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DESCRIPTION OF THE CEPHALIC MUSCLES AND GLAND MORPHOLOGY OF *CLELIA PLUMBEA* AND THREE PRESUMABLY RELATED SPECIES (SERPENTES, XENODONTINAE)

HUSSAM ZAHER

ABSTRACT

The cephalic muscles and glands of Clelia plumbea *are described and compared with those of* C. rustica, Oxyrhopus petola *and* Pseudoboa nigra. *Intraspecific as well as intra- and intergeneric variations of the cephalic muscles are given for each species.*

Intra- and intergeneric variations occur in the shape of the Duvernoy's gland, the size of the rictal gland, the length of the posteroventral region of the nasal gland, the width of the quadrato-maxillary ligament, the presence of an anterior bundle of the M. adductor mandibulae externus superficialis, the size of the insertion site of the deep part of the Mm. adductor mandibulae externus profundus and adductor posterior, the presence and length of an occipital head of the M. depressor mandibulae, the size of the insertion site of the M. intermandibularis posterior pars anterior, the presence of a pars mucosalis belonging to the M. transversus branchialis, the site of origin of the M. protractor laryngeus and site of insertion the lateral fibers.

Intraspecific variation occurs in the width of the M. constrictor colli, the site of insertion of the Mm. cervicomandibularis, intermandibularis anterior pars anterior and pars glandularis, and the tranversus branchialis, the site of origin of the Mm. pseudotemporalis, protractor pterygoidei,

Departamento de Vertebrados, Museu Nacional-UFRJ, Quinta da Boa Vista, CEP 20940-040-São Cristovão, Rio de Janeiro-RJ, Brasil.
Present adress: Departamento de Zoologia, Universidade de São Paulo, Cidade Universitária, CEP 05508-900, São Paulo - SP, Brasil.

protractor quadrati, genioglossus and geniotrachealis, and the lenght of the Mm. hyoglossus and hyotrachealis.

Keywords: Xenodontinae; Pseudoboini; Anatomy; Head muscles; *Clelia plumbea; Clelia rustica; Oxyrhopus petola; Pseudoboa nigra.*

INTRODUCTION

Anatomical studies on the cephalic musculature[1] of squamate provide an impressive amount of detail. However, considerable gaps remain in the knowledge of ophidian structure and principally of colubrid snakes. For instance, little attention has been paid to the analysis of differences in the musculature below the family level. Cowan & Hick (1951) provided the first detailed comparison among three species of the colubrid genus *Thamnophis.* Varkey (1979) gave an extensive analysis of North American natricine genera. Recently, Cundall (1986) described and discussed differences of cephalic muscles among and within the colubrid genera *Entechinus, Opheodrys* and *Symphimus.*

Few studies have dealt with the musculature of Neotropical colubrid snakes. Only Weaver (1965), Romano & Hoge (1972), Kardong (1980), and, to some extent, McDowell (1986), provided descriptions. The first aim of the present study is to amplify data on the topic, by describing the cranial musculature and gland morphology of four species currently assigned to the South American xenodontine genera, *Clelia, Pseudoboa* and *Oxyrhopus.* This report offers information on interspecific differences among genera as well as intraspecific variations within each of the species: *Clelia plumbea, Clelia rustica, Pseudoboa nigra* and *Oxyrhopus petola.* The genera *Clelia, Oxyrhopus,* and *Pseudoboa* are placed in the tribe Pseudoboini along with *Tripanurgos, Rhachidelus, Siphlophis, Phimophis* and *Drepanoides,* an arrangement first proposed by Bailey (1939, 1967) who recognized the close affinities between them. The genera *Clelia, Pseudoboa* and *Oxyrhopus* also share a long and controversial taxonomic history since they are generally viewed as closely related, and have been considered synonyms at least once since Duméril, Bibron & Duméril (1854). However, their distinct patterns of head muscles and glands, illustrated by various important morphological differences, point to a complex evolutionary history.

The anatomical information obtained from the present comparative analysis provided a framework for the choice of phylogenetically informative characters used in a cladistic analysis of the tribe Pseudoboini to be presented elsewhere (Zaher, 1994a; in prep.).

