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CRANIAL OSTEOLOGY AND MYOLOGY OF THE JAW APPARATUS IN THE GALBULIDAE (AVES, PICIFORMES)*

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ABSTRACT

The nature of the relationship among six species of Galbulidae was analysed in terms of cranial osteology, ligaments and myology of the jaw apparatus. A detailed description of G. ruficauda *followed by a comparison with* G. albirostris, G. galbula, G. cyanicollis, Brachygalba lugubris *and* Jacamerops aurea *was made.*

This study showed a close relationship among the species of Galbula *with* Brachygalba lugubris; J. aurea, *on the other hand, presented many differences mainly in osteological structures. Among the species of* Galbula, G. cyanicollis *differed from the general pattern of the genus while* G. ruficauda *and* G. galbula *showed many common characteristics. Key-words: Birds; Galbulidae; osteology; musculature.*

I — INTRODUCTION

The Galbulidae or Jacamars can be defined according to Ridgway (1914) as "small to median-sized desmognathous Picarian birds with long, straight, pointed bill, having both culmen and gonys carinate, a small aftershaft to the contour feathers, vomer absent, and pectoral pteryla with a narrow lateral (clavicular) and an inner (gular) branch; plumage usually metallic (green, bronze, or purplish) on upper parts, sometimes across breast also".

The Galbulidae consist of seventeen species (Haffer, 1974) restricted to the Neotropics. This author shows the family in terms of genera and superspecies. Thus, two genera are monotypic (*Jacamerops* and *Jacamaralcyon*), two are *quasi-monotypic*, *i.e.*, they present only one superspecies each (*Galbalcyrhynchus* and *Brachygalba*) and only *Galbula* possesses two superspecies (*Galbula albirostris* and *Galbula galbula*) as well as two species not placed in superspecies (*Galbula dea* and *Galbula leucogastra*).

The Galbulidae feed on insects in forests and savanna country. They usually wait for the approach of the prey which they capture in the air. After capture they return to the same perch they left (Meyer de Schauensee, 1982). Fry (1970) reported that Hymenoptera account for 85% of the average of the stomach content of *G. ruficauda*. They build their nests in banks by excavating holes about one meter long; male and female participate in this action (Van Tyne & Berger, 1976 and Sick, 1985).

Most papers on Jacamars deal with their occurrence and distribution (Sclater & Salvin, 1869;

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Salvin & Goodman, 1896; Hellmayr, 1907 and 1908; Cory, 1913; Ridgway, 1914; Cherrie, 1916; Chapman, 1917 and 1921; Underdown, 1929; Todd, 1932 and 1943; Zimmer & Phelps, 1947; Novaes, 1952; Maria & Olivares, 1967 and Fitzpatrick & Willard, 1982). Others deal with taxonomy (Sclater, 1879-82; Miller, 1919; Steinbacher, 1937; Sibley, 1956 and Lanyon & Zink, 1987), biology (Skutch, 1937, 1963, 1968 and 1970; Haverschmidt, 1958; Wetmore, 1968 and Burton, 1976) and speciation patterns (Haffer, 1974).

Steinbacher (1937), after studying the skull, the pectoral and pelvic girdles and the digestive system, pointed out that there is a close relationship between the Galbulidae and Bucconidae. However, the former differ from the latter in the structure of the bill and clavicle, in pterylosis and by an aftershaft (Sclater, 1879-82; Sibley, 1956 claims an aftershaft in Galbulidae, although less well developed than in Bucconidae). Forbes (apud Sclater, 1879-82), on the other hand, affirms that the Meropidae, Coraciidae and Leptosomatidae share many common characteristics with the Galbulidae but differ in the distribution of the plantar tendons and the structure of the feet. Sibley & Ahlquist (1972) after their study of the eggwhite proteins in birds, suggested that the Galbulidae and the Bucconidae may be most closely allied to the Alcedinidae (Coraciiformes).

After the introduction of Hennig's phylogenetic systematics (1966) and the evolution of the phylogenetic hypothesis within the class Aves, there developed a controversy among the researchers in relation to the systematic position of the Galbulidae in the order Piciformes.

Thus, Simpson & Cracraft (1981) and Swierczewisky & Raikow (1981) have independently reached the conclusion that the Piciformes form a natural (monophyletic) group. Olson (1982 and 1983), based on the characteristics described by Simpson & Cracraft (op.cit.) excluded the possibility of the Piciformes forming a natural group, and after criticizing these authors suggested a polyphyletic origin for the group. Burton (1984) studying the anatomy and evolution of the Coraciiformes and Piciformes, suggested a polyphyletic origin for the group formed by these two orders. Thus, the author put together Galbulidae, Bucconidae (Piciformes), Leptosomatidae, Coraciidae and Brachypterociidae (Coraciiformes). Moreover, he pointed out that the Galbulidae and Bucconidae differ from other families of the Piciformes but they have much in common with the Coraciiformes. He considered the Capitonidae, Ramphastidae, Indicatoridae and Picidae as true Piciformes.

As can be observed, the researchers defend two divergent points of view concerning the position of the Galbulidae in the order: that established by Simpson & Cracraft, Swierczewisky & Raikow, and that established by Olson and Burton.

The study of anatomy in birds gives us a great understanding of the mechanisms related to the life of these animals, such as flight and feeding, for example. However, in order to understand them, it is necessary to focus on the aspects of the descriptive anatomy as well as on those of functional anatomy. One can, through an analysis of the jaw musculature, understand the range of possible movements available to a bird for obtaining and preparing food by its bill.

In this field of research, many authors investigated the jaw musculature and its implication on the feeding of birds (Beecher, 1951; 1953; Starck & Barnikol, 1954; Zusi, 1962; Bühler, 1970; Burton, 1974; Bühler, 1981; Höfling & Gasc, 1984a and 1984b and Gennip, 1986).

The scope of this paper is to describe and compare the cranial osteological anatomy, jaw musculature and ligaments of the skull and jaws of the species of Galbulidae here considered.

II — METHODS AND MATERIAL

Six species of Galbulidae were utilized in this work: *Galbula albirostris* (MPEG — A1616), *Galbula ruficauda* (MPEG — A3542; A3543), *Galbula galbula* (MPEG — A346), *Galbula cyanicollis* (MPEG — A357), *Brachygalba lugubris* (MPEB — A384) and *Jacamerops aurea* (MPEG — A403). The specimens were provided by the Museu Paraense Emílio Goeldi (MPEG), Belém, Pará (Brazil) and were composed of a complete skeleton of *Galbula albirostris* and one specimen of each of the other species preserved in ethylic alcohol 70% v/v.

Galbula albirostris had its skull studied and drawn; afterwards, the jaw musculature, osteology and ligaments of the other species were examined. A stereomicroscope Nikon (10-40X) was utilized for the description of the anatomical components of this work.

Galbula ruficauda was used as a pattern on which the anatomical descriptions are based. Consequently, for the other species in this study only the structural differences from *G. ruficauda* are presented and discussed.

The nomenclature used for the description of the jaw musculature was the same as that of Lakjer (1926); that used for crests, processes and other associated bony structures followed the *Nomina Anatomica Avium* (Baumel et al., 1979) except in cases where there were no corresponding structures. In this case, numbers and letters were used to avoid the creation of new names.

The numbering of the aponeuroses followed the method of Höfling & Gasc (1984a), *i.e.*, those of origin are designed by Arabic numerals while those of insertion are showed by Roman numerals.

The nomenclature of the species follows Sick (1985).

III — RESULTS AND DISCUSSION

A. ANATOMY

1. Osteology

In adult birds it is not possible to distinguish the bones of the braincase, upper and lower jaws once they are completely fused. Consequently, the term region is used here to define a particular component pertaining to the bone.

1.1. Skull

The frontal region (F — Figs. 1-6) covers part of the cranial roof. It is limited rostrally by the nasal region through the frontonasal suture (SFN — Figs. 1-6) where one can observe a small concavity (Cm — Figs. 1-6) well delimited in its median portion, disposed in the rostrocaudal axis of the skull. This structure is also well developed in *G. albirostris* (Fig. 2) and *G. galbula* (Fig. 3) but it is not present in *G. cyanicollis* (Fig. 4); in *B. lugubris* and *J. aurea* it is not conspicuous. In its rostrolateral portion the frontal region is limited by the lacrimal bone (L — Figs. 1-12) through the frontolacrimal suture (SFL — Figs. 1-6). In the laterocaudal portion of the orbit it extends to the postorbital process (PrPo — Figs. 7-12) and in the dorsocaudal portion to the parietal region (P — Figs. 1-12).

The lacrimal bone (L — Figs. 1-12) becomes linked laterorostrally with the set of bones that form the upper jaw through the nasolacrimal suture (SNL — Figs. 7-12) located lateroventrally. In *G. ruficauda* the lacrimal bone forms only a slightly pronounced dorsolateral process (PrL — Fig. 1) as we found in *G. galbula* (Fig. 3). In *G. albirostris* (Fig. 2), *G. cyanicollis* (Fig. 4) and *B. lugubris* (Fig. 5) the same is well developed; in *J. aurea* (PrL — Fig. 6) there is no dorsolateral process but a slightly developed ventrolateral process (Fig. 6). Also in the latter one finds a posterior conspicuous bony projection of the lacrimal bone (PrjO — Fig. 12), located in the contact region between the lacrimal and the ectethmoid bones. Cracraft (1968), in his study of the lacrimal bone complex in birds, observed that the lacrimal bone articulates with the frontal and nasal bones in the majority of the birds but it could only either articulate with the frontal bone as observed in Psittacidae, or it could articulate with the nasal bone as observed in Threskiornithidae. In Galbulidae the lacrimal bone articulates either with the frontal or with the nasal bones, although there are some differences among species as mentioned above.

Jollie (1957) discusses the correct name for this bone. The author affirms that Cuvier (1835) and Owen (1879) *apud* Jollie, *l.c.* use lacrimal probably in association with the same position of this bone in mammals. However, he adds that in order to analyse this matter it would be necessary to have it compared directly with the reptiles from which the birds originated. He affirms that the prefrontal bone is equivalent to that found in reptiles; the lacrimal bone, however, could not be confirmed in relation to the position of the lacrimal duct which has no correspondence in birds except in Struthioniformes, Rheiformes, Casuariformes and Apterygiformes. Therefore, according to Jollie, *(op. cit.)*, the best term to employ is prefrontal. *Nomina Anatomica Avium* (Baumel *et al.*, 1979) utilizes the two terminologies; on that account and following the nomenclature of other authors (Bock, 1964; Cracraft, 1968; Burton, 1974; Höfling & Gasc, 1984a) I decided to use lacrimal bone.

The postorbital process (PrPO — Figs. 7-12) is composed of the frontal and squamosal bones and perhaps the orbitosphenoid (Jollie, 1957). It is long, thin and well developed — it reaches more than a half of the distance between the skull and the jugal bar — in all species of Galbulidae except *J. aurea* where it is enlarged at its base and short (Fig. 12).

The parietal region (P — Figs. 1-12) lies between frontal and occipital regions. Its median posterior boundary reaches the supraoccipital region (SO — Figs. 7-24). Laterocaudally it contacts the exoccipital regions through the occipital crest (CrO — Figs. 7-24). Laterally it keeps contact with the squamosal region (E — Figs. 7-12) through the superior temporal crest (CrTS — Figs. 7-12) which delimits superiorly the temporal fossa (FT — Figs. 7-12).

The squamosal region (E — Figs. 7-12) is dorsolaterally bordered by the superior temporal crest (CrTS — Figs. 7-12), laterocaudally by the occipital crest (CrO — Figs. 7-24), and laterorostrally by the anterior temporal crest (CrTA — Figs. 7-12). The squamosal region is well developed and bounds the temporal fossa where *m. adductor mandibulae externus superficialis originates*. It is longer vertically than horizontally in most of the species; however, in *J. aurea* (Fig. 24) it is longer in the horizontal dimension. Burton (1984) had already noticed that the temporal fossae in *J. aurea* almost meet each other on the caudal region of the skull. The length and the width are important because they show the stage of development of the adductor mandible muscles. The squamosal process (PrE — Figs. 7-12) is more developed in *J. aurea* (Fig. 12); in the other species it is inconspicuous.

The exoccipital region (EX — Figs. 7-24) presents a small intumescence (INT — Figs. 13-18) situated laterally in relation to the foramen magnum (FOM — Figs. 13-18). The limits of the exoccipital region are the following: dorsolaterally with occipital crest (CrO — Figs. 7-24); dorsomedially with the supraoccipital region (SO — Figs. 7-24); ventrolaterally with *ala tympanica* (AT — Figs. 7-12) through tympanic crest (CrTI — Figs. 7-12) and ventromedially with the basioccipital region (BA — Figs. 13-18). The last one shows a small occipital condyle (CO — Figs. 13-18); in its base there is a reduced *fossa subcondilaris* (Fsc — Figs. 13-18). The basioccipital region contacts lateroventrally the tympanic crest; rostroventrally the basisphenoid region (BS — Figs. 13-18) through basioccipital crest (CrBA — Figs. 13-18) and basioccipital process (PrBA — Figs. 13-18). In the basioccipital region there are two pairs of foramina: one is near the tympanic crest the other is close to the basioccipital process (FOR — Figs. 13-18). The supraoccipital region (SO — Figs. 7-24) presents a *proeminentia cerebralis* characteristic of all species of Galbulidae but it is less pronounced in *J. aurea* (Fig. 18). Also common to the Galbulidae is a crest and a pair of basioccipital processes delimiting the basioccipital and the basisphenoid regions. Höfling & Gasc (1984a), in contrast, adopted the term basiparasphenoidean blade to characterize the same region where the process and the crest were absent.

