the effect of this loss, and the change in behavio which could favour such loss are unknown.

It could be suggested that ossification of the hyoid plate in Austral Papuan hylids is a consequence of loss of the vocal sac (as opposed to bei directly or indirectly responsible for it), because of the existence of speci lacking both ossification and vocal sacs. However here I have only demo strated that the presence of ossification and loss of the vocal sac are associat phenomena in Australo-Papuan hylids.

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