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[1] The abbreviations used in the text are: M., muscle; Mm., muscles.

Material and Methods

Complete anatomical descriptions of cephalic glands and muscles of *Clelia plumbea* start the descriptions. Dissections of *Clelia rustica*, *Oxyrhopus petola* and *Pseudoboa nigra* are compared directly in a section based on the previous description of *C. plumbea*.

The selection of these species to illustrate the comparative section was made upon two criteria: 1) to provide a detailed anatomical work within the Pseudoboini in which the majority of the myological and glandular differences are described and illustrated in a minimum of space; 2) to show the array of such differences within presumably closely related genera.

One specimen of each species has been used for complete description of the cephalic glands and muscle complexes. Other specimens have subsequently been dissected to check the anatomical stability of the structures illustrated in the drawings. A specimen of *Clelia rustica* (MNHN 7803) was sacrificed and Rhodopax AX 85/15, dissolved in acetone and colored with alcian blue, was injected in the arterial system (carotid artery). This manipulation allowed visualization with increased precision of the course of the cephalic blood system and its differentiation from the nervous system. Nevertheless, peripheral blood vessels are hardly stained and some of them were lost during the dissection.

Dissections were performed with the help of a stereomicroscope Wild M5 (using 6X or 12X magnification) equipped with a *camera lucida* for drawings. Both sides of the head of each specimen were dissected in order to check for possible bilateral assymetry.

Museum and Institute collections are denoted by the following abbreviations: IBH, Instituto Butantan; IVB, Instituto Vital Brazil; MNHN, Muséum national d'Histoire naturelle de Paris.

Specimens dissected for the comparative section are: *Clelia plumbea*: IVB 598- Motel Farol, Maria Paula, Niterói, state of Rio de Janeiro, Brazil; CEPLAC 576 - Ilhéus, state of Bahia, Brazil; IBH 49305 - Juquitiba, state of São Paulo, Brazil. *Clelia rustica*: MNHN 7803- Buenos Aires, Argentina; MNHN 1990.4301- Argentina; IBH 25135- Guarapuara, state of Paraná, Brazil; IBH 32622- Campo Largo, state of Rio Grande do Sul, Brazil. *Pseudoboa nigra*: IVB 630 and 637- Itaparica barrage, state of Bahia, Brazil; IBH 53289- Rosana, state of São Paulo, Brazil; IBH 53621- Pompéia, state of São Paulo, Brazil. *Oxyrhopus petola*: IVB 472- Tijuca forest, Rio de Janeiro, state of Rio de Janeiro, Brazil; IVB 678- Itaipu, Niterói, state of Rio de Janeiro, Brazil; IBH 54124 and 54131-Usina Três Irmãos, Pereira Barreto, state of São Paulo, Brazil.

Muscular terminology employed

The terminology for the adductor externus musculature is in a state of chaos. The most commonly employed terminology is that of Lakjer (1926), as used by Haas (1930, 1931a,b, 1962). Haas (1973) showed the weakness of Lakjer's terminology to reflect the homologies between the lacertilian and ophidian adductor externi muscles and tried to remediate this problem in providing a new interpretation. However, Haas (1973: 471) clearly encouraged the conservation of Lakjer's terminology in order to avoid confusion. Rieppel (1980a) reviewed the question of homologies, providing a careful analysis based on the topographical relations between the bundles of the adductor muscles and the aponeurotic system of Anguimorph lizards and Iguana on the one hand and anilioid snakes on the other hand. McDowell (1986, 1987) rejected Rieppel's (1980a) homologies and proposed a new terminology for the three adductores externi muscles. Paradoxically, McDowell (1986) misregarded the anilioid and "booid" snakes, as well as Rieppel's (1980a) findings, and focused his analysis in Colubroid snakes. Subsequently, Rieppel (1988) reanalyzed his previous conclusions and rejected McDowell's (1986) views. However, Rieppel (1980a, 1988) did not propose a new terminology. Recently, Zaher (1994b) discussed both Rieppel's and McDowell's conclusions and presented a reinterpretation of the jaw adductor muscles, comparing representatives of