The basisphenoid region (BS — Figs. 13-18) is rostral to the basioccipital region; it contacts rostrally the parasphenoid region (PAR — Figs. 13-18) where there is no characteristic to distinguish between these two regions. The parasphenoid region articulates rostrally with the pterygoid (PT — Figs. 7-24) and palatine (PA — Figs. 7-18); dorsally it joins the interorbital septum (SI — Figs. 7-12). This region forms a narrow blade in *B. lugubris* (Fig. 17) and in *J. aurea* (Fig. 18); in the other species this characteristic is much variable.

The palatal region is composed of the palatine (PA — Figs. 7-18) and the pterygoid (PT — Figs. 7-24) bones. The palatine articulates caudally with the pterygoid and with the parasphenoid region; rostrally it fuses with the upper jaw. In its median portion it shows *fossa medialis* (FM — Figs. 13-18) which has a narrow slotlike aspect, surrounded by the ventral palatine crest (CrPV — Figs. 13-18). Laterally there is the lateral palatine crest (CrPL — Figs. 13-18) where the fibers of *m. pterygoideus ventralis lateralis* originates. The pterygoid also articulates laterocaudally with the medial region of the quadrate. *Fossa medialis* is wider in *G. albirostris* (Fig. 14), *G. galbula* (Fig. 15) and *G. cyanicollis* (Fig. 16); in *J. aurea* the lateral palatine crest (CrPL — Fig. 18) is not expanded laterally as in other species so that the two crests — lateral and ventral of the palatine — are very closely associated.

The orbithosphenoid region extends from the interorbital septum (SI — Figs. 7-12) up to the postorbital process (PrPO — Figs. 7-12) and temporal fossa (FT — Figs. 7-12).

The interorbital septum (SI — Figs. 7-12) is limited rostrally with the ectethmoid bone (ET — Fig. 7-12) with which it is fused. Lateroventrally the interorbital septum articulates with the palatine and pterygoid bones. In *J. aurea* only the ventrolateral part of the interorbital septum is fused with ectethmoid bone.

The ectethmoid region is fused dorsally with the frontal region; ventrally it forms a conspicuous bony projection (PrET — Fig. 7-11) which recovers the palatine bone (PA — Fig. 7-12). In *J. aurea* (Fig. 12) there is not any depression on the median concavity of the ectethmoid bone and its ventral bony projection is less conspicuous than that found in other Galbulidae. Cracraft (1968) observed in *Galbula*, *Galbalcyrhynchus* and *Brachygalba* that the ectethmoid bone is a great bulbous structure fused dorsolaterally with the frontal bone and sometimes with the lacrimal bone; in none of the species of the genus *Galbula* here studied the ectethmoid bone presented a bulbous structure.

The quadrate bone presents two processes: the otic process (PrOtQ — Figs. 7-12) — which articulates dorsally with the squamosal region — and the orbital process (PrOrQ — Fig. 7-12). It also presents three condyles: lateral (CoLQ — Figs. 13-18), medial (CoMQ — Figs. 13-18) and posterior (CoPQ — Figs. 13-18). The last one is actually a small extention of the well developed medial condyle. Bock (1960) pointed out that the medial condyle is the most developed one. This can be perfectly observed in this paper. The articular surfaces of the mandible for these condyles are continuous and form a lateromedially concave surface. This disposition prevents lateral or posterior movement of the mandible in relation to the skull. The quadrate bone also articulates with the jugal bar (J — Figs. 1-18) laterally and with the pterygoid bone ventromedially.

The jugal bar — a fusion of the quadratojugal and jugal — is rostrally fused with the upper jaw which is formed by the premaxillae, maxillae and nasals.

In general, the upper jaw is about twice the length of the skull in all species except in *J. aurea*. The nares (NA — Figs. 1-12) have about 1/7 of the length of the skull.

1.2. Mandible

According to Jollie (1957) the bones of the mandible are usually six and include all those known from the reptiles except the coronoid bone. Thus, the mandible of a bird is formed by the articular, angular, suprangular, dentary, splenial and the prearticular fused together.

In all species of Galbulidae studied except *J. aurea*, the *pars symphysialis mandibulae* occupies about 2/3 of the total length of the mandible (Fig. 25); in that species it is about half of the total length of the mandible (Fig. 26).

On the dorsal mandibular region one can observe a small conspicuous coronoid process (PrC — Figs. 33-38).

On the articular region caudal to the coronoid process one can distinguish the *crista intercotylaris* (CrI — Figs. 45-50) which separates rostrally the *cotyla laterales* from the *cotyla mediales* where the lateral and medial condyles, respectively articulates. The *crista intercotylaris* is more developed in *J. aurea* (Fig. 56) where one can observe a continuity among the lateral, posterior and medial *cotylae*. Together they form a concave surface lateromedially disposed, as observed in *Ramphastos tucanus* by Höfling & Gasc (1984a). On the dorsocaudal edge of the mandible there rises a tuberosity Y (TY — Figs. 51-56).

The caudal surface of the mandible forms a depression called *fossa caudalis* (FC — Figs. 51-56). Laterally there is a lateral crest (CrLM — Figs. 51-56) and medially the medial crest (CrM — Figs. 51-56). In *J. aurea*, the *fossa caudalis* is less conspicuous. Laterocaudally the T crest (CrT — Figs. 33-38) is shown with a small tuberosity T (TT — Figs. 33-38). On the ventral region an apophysis is formed which is the vertex of the angular (VA — Figs. 51-56).

The most proeminent feature of the medial surface of the mandibular region is the *fossa aditus canalis mandibulae* (Facm — Figs. 27-32) which shows a mosaic pattern of development depending on the species (Figs. 27-32).

The medial process of the mandible (internal process of the mandible, Burton, 1984; medial process of the angular, Höfling & Gasc, 1984a) is sharp and thin (PrM — Figs. 27-31; 33-37; 39-43; 45-49; 51-55) in all species except in *J. aurea* (Figs. 32, 38, 44, 50, 56) where it is enlarged and short.

2. Musculature (Fig. 67)

The adductor mandibular system presents two groups of muscles: one external and one internal. The former is represented by *m. adductor mandibulae externus superficialis, m. a.m.e. medialis, m. a.m.e. profundus* and *m. a.m. posterior.* The primary action of the external group is to elevate the lower jaw in order to close the bill. This system links the temporal fossa and the proximal region of the orbital process of the quadrate to the mandible. The internal system presents two muscles: *m. pseudotemporalis superficialis* and *m. pseudotemporalis profundus*. The first one plays the same role of the adductor mandibular group; *m. pseudotemporalis profundus* has a double action: it retracts the upper jaw and elevates the mandible (Zusi, 1962). This system links the orbitosphenoid region and the rostral surface of the orbital process of the quadrate to the mandible.

The *pterygoideus system* retracts the upper jaw as its primary action and also adducts the mandible. It links the palatal region of the skull to the caudolateral and caudomedial portions of the mandible.

The muscle *protractor quadrati* and the muscle *protractor pterygoideus s.s.* protract the upper jaw; their fibers are inserted respectively on the medial surface of the quadrate and on the dorsocaudal end of the pterygoid. This makes possible the rotation of the quadrate and thus allows the elevation of the upper jaw in relation to the braincase. These muscles link the orbitosphenoid region and the interobital septum to the medial surface of the orbital process of the quadrate.

The *depressor mandibulae* system depresses the lower jaw to open the bill; it links the caudolateral region of the skull to the caudolateral and caudal regions of the mandible.

According to Lakjer (1926) the external adductor mandibular system is divided in three parts: *superficialis, medialis* and *profundus.* Many authors follow this nomenclature (Hofer, 1945; Höfling & Gasc, 1984 a); others follow that of Starck & Barnikol (1954), who propose an analysis of this system based on three main aponeuroses; he was followed by Zusi (1962) and Burton (1974). Burton (1984) follows Lakjer but with some modifications from Richards & Bock (1973). Other authors utilize differents methods and nomenclature to describe this muscular system (Table 1). In the present work I follow Lakjer's (1926) nomenclature.

2.1. Adductor Mandibular System

2.1.1. External Adductor Mandibular system

2.1.1.1. *M. adductor mandibulae externus superficialis (m.a.m.e.s.)*

a. *Pars dorsalis*

It presents a fleshy origin on the caudolateral surface of the skull on the temporal fossa from its limit on the temporal superior crests up to the occipital crest. It presents two bundles of fleshy fibers which insert on the rostral and caudal surface of the aponeurosis I; this arrangement gives an aspect of a bipinnate muscle. The aponeurosis I is inserted on the dorsal surface of the coronoid process on the mandible (Fig.57).

b. *Pars ventralis*

There are two fleshy origins from the temporal fossa: the first one originates on the rostrodorsal part of the temporal fossa and inserts on the lateral surface of aponeurosis II; the second one originates on the rostroventral part of the same fossa and inserts on the lateral surface of aponeurosis III; these two aponeuroses are linked together with aponeurosis I (Fig. 57).

All the species analysed presented *m.a.m.e. superficialis* divided into *pars dorsalis* and *ventralis.* This is significant as it is not commonly found in many groups of birds but only in a few (Burton, 1974; and Höfling & Gasc, 1984 a). Aponeurosis I is more developed in *J. aurea* and poorly developed in *B. lugubris.*

2.1.1.2. *M. adductor mandibulae externus medialis (m.a.m.e.m.)*

It originates on the lateral surface of a thick aponeurosis 1 (Fig. 58), which originates on the anterior temporal crest and on the squamosal process of the skull. The fleshy muscular fiber inserts on the lateral surface of the mandible, on the suprangular region where it shows a fanlike aspect (Fig. 67). Aponeurosis 1 is thicker in *J. aurea* and badly developed in *B. lugubris.*

2.1.1.3. *M. adductor mandibulae externus profundus (m.a.m.e.p.)*

The superficial fibers of this muscle originate ventrally to aponeurosis 1 on the laterosuperior surface of the otic process of the quadrate; part of these fibers insert on the medial surface of aponeurosis IV (Fig. 58), and part insert directly on the dorsomedial surface of the mandible; aponeurosis IV inserts on the dorsal and dorsomedial surface of the mandible laterally to the fleshy fibers and caudally to the insertion of the fibers of the *m.a.m.e. superficialis*. The deeper fibers originate on the medial surface of aponeurosis 2 (Fig. 58) which originates on the laterobasal surface of the otic process of the quadrate; it inserts through fleshy fibers on the suprangular region, medially to the superficial fibers.

This muscle shows some modifications among the species of Galbulidae analysed in this paper: in the species of *Galbula* the fleshy fibers originate from aponeurosis 2 (Fig. 58); in *J. aurea* and in *B. lugubris* aponeurosis 2 was not observed and the origin of the muscle is fleshy while its insertion is from aponeurosis V (Fig. 59). Zusi (1962) and Burton (1984) agree that there are many differences in the structure of this muscle and aponeurosis among species they analysed: the aponeurosis can be disposed only in the terminal portion of the muscle, or the muscle can originates directly from an aponeurosis and be inserted through fleshy fibers on the mandible; or, the aponeurosis can be absent. Burton (1974) observed in *Rostratula* (Rostratulidae) that the structure of this muscle was quite different among the members of the suborder Charadrii. I found a similar result comparing the *Galbula* species to *J. aurea* and *B. lugubris* as described above.

2.1.1.4 *M. adductor mandibulae posterior (m.a.m.p.)*

It originates on the laterocaudal surface of the orbital process of the quadrate near the otic process; it runs parallel to *m. pseudotemporalis profundus* where a branch of the trigeminal nerve separates them. It inserts caudally in relation to the insertion of *m.a.m.e. profundus* on the medial and dorsal surfaces of the lower jaw.

In this muscle the same pattern of structure was found in the species of *Galbula*. However, no aponeurosis was found as observed by Burton (1974) in Charadriiformes or by Höfling & Gasc (1984a) in *Ramphastos*; in *J. aurea* and in *B. lugubris* this muscle is poorly developed; this might be related to the well developed *m. pseudotemporalis profundus* which occupies almost the entire surface of the orbital process of the quadrate.

2.1.2. Internal Adductor Mandibular system

2.1.2.1. *M. pseudotemporalis superficialis (m. pt.s.)*

In Galbulidae this is a poorly developed muscle which originates on the orbitosphenoid region dorsally to the foramen of the trigeminal cranial nerve. It runs ventrally to the mandible where it is connected medially on a thin aponeurosis VI (Fig. 58) which inserts on the medial surface of the mandibular ramus, caudally to the coronoid process. In *B. lugubris* the *m.pt. superficialis* is not present.

2.1.2.2. *M. pseudotemporalis profundus (m. pt.p.)*

This muscle presents superficial and deeper fibers. The former originate on the lateral surface of a thin aponeurosis 3 (Fig. 60) which itself originates on the laterorostral surface of the orbital process of the quadrate. It runs ventrally to the mandible where it inserts rostrally in relation to the insertion of *m. pseudotemporalis superficialis*. The deeper fiber is poorly developed; it originates ventrally in relation to the anterior fiber and runs to the medial surface of the mandible where it inserts together with the superficial fiber. This muscle shows the same pattern among the species of Galbulidae except *J. aurea* where it is more developed and presents a fanlike aspect.

2.2.1. *M. protractor quadrati (m. pr.qt.)*

A well developed muscle originating on the orbitosphenoid region (Fig. 67) inserts medially in relation to the origin of m. *pseudotemporalis superficialis*. It shows a distinct characteristic in *J. aurea*; the first part of this muscle originates on the interorbital septum ventrally to the optic foramen; the second one originates on the orbitosphenoid region and is more developed than in other species of Galbulidae here studied. Thus, in this species there are two different areas of origin on the orbital region while in the other species there is just one. Burton (1984) proposed a division of this muscle according to its place of origin: the one originating on the interorbital septum he called *m. protractor quadrati 1* and the one originating on the orbitosphenoid region, *protractor quadrati* 2. In this case, the nomenclature establised by him is followed in the present paper. *Protractor quadrati 1* inserts through fleshy fibers on the rostromedial surface of the orbital process of the quadrate while *protractor quadrati 2* inserts on the caudomedial surface of the same process.

2.2.2. *M. protractor pterygoidei* (*m. pr.pt.*)

It originates through fleshy fibers on the caudal portion of the interorbital septum, rostroventrally to the optic foramen and rostrolaterally in relation to the *m. protractor quadrati.* The fleshy fibers insert on the medial surface of aponeurosis VII, which inserts on the dorsal posterior surface of the pterygoid.

2.3. Pterygoideus system

The nomenclature of this muscular system differs significantly among authors (Lakjer, 1926; Hofer, 1945; Beecher, 1951; Starck & Barnikol, 1954; Merz, 1963, among others — Table 1). In order to avoid misunderstandings I followed the nomenclature of Lakjer (1926).

2.3.1. *M. pterygoideus ventralis*

2.3.1.1. *M. pterygoideus ventralis medialis* (*m. pt.v.m.*)

It consists of four muscular bundles: the first one, more ventrally situated, originates from aponeurosis 4 (Fig. 61) and inserts medially through fleshy fibers medially to the angular vertex of the mandible (Fig. 62); the aponeurosis 4 originates on the palatine region. The second fiber originates dorsally from aponeurosis 5 (Fig. 61) which originates on the anterior half of the ventral palatine crest; it inserts ventrally on the aponeurosis VIII which is attached on the caudomedial surface of the mandible (Figs. 61 and 62). The third one originates on the dorsal part of aponeurosis 6 (Fig. 61) which originates on the posterior half of the palatine crest; it inserts on the ventral surface of aponeurosis IX which inserts on the dorsomedial surface of the medial process of the mandible (Fig. 62). The fourth fleshy fiber originates on the ventral palatine crest, near the palatine/pterygoid articulation and inserts through aponeurosis X on the ventromedial surface of the medial process of the mandible (Figs. 61 and 62). In general the species of Galbulidae showed the same pattern of structure; *J. aurea* showed a greater development of its muscular fibers and aponeurosis. Moreover, all species presented the two apouneurosis of insertion on the medial process of the mandible.

2.3.1.2. *M. pterygoideus ventralis lateralis* (*m. pt.v.l.*)

It originates from a well developed aponeurosis 7 (Fig. 61), which originates on the lateral palatine crest and runs perpendicularly to the muscular fibers. The two muscle fibers present different places of insertion: the one that originates on the lateral surface of aponeurosis 7 inserts on the caudolateral surface of the mandible (Fig. 62); the one medially situated to aponeurosis 7 inserts on the caudomedial portion of the mandible ventrally to aponeurosis VIII (Fig. 62). Both fibers are fleshy at the point of insertion. Burton (1984) observed that there is no distinction between this muscle and *m. pt. dorsalis lateralis* in Galbulidae; they form a reduced unit quite different from other groups of birds. *J. aurea* showed a well developed insertion on the caudolateral surface on the mandible if compared with other Galbulidae; it occupies a great part of the angular region laterally and also part of the suprangular region.

2.3.2. *M. pterygoideus dorsalis* (*m. pt.d.*)

It originates as fleshy fibers on the caudodorsal part of the palatine and on the rostrolateral surface of the pterygoid; these fibers diverge caudally and insert on the dorsal surface of aponeurosis XIa and aponeurosis XIb respectively; these aponeurosis are linked together just before insertion at *crista intercotylaris* (CrI - Fig. 45-50).

2.4. Depressor Mandible System

2.4.1. External Depressor Mandible System

2.4.1.1. *M. depressor mandibulae externus superficialis* (*m. d.m.e.s.*)

It consists of three parts without any aponeurosis of origin: the superficial one originates on the caudolateral surface of the skull on the tympanic crest (CrTI - Figs. 7-12) and lateral surface of the occipital region. Its fleshy fibers run lateroventrally and insert on the lateral surface of aponeurosis XII (Fig. 63); this aponeurosis inserts on the caudolateral surface of the mandible next to the lateral mandibular crest; the intermediate part originates ventrally to the superficial one on the internal surface of the tympanic crest and inserts on the anterior surface of aponeurosis XIII; this one inserts on the caudal surface of the mandible caudally to aponeurosis XII and near the angular vertex (Fig. 63); the deeper fiber originates ventrally to the intermediate portion and it inserts on the mandible through aponeurosis XIV (Fig. 63); this one is attached to the caudal surface of the mandible, on *fossa caudalis.*

2.4.1.2. *M. depressor mandibulae externus profundus* (*m. d.m.e.p.*)

It originates from the caudolateral surface of the occipitomandibular ligament (LOM - Figs. 65 and 66); it inserts on the mandible through aponeurosis XV which attaches to the caudal surface of the mandible (Fig. 63). In *J. aurea* aponeurosis XV is more developed than in other Galbulidae (Fig. 64).

2.4.2. Internal Depressor Mandible System

2.4.2.1. *M. depressor mandibulae internus*

It originates through fleshy fibers on the rostromedial surface of the occipitomandibular ligament; it is fleshy at insertion on the dorsocaudal part of the mandible medially to tuberosity Y (TY - Fig. 51).

Burton (1984) indicates that, in general, the muscles of the depressor mandible system show poorly developed aponeuroses except in Upupidae and Phoeniculidae (Coraciiformes). However, in all species here analysed these aponeuroses among the Coraciiformes and Piciformes were well developed; this condition agrees with that found by Höfling & Gasc (1984a) in *Ramphastos.*

3. Ligaments

3.1. Postorbital ligament (LPO)

It originates on the lateral surface of the postorbital process (LPO - Fig. 65) and runs lateroventrally to the mandible where it covers the articulation of the jugal bar with the quadrate. It inserts on the lateral surface of the mandible on its tuberosity T (TT - Figs. 33-38). It is particularly well developed in *J. aurea.*

3.2. Occipitomandibular ligament (LOM)

It originates medially to the tympanic crest and inserts on the dorsocaudal part, tuberosity Y on the mandible (Figs. 51-56 and LOM - Figs. 65 and 66). It is well developed in all species of Galbulidae here analysed.

3.3. Lateral jugomandibular ligament (LJML)

It runs laterally from the caudal end of the jugal bar (LJML - Fig. 65) to insert also laterally on the mandible, caudally to the insertion of the postorbital ligament.

3.4. Medial jugomandibular ligament (LJM)

This ligament connects the caudolateral surface of the jugal bar to the caudal region of the mandible. In this region it shows two sesamoid bones: one lateral and the other posterior (SE - Fig. 66) as seen in *G. ruficauda.* In *J. aurea* sesamoid bones are more developed than in other jacamars.

IV — CONCLUSIONS

Among all species of Galbulidae analysed in this paper *J. aurea* differs significantly from the general pattern found in relation to other species: morphologically, by the size of the body and by the aspect of the bill, thick, short and slightly curved; in relation to the osteology it presents a greater development of bony structures except for the poor development of the postorbital process and for the medial process of the mandible. The ventrolateral process is also unique to this species. In terms of myology it is distinguished by the greater development of its muscular fibers and associated aponeuroses. The poor development of the *m. adductor mandibulae posterior* seems to be compensated by the great development of *m. pseudotemporalis profundus* which occupies almost all the lateral surface of the orbital process of the quadrate. Moreover, the m. *protractor quadrati* has two regions of origin against just one in other Galbulidae.

Brachygalba lugubris shows many similiarities with the species of genus *Galbula* except for the absence of *M. pseudotemporalis superficialis* — unique to *B. lugubris* — and the poor development of *m. adductor mandibulae posterior.* This last characteristic is the only one which shows a clôser relationship between *B. lugubris* and *J. aurea*. The similiarities between *B. lugubris* and the species of *Galbula* are the following: medial process of the mandible, long and thin; *pars symphisialis mandibulae* about 2/3 of the total length of the mandible; squamosal process poorly developed; temporal fossa larger than longer and postorbital process long and thin.

Among *Galbula* species, *G. cyanicollis* is the one that most differs from the general pattern of the genus. *G. ruficauda* and *G. galbula* are more closely associated with each other than with other *Galbula* species.

The anatomical data presentend in this paper will be considered elsewhere mainly for systematic considerations on the position of the Galbulidae, whether in the order Piciformes on in the order Coraciiformes.

ACKNOWLEDGMENTS

I would like to express my appreciation and thanks to many people who helped me in many ways throughout this study. I am particularly indebted to Dr. Elizabeth Höfling, my adviser, who offered me information, much of her own time and valuable criticism. Special thanks to Dr. Norma Gomes, Dr. Miguel T. Rodrigues and Dr. Douglas Stotz who read and criticized the manuscript. In addition, I whish to thank Seomara who helped me with the illustrations, José M. Martins and Thomas who helped me in my field work in my continuous search for *Jacamaralcyon tridactyla*.

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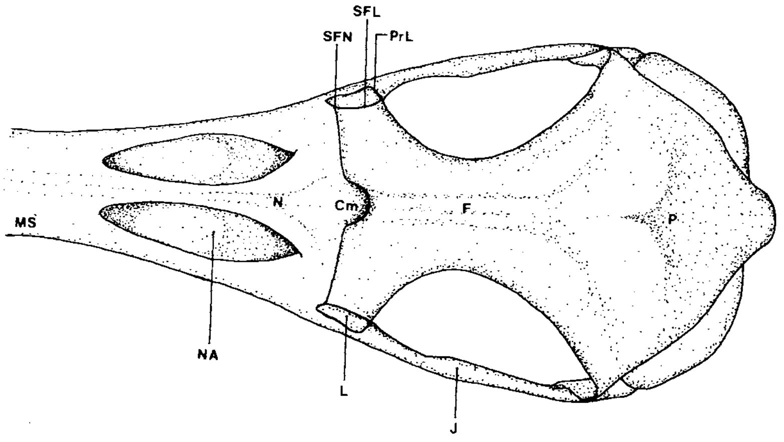

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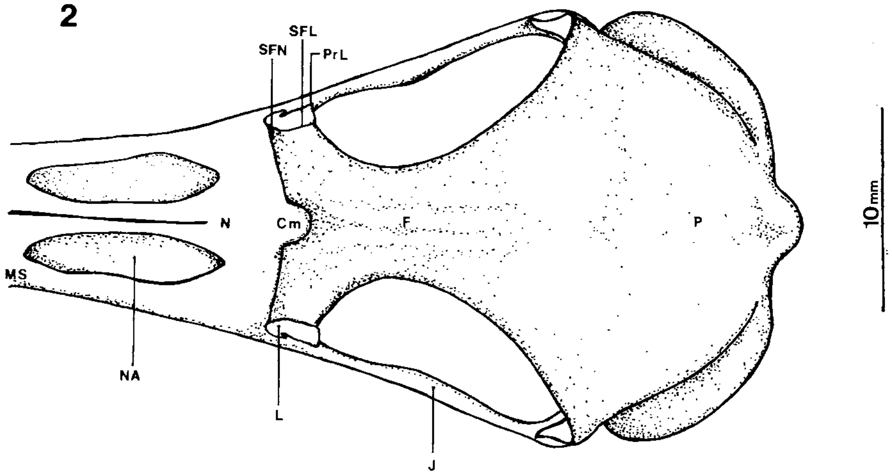

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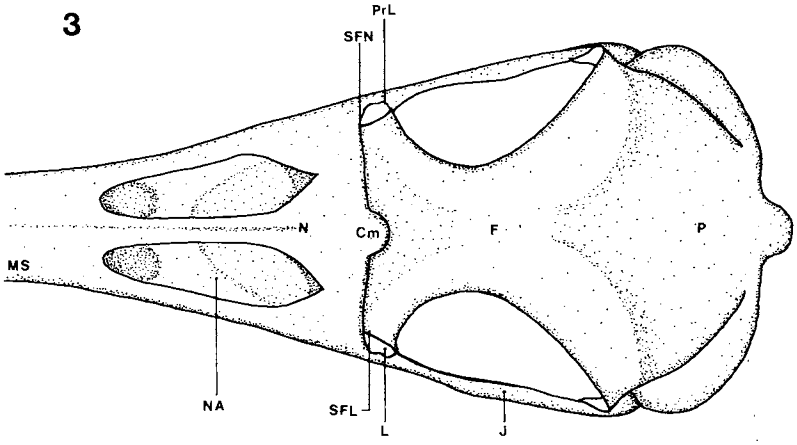

Fig.1, dorsal view of the skull of *Galbula ruficauda;* fig. 2, dorsal view of the skull of *Galbula albirostris;* fig. 3, dorsal view of the skull of *Galbula galbula.*

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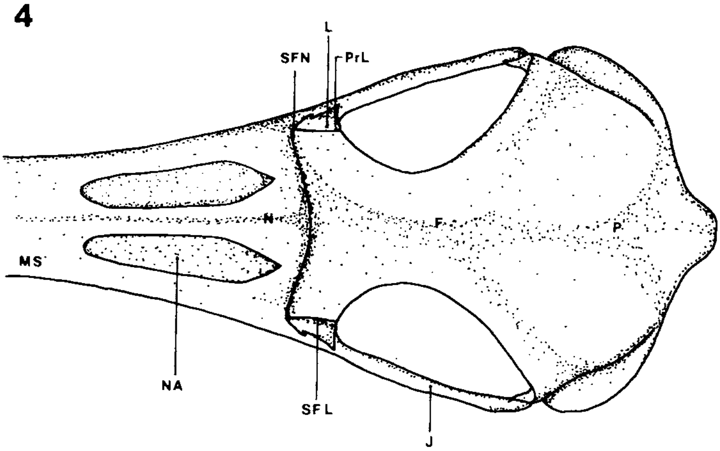

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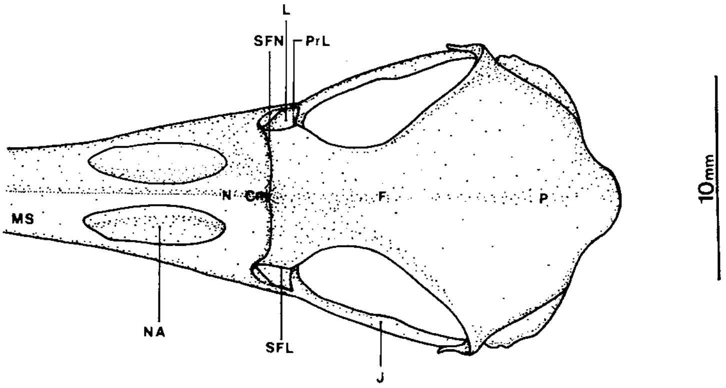

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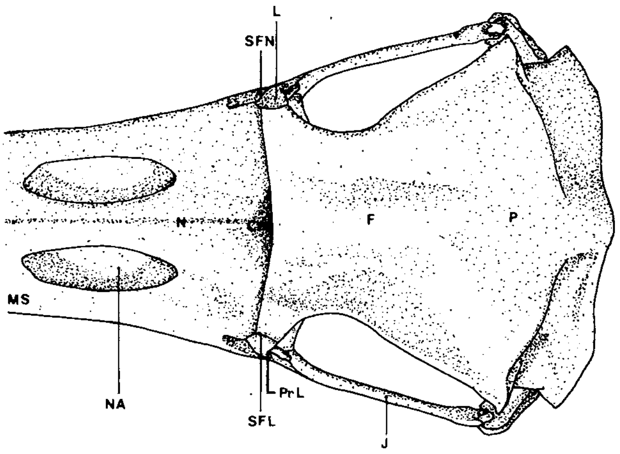

Fig.4, Dorsal view of the skull of *Galbula cyanicollis;* fig. 5, dorsal view of the skull of *Brachygalba lugubris*; fig. 6, dorsal view of the skull of *Jacamerops aurea.*

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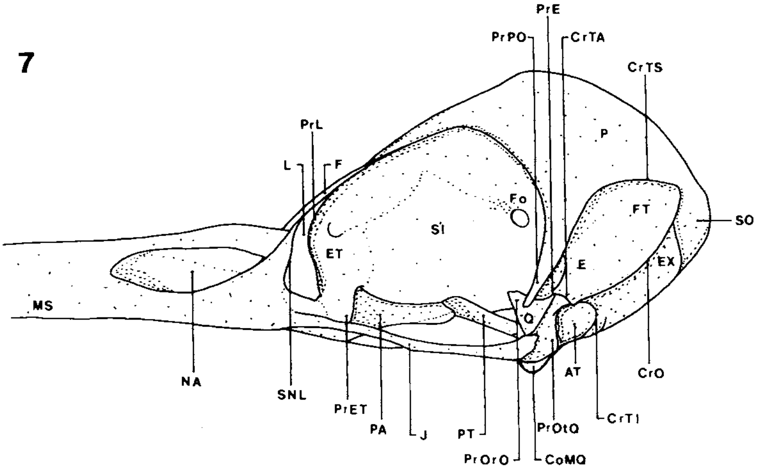

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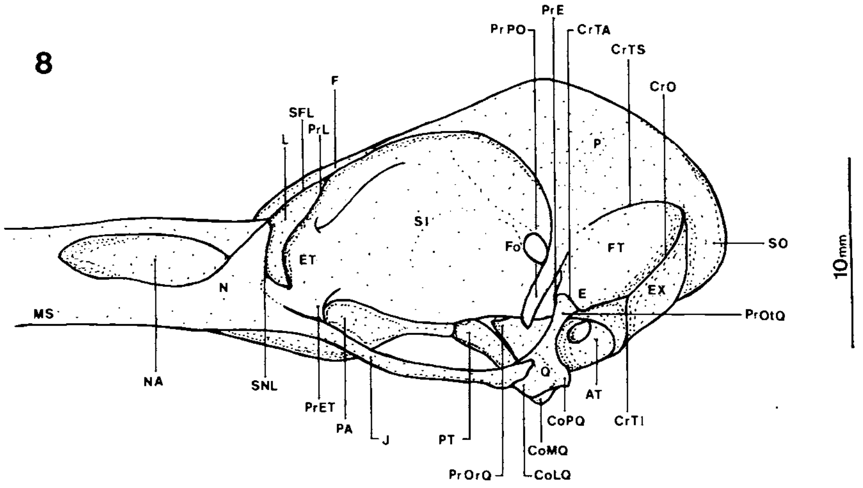

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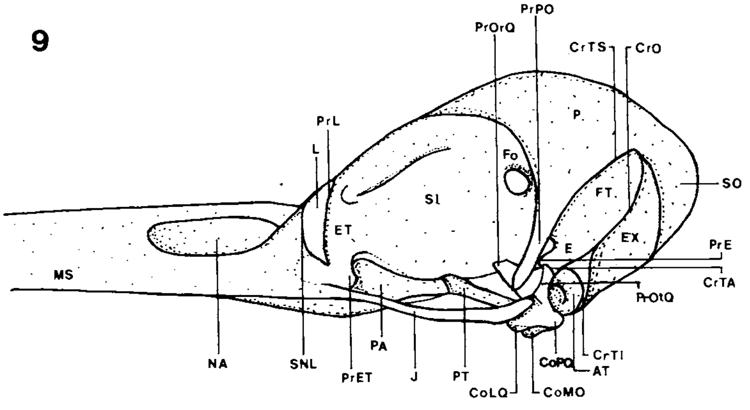

Fig. 7, Lateral view of the skull of *Galbula ruficauda;* fig. 8, lateral view of the skull of *Galbula albirostris;* fig. 9, lateral view of the skull of *Galbula galbula.*

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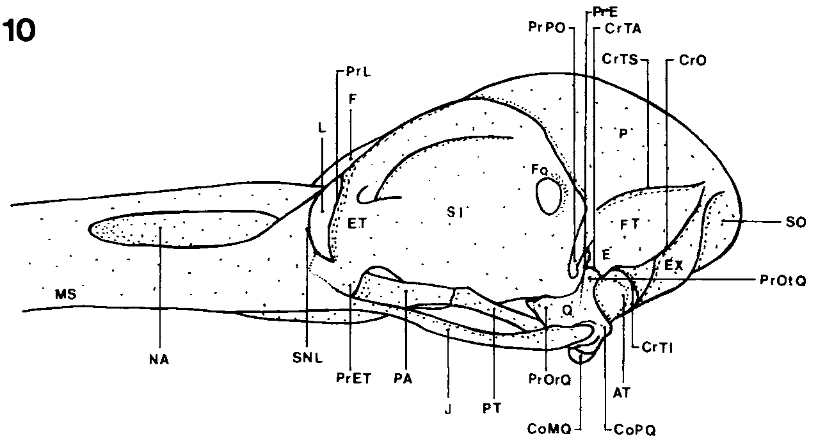

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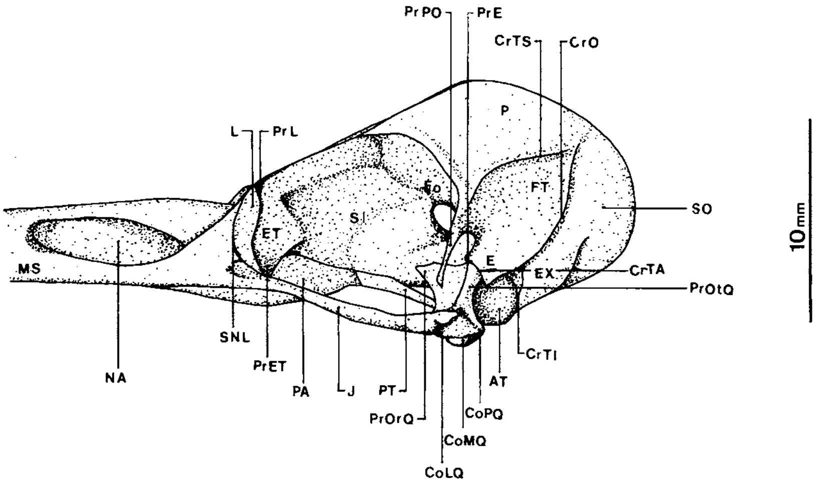

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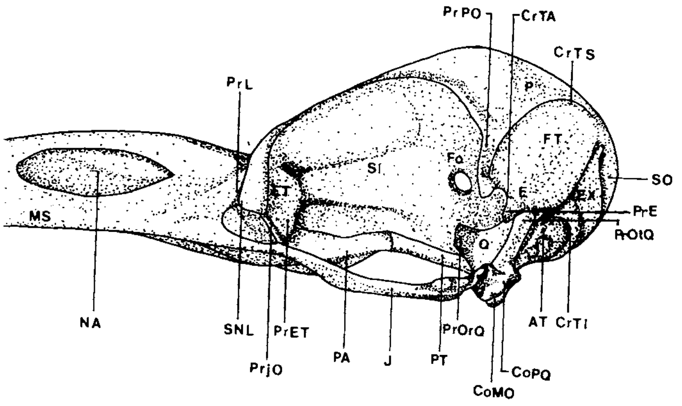

Fig. 10, Lateral view of the skull of *Galbula cyanicollis;* fig. 11, lateral view of the skull of *Brachygalba lugubris;* fig. 12, lateral view of the skull of *Jacamerops aurea.*

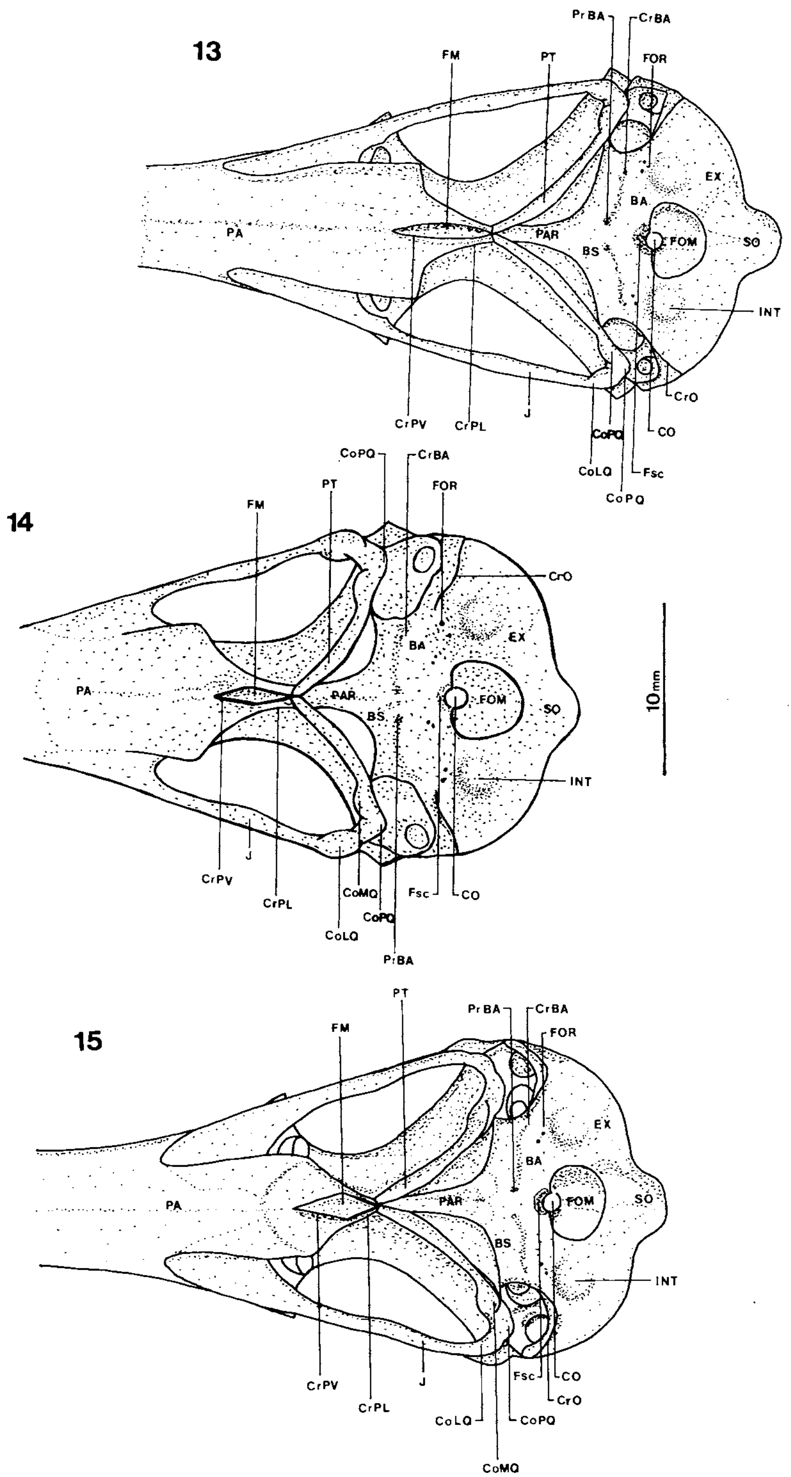

Fig. 13, Ventral view of the skull of *Galbula ruficauda;* fig. 14, ventral view of the skull of *Galbula albirostris;* fig. 15, ventral view of the skull of *Galbula galbula.*

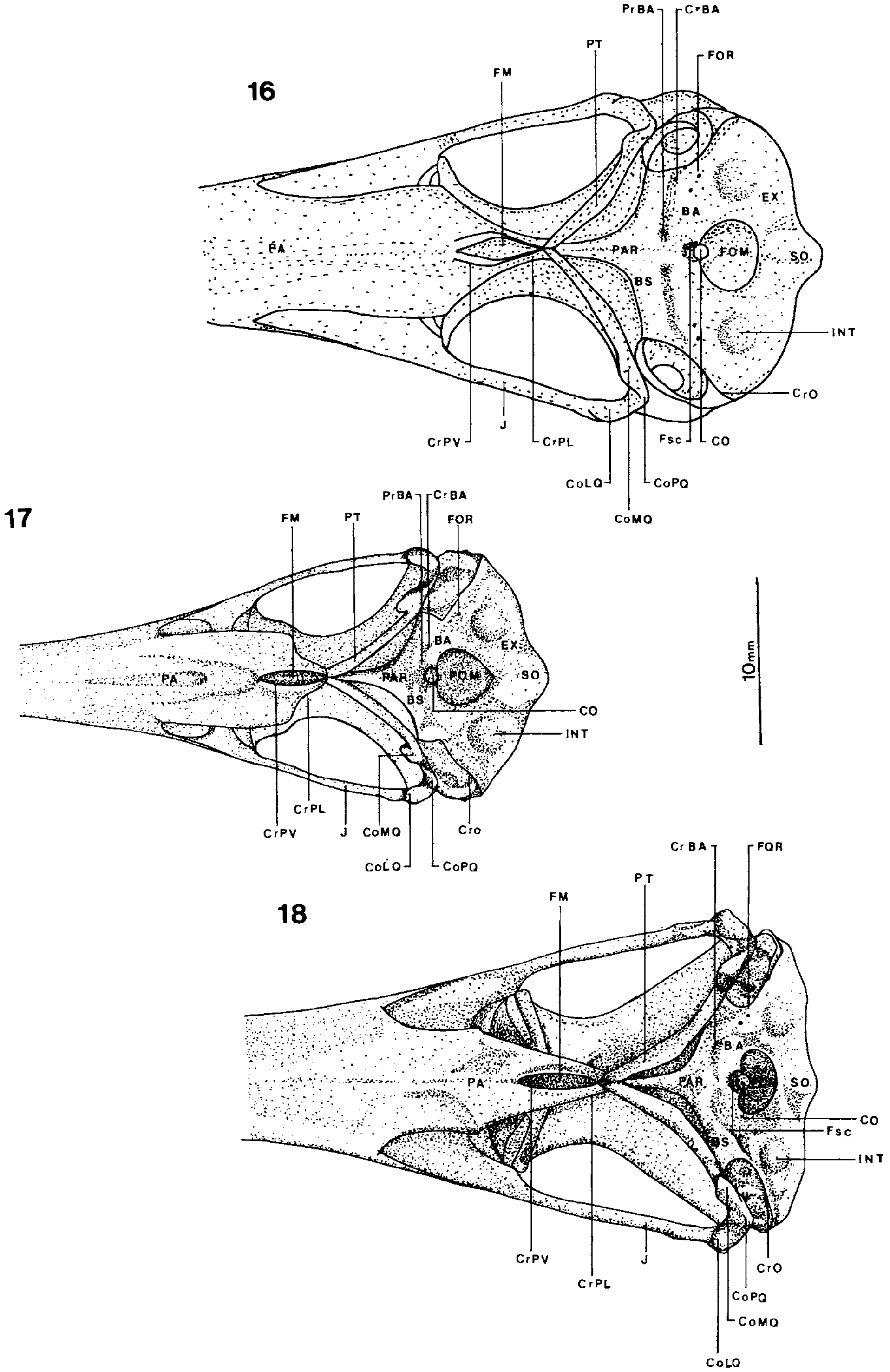

Fig. 16, Ventral view of the skull of *Galbula cyanicollis;* fig. 17, ventral view of the skull of *Brachygalba lugubris;* fig. 18, ventral view of the skull of *Jacamerops aurea.*

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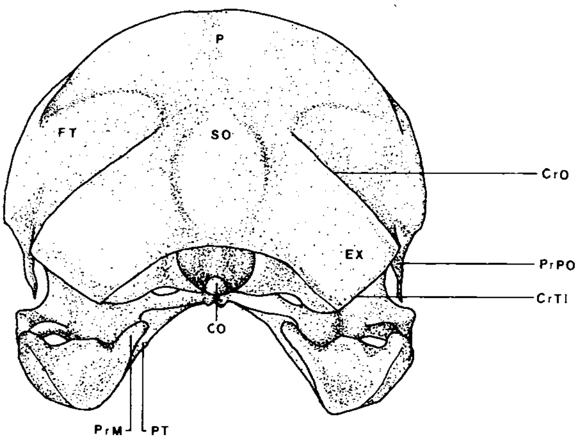

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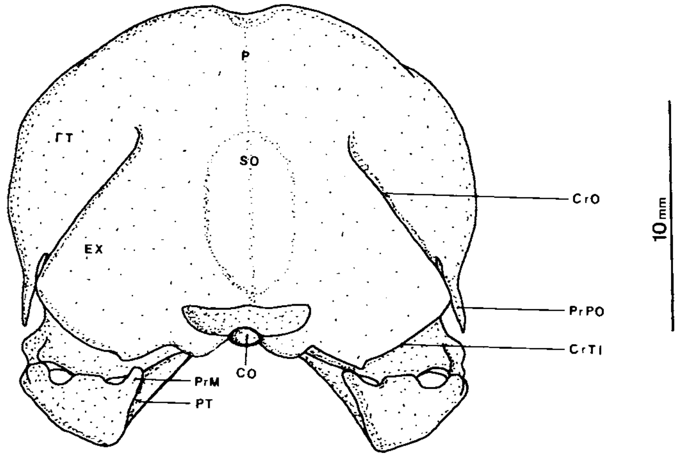

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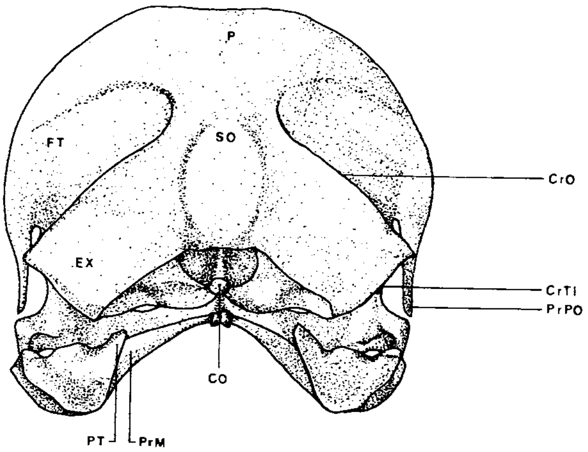

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Fig. 19, Posterior view of the skull of *Galbula ruficauda;* fig. 20, posterior view of the skull of *Galbula albirostris;* fig. 21, posterior view of the skull of *Galbula galbula.*

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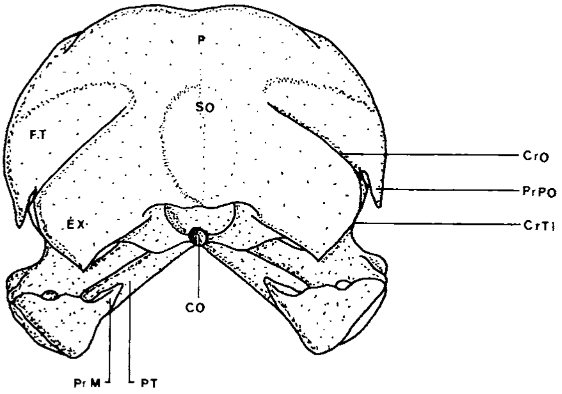

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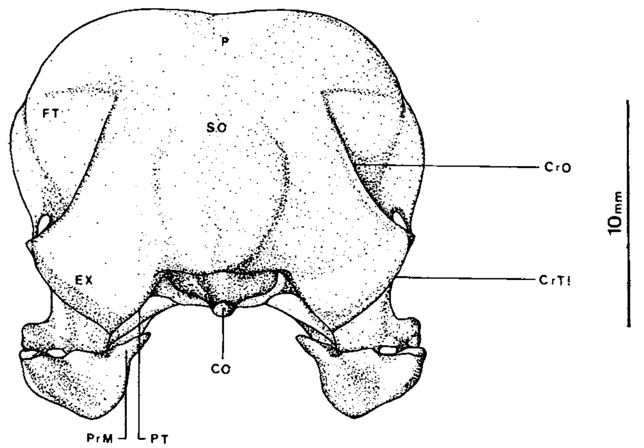

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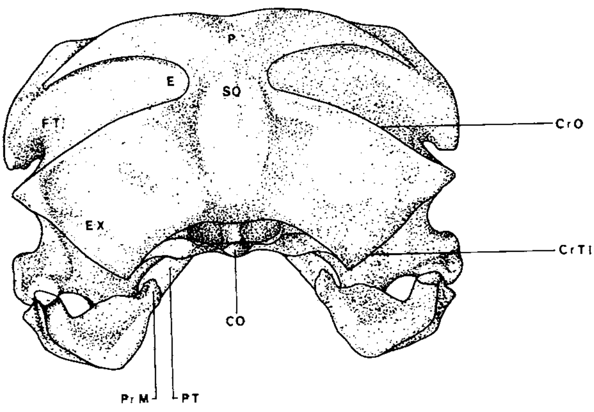

Fig. 22, Posterior view of the skull of *Galbula cyanicollis;* fig. 23, posterior view of the skull *Brachygalba lugubris;* fig. 24, posterior view of the skull of *Jacamerops aurea.*

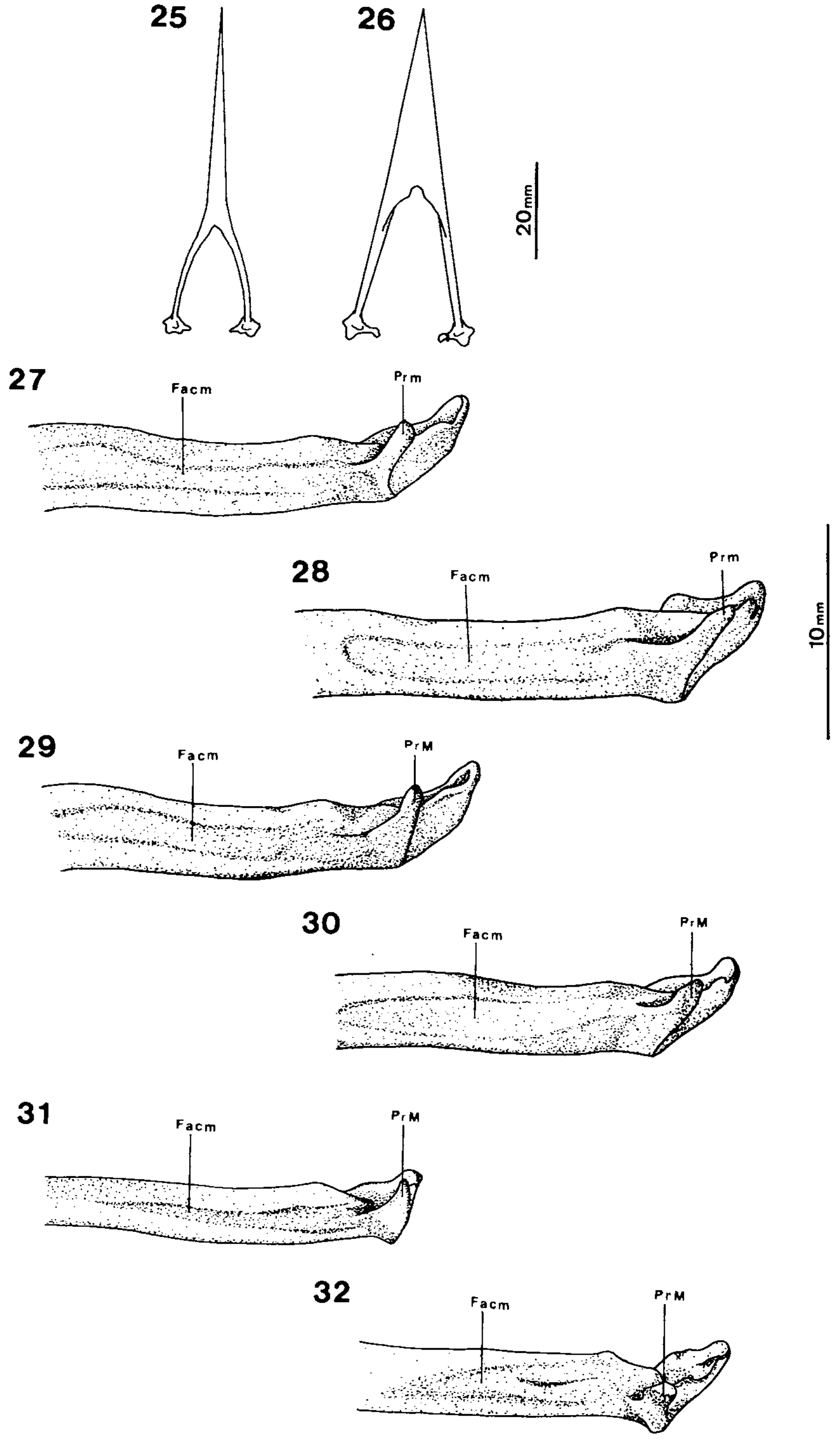

Fig. 25, Dorsal view of the lower jaw showing the *pars symphisialis mandibulae* of *Galbula ruficauda;* fig. 26, dorsal view of the lower jaw showing the *pars symphisialis mandibulae* of *Jacamerops aurea;* fig. 27-32, medial view of the lower jaw of *Galbula ruficauda* (27); *Galbula albirostris* (28); *Galbula galbula* (29); *Galbula cyanicollis* (30); *Brachygalba lugubris* (31) and *Jacamerops aurea* (32).

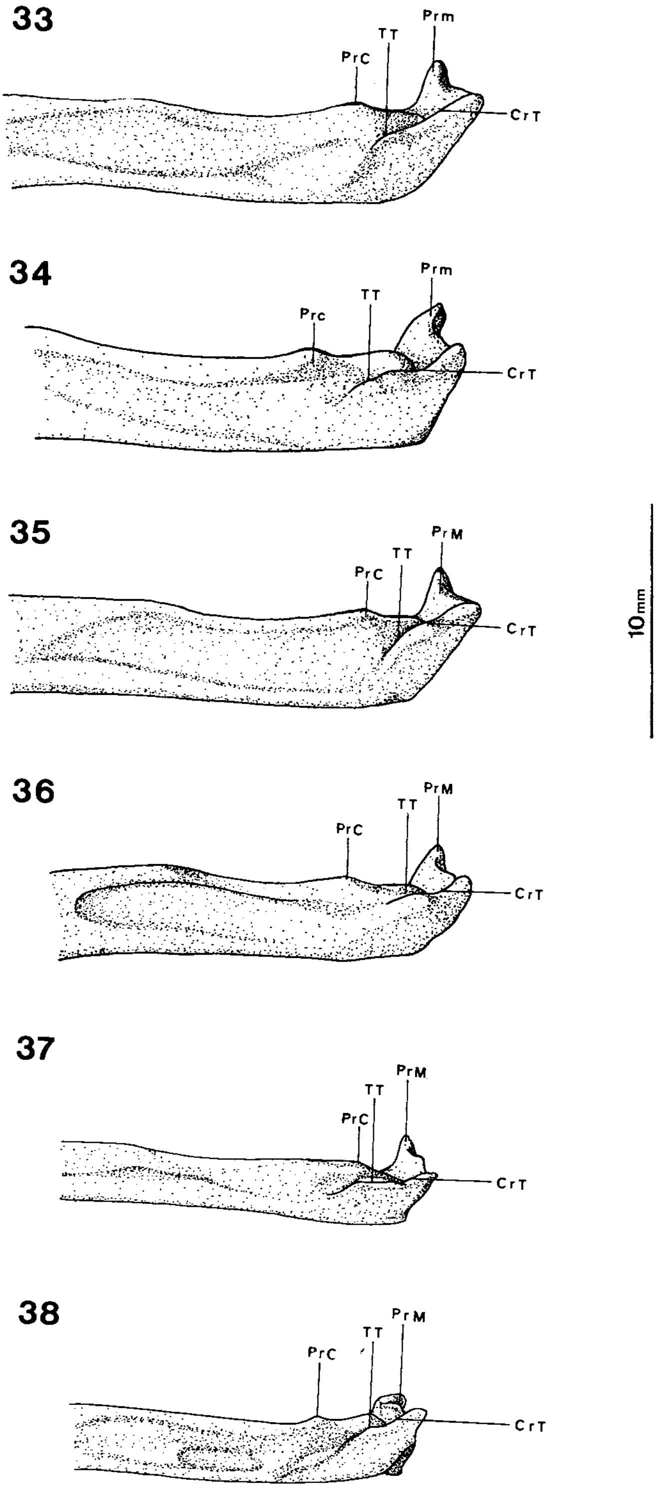

Fig. 33-38, Lateral view of the lower jaw of *Galbula ruficauda* (33); *Galbula albirostris* (34); *Galbula galbula* (35); *Galbula cyanicollis* (36); *Brachygalba lugubris* (37) and *Jacamerops aurea* (38).

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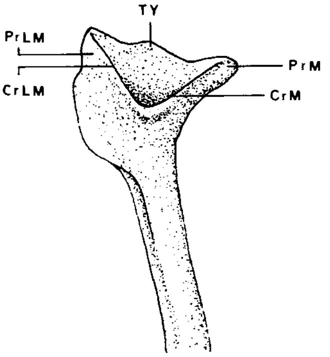

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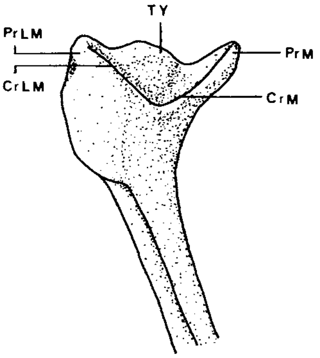

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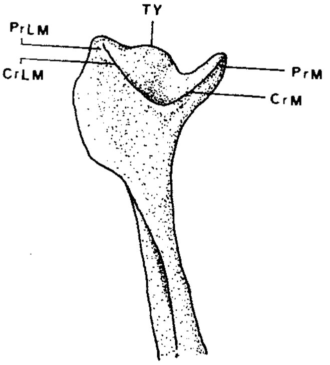

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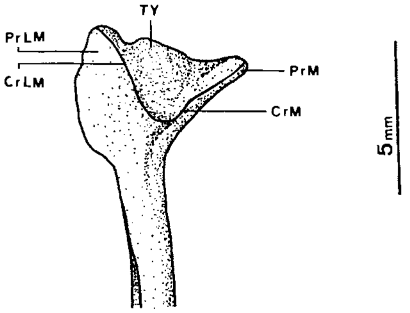

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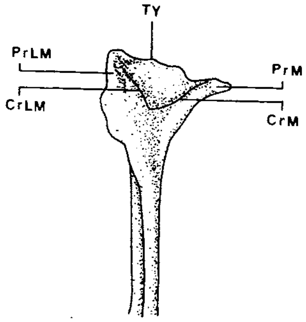

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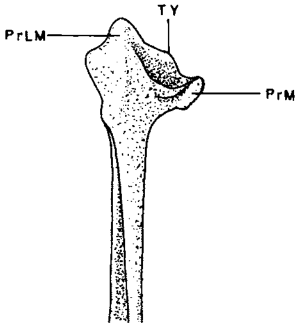

Fig. 39-44, Ventral view of the lower jaw of *Galbula ruficauda* (39); *Galbula albirostris* (40); *Galbula galbula* (41); *Galbula cyanicollis* (42); *Brachygalba lugubris* (43) and *Jacamerops aurea* (44).

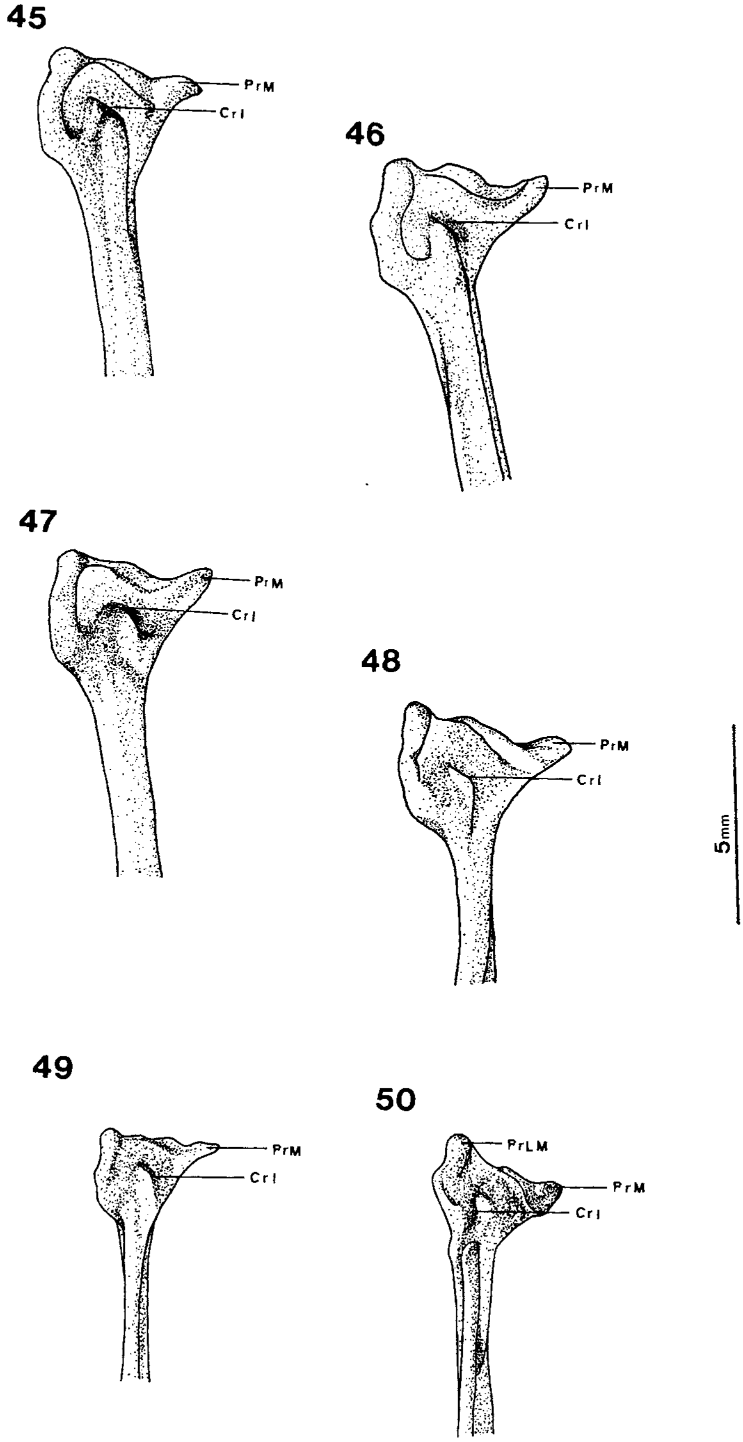

Fig. 45-50, Dorsal view of the lower jaw of *Galbula ruficauda* (45); *Galbula albirostris* (46); *Galbula galbula* (47); *Galbula cyanicollis* (48); *Brachygalba lugubris (49)* and *Jacamerops aurea* (50).

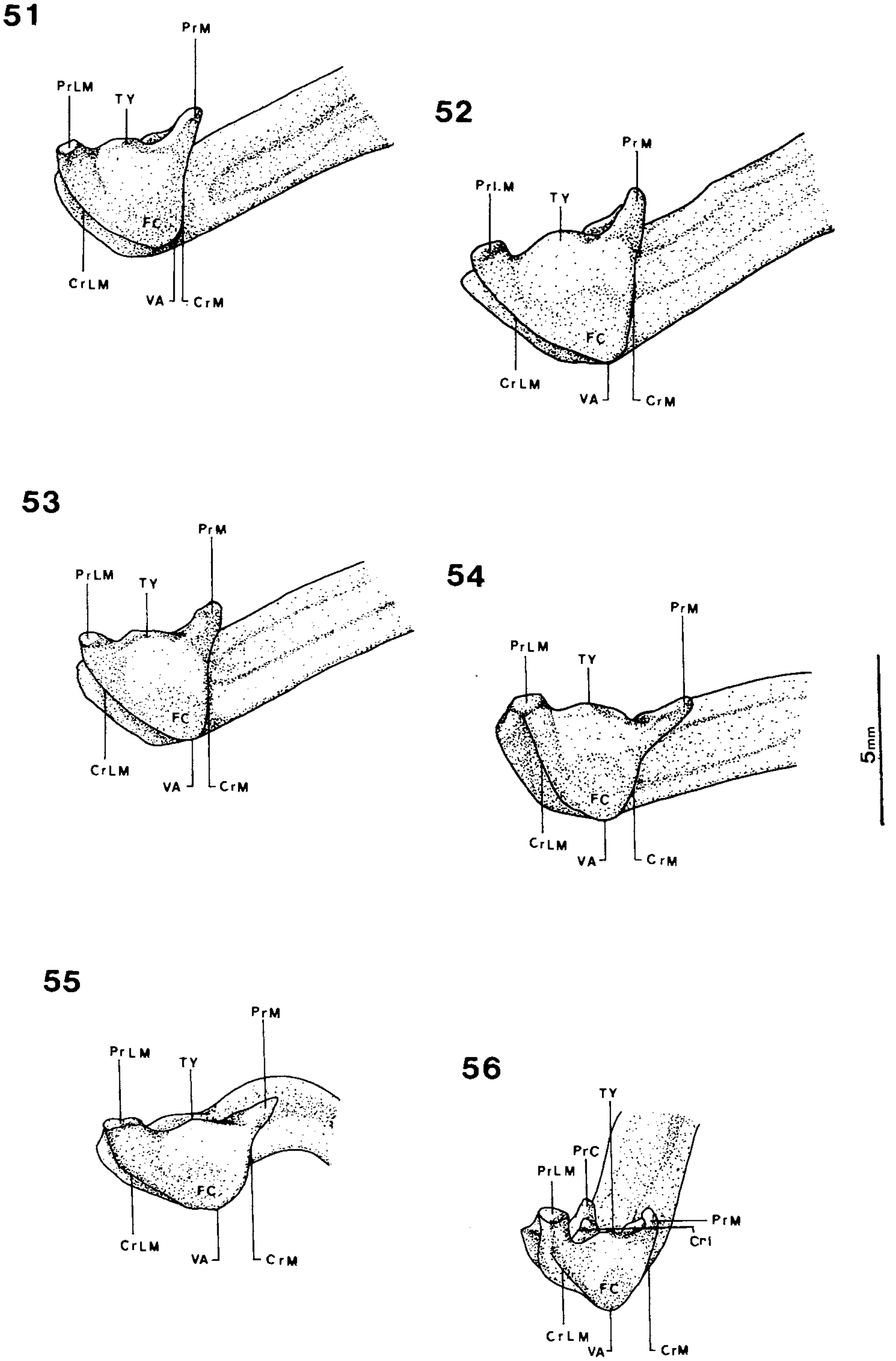

Fig. 51-56, Caudal view of the lower jaw of *Galbula ruficauda* (51); *Galbula albirostris* (52); *Galbula galbula* (53); *Galbula cyanicollis* (54); *Brachygalba lugubris* (55) and *Jacamerops aurea* (56).

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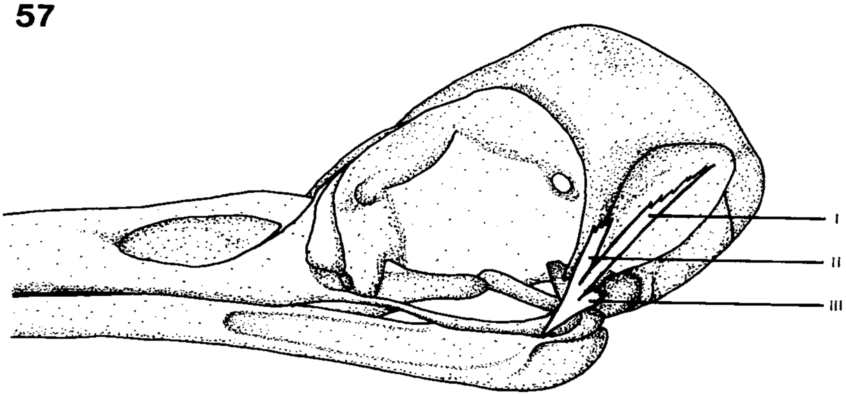

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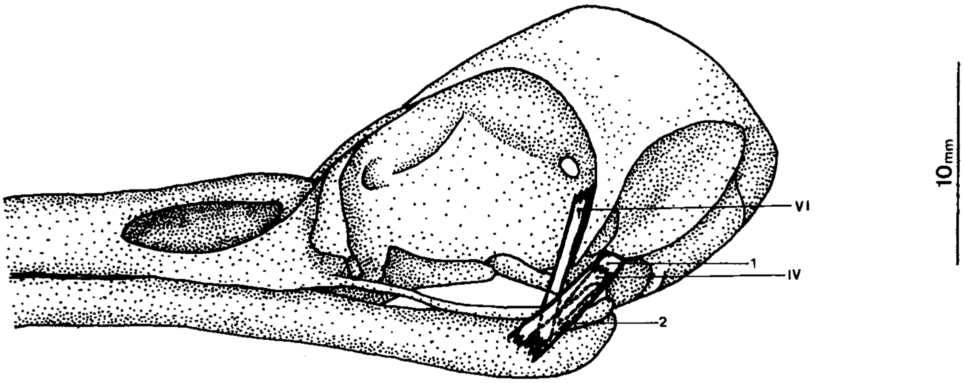

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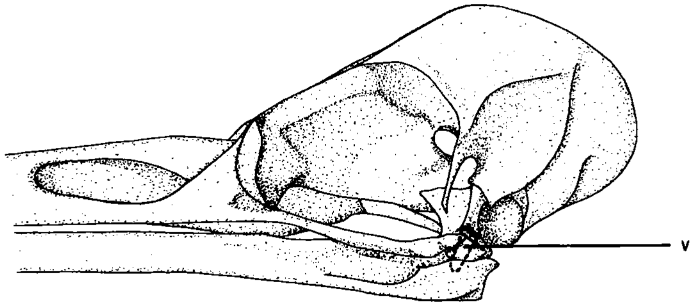

Fig. 57, Aponeurosis I, II and III of the *m. adductor mandibulae externus superficialis* represented in *Galbula ruficauda;* fig. 58, aponeurosis I of the *m. adductor mandibulae externus medialis;* aponeurosis 2 and IV of the *m. adductor mandibulae externus profundus* and aponeurosis VI of the *m. pseudotemporalis superficialis* represented in *Galbula ruficauda;* fig 59, aponeurosis V of the *m. adductor mandibulae externus profundus* represented in *Brachygalba lugubris.*

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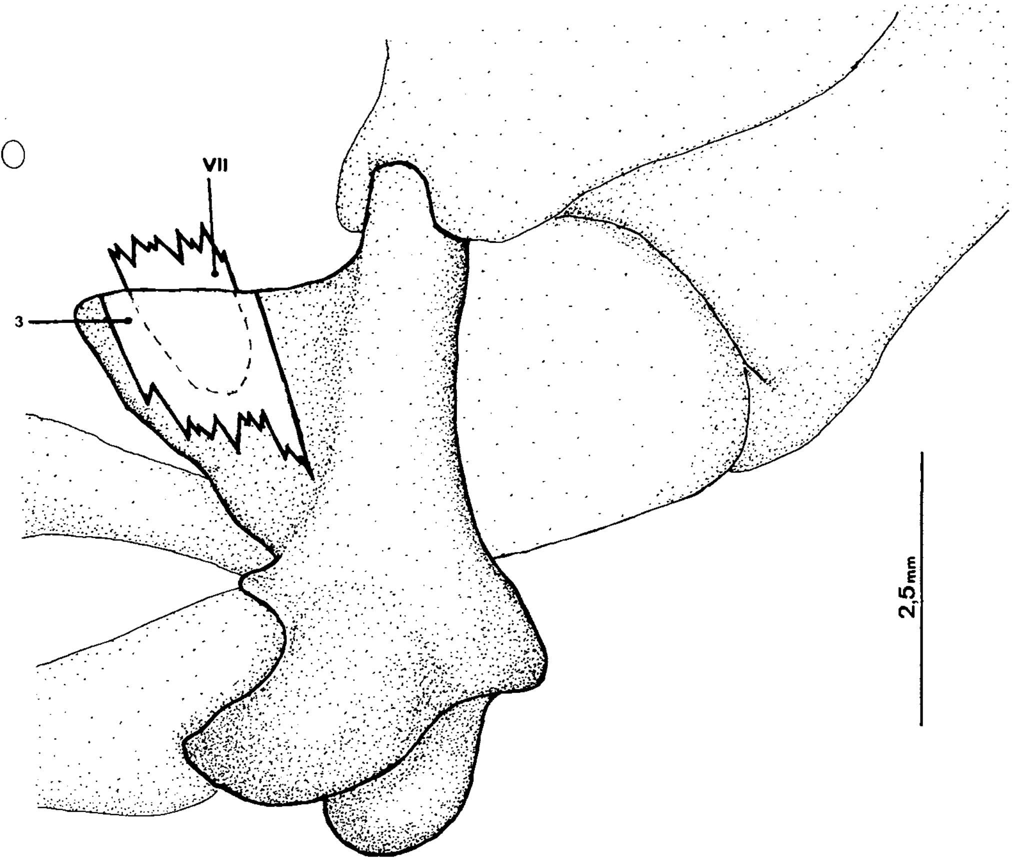

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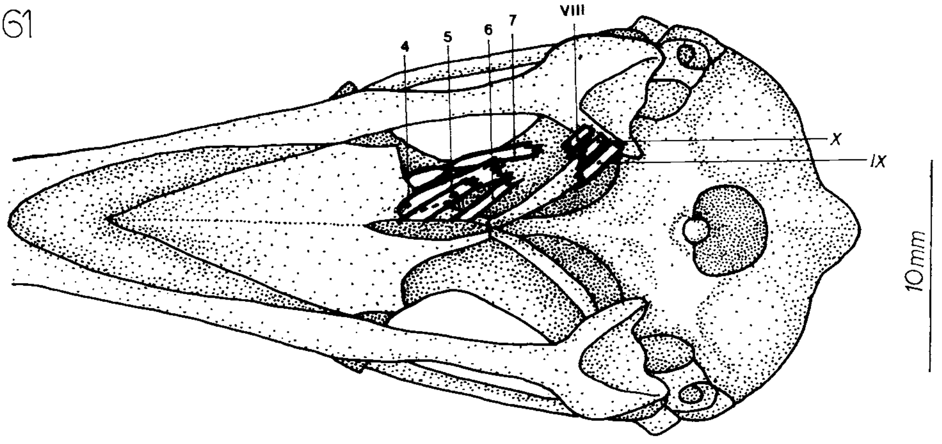

Fig. 60, Aponeurosis VII of the *m. protractor pterygoidei* s.s. and aponeurosis 3 of the *m. pseudotemporalis profundus* represented in *Galbula ruficauda*; fig. 61, aponeurosis of the *pterygoideus ventralis* system represented in *Galbula ruficauda*.

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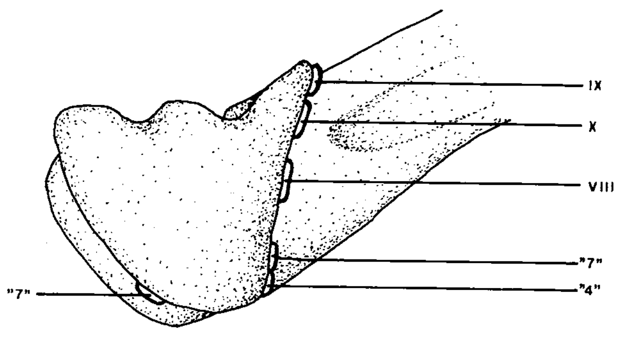

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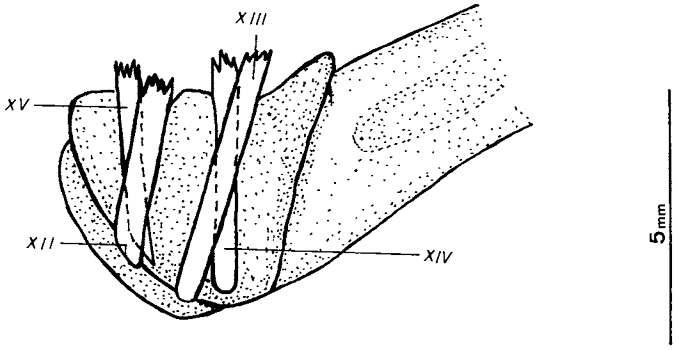

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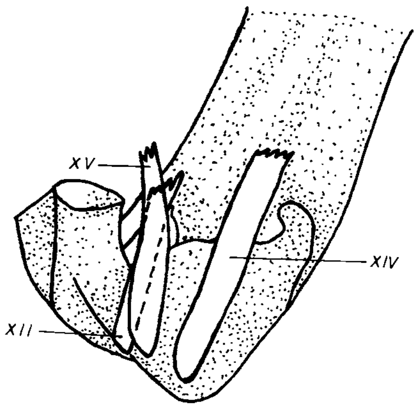
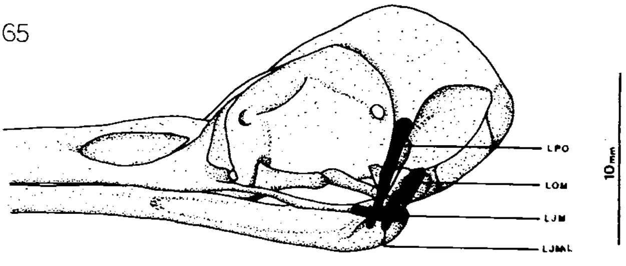


Fig. 62, muscular insertion on the lower jaw; Arabic numerals represent insertions areas of fleshy fibers and Roman numerals represent insertions of aponeuroses; fig 63, aponeuroses of the *m. depressor mandibulae externus* represented in *Galbula ruficauda;* fig. 64, aponeuroses of the *m. depressor mandibulae externus* represented in *Jacamerops aurea.*

65



66

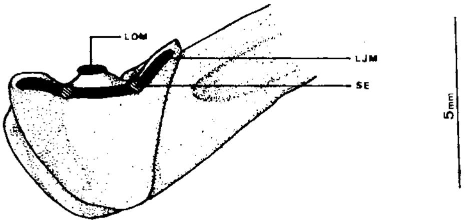


Fig. 65, Lateral view of the skull of *Galbula ruficauda* showing cranial jaw ligaments: LPO (Posterorbital ligament); LOM (Occipitomandibular ligament) LJM (Medial Jugomandibular ligament) and LJML (Lateral Jugomandibular ligament); fig. 66, caudal view of the lower jaw showing the insertions of the Occipitomandibular ligament (LOM) and of the Medial Jugomandibular ligament (LJM).

67

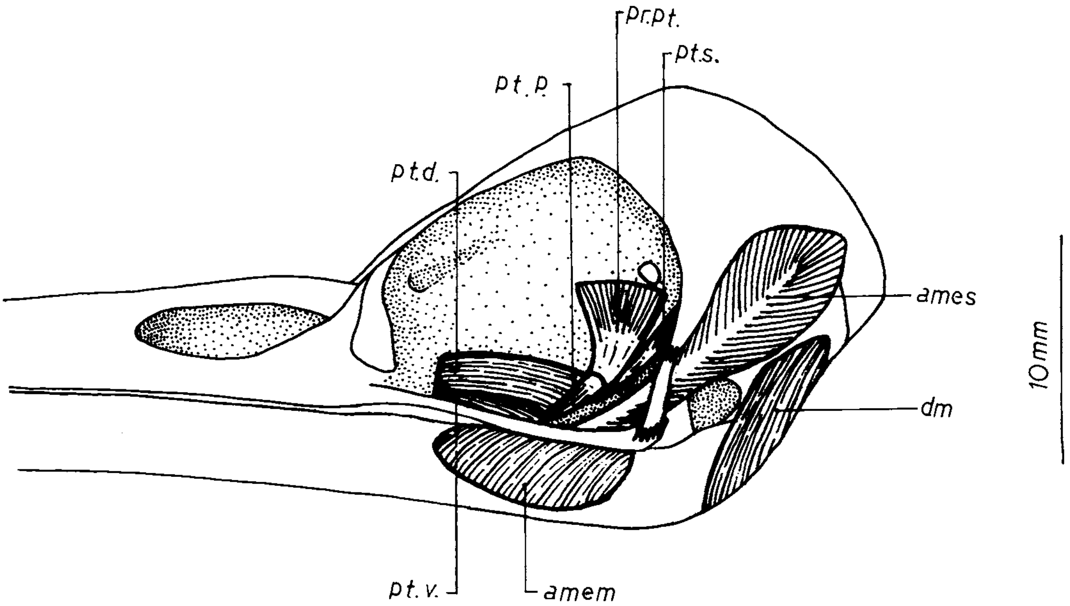


Fig. 67, Lateral view of the skull of *Galbula ruficauda* showing the muscles of the jaw apparatus. The quadrate bone was removed.

Table 1.

Present paper	Shufeldt (1890) apud Merz (1963)	Gadow (1891) apud Merz (1963)	Lakjer (1926)	Edgeworth (1935) apud Merz (1963)	Adams (1942) apud Merz (1963)
M. adductor mandibulae externus superficialis	part of M. temporalis	parts 1 and 2 of M. temporalis	+	part of M. adductor mandibulae externus	M. capiti mandibularis medius et profundus
M. adductor mandibulae externus medialis	part of M. masseter and temporal	parts 1 and 2 of M. temporalis	+	part of M. adductor mandibulae externus	M. capiti mandibularis superficialis, 1st part
M. adductor mandibulae externus profundus	part of M. masseter and m. temporalis	part 2 of M. temporalis	+	part of M. adductor mandibulae externus	M. capiti mandibularis medius and 2nd part of M. capiti mand. superficialis
M. psedotemporalis superficialis	part of M. temporalis	M. sphenomaxillaris	+	part of M. adductor mandibulae medius	M. pterygoideus posterior
M. adductor mandibulae posterior	part of M. temporalis	part of M. temporalis	+	part of M. adductor mandibulae medius	part M of M. pterygoideus posterior
M. pseudotemporalis profundus	part of M. pterygoideus externus	M. quadrato maxillaris	+	part of M. adductor mandibulae medius	part M of M. pterygoideus posterior
M. protractor quadrati	part of M. entotympanicus	parts 4a and 4b of M. temporalis and M. orbito-quadratus	+	M. sphenopterygo-quadratus	
M. protractor pterygoidei	part of M. entotympanicus	parts 4a and 4b of M. temporalis and M orbito-quadratus	+	M. sphenopterygo-quadratus	
M. pterygoideus ventralis medialis	part of M. pterygoideus internus	part of M. pterygoidei	+	part of M. adductor mandibulae internus	part of M. pterygoideus anterior
M. pterygoideus ventralis lateralis	part of M. pterygoideus internus	part of M. pterygoidei	+	part of M. adductor mandibulae internus	part of M. pterygoideus anterior
M. pterygoideus dorsalis	part of M. pterygoideus internus	part of M. pterygoidei	+	part of M. adductor mandibulae internus	part of M. pterygoideus anterior
M. despressor mandibulae	+	+			
M. despressor mandibulae externus superficialis	M. biventer maxillae	M. digastricus			
M. despressor mandibulae externus profundus					

Synonymy of the jaw

Hofer (1950)	Beecher (1951)	Starck & Barnikol (1954)	Bams (1956)	Zusi (1962)	Merz (1963)
+	M. superficialis (part)	portion ap. 1 of M.a.m.e.s. —	M. adductor mandibulae externus et posterior	part M and part A, dorsal portion of M.a.m. externus	+
M.a.m.e. medius and superficialis (part)	M. superficialis (part) and medialis	portion ap.2 of. M.a.m.es.	M. aductor mandibulae externus et posterior	part A, ventral portion of M.a.m. externus	+
+	+	portion ap.3 of M.a.m.e.s	M. adductor mandibulae externus et posterior	part B of M. adductor mandibulae externus	+
part of M. pseudotemporalis	+	+	M. adductor mandibulae internus et pseudotemporalis	+	+
+	+	+		+	+
M. quadrati mandibularis	+	+	M. adductor mandibulae externs profundus	+	+
M. protractor quadrati et pterygoidei	M. protractor quadrati et pterygoidei	M. protractor quadrati et pterygoidei	M. protractor quadrati et pterygoidei	M. protractor quadrati et pterygoidei	M. protrator quadrati et pterygoidei
M. pterygoidei ventralis	M. ventralis anterior	M. pterygoideus ventralis lateralis (part) and ventralis medialis	M. adductor mandibulae internus pterygoideus (ventromedial portion)	part N of M. pterygoideus	
M. pterygodei ventralis lateralis et dorsalis lateralis	M. ventralis posterior	M. dorsalis lateralis et ventralis lateralis	M.a.m.i.p. ventro and dorso lateral portion	part M of M. pterygoideus dorsalis lateralis	+
M. pterygoidei dorsalis, lateralis et medialis	M. dorsalis anterior et posterior	M. dorsalis medialis	M.a.m.i. pterygoideus dorsalis	part O of. M. pterygoideus	+
+	+		+	+	+
					M. superficialis medialis
					M. superficialis lateralis et. med.

Apparatus

Burton (1974)	Zweers (1974)	Höfling & Gasc (1984a)	Burton (1984)	Zusi 1984)
part M and part A of M.a.m. externus	M.a. m. externus pars caudolaterais	+	M.a. m. externus rostralis temporalis	M.a.m. externus pars rostralis
part A of M.a.m. externus (ventral portion)	M.a.m. externus pars rostromedialis	+	M.a.m.e. ventralis	M.a.m.e. pars ventralis
part B of M.a.m. externus	+	+	M. adductor mandibulae externus caudalis	
+	+	+	+	+
+	+	+	+	M. adductor mandibulae caudalis
+	+	+	+	+
M. protractor quadrati pterygoidei	+	+	M. protractor quadrati et pterygoidei	M. protractor quadrati et pterygoidei
	+			
part N of M. pterygoideus	+	+	+	+
part M of M. pterygoideus	+	+	+	+
part O of M. pterygoideus	+	+	+	+
+	+	+	+	+
	M.d.m. grandis pyramidalis (part) and M.d.m. triangularis	+		
	M.d.m. cuboides, pars lateralis	+		

Legend:
M.: muscle
+: same nomenclature of the present paper
ap.: aponeurosis
M.a.m.: muscle adductor mandibulae
M.a.e. (for ext.): muscle adductor mandibulae externus
M.a.m.e.s.: muscle adductor mandibulae externus superficialis
mand.: mandibularis
M.a.m.i.p.: muscle adductor mandibulae internus pterygoideus
M.d.: muscle depressor mandibulae
med.: medialis

ABREVIATIONS

a.m.e.m. — *adductor mandibulae externus medialis*
a.m.e.p. — *adductor mandibulae externus profundus*
a.m.e.s. — *adductor mandibulae externus superficialis*
An — angular region of the lower jaw
Ar — articular region of the lower jaw
AT — *ala tympanica*
BA — basioccipital region
BS — basisphenoid region
Cm — median concavity
CO — occipital condyle
CoLQ — lateral condyle of the quadrate
CoMQ — medial condyle of the quadrate
CoPQ — posterior condyle of the quadrate
CrBA — basioccipital crest
CrI — *crista intercotylaris*
CrLM — lateral crest of the lower jaw
CrM — medial crest of the lower jaw
CrO — occipital crest
CrPL — lateral palatine crest
CrPV — ventral palatine crest
CrT — T crest of the lower jaw
CrTA — anterior temporal crest
CrTI — tympanic crest
CrTS — superior temporal crest
d.m. — *depressor mandibulae*
E — esquamosal region
ET — ectethmoid region
EX — exoccipital region
F — frontal region
Facm — fossa aditus canalis mandibulae
FC — *fossa caudalis*
FM — *fossa medialis*
FO — optical foramen
FOM — foramen magnum
FOR — foramen
Fsc — *fossa subcondilaris*
FI — temporal fossa
INT — intumescentia exoccipitalis
J — jugal bar
L — lacrimal bone
MS — upper jaw
N — nasal region
NA — nostril
O — occipital region
P — parietal region
PA — palatine bone
PAR — parasphenoid region
PrArQ — articular process of the quadrate
PrBA — basioccipital process
PrC — coronoid process
PrE — squamosal process
PrET — ectethmoid process
Prjo — bony projection
PrL — lacrimal process
PrLM — lateral process of the lower jaw
PrM — medial process of the mandible
PrOtQ — optical process of the quadrate
PrOrQ — orbital process of the quadrate
PrPO — postorbital process
pr.qt. — *protractor quadrati*
pr.pt.s.s — *protractor pterygoidei s.s.*
PT — pterygoid
pt.d. — *pterygoideus dorsalis*
pt.p. — *pseudotemporalis profundus*
pt.s. — *pseudotemporalis superficialis*
pt.v.l. — *pterygoideus ventralis lateralis*
pt.v.m. — *pterygoideus ventralis medialis*
Q — quadrate
SA — suprangular region of the jaw
SE — sesamoid
SFL — frontolacrimal suture
SFN — frontonasal suture
SI — septum interorbital
SNL — nasolacrimal suture
SO — supraoccipital region
TT — T tuberosity of the lower jaw
TY — Y tuberosity of the lower jaw
TZ — Z tuberosity of the lower jaw
VA — angular vertex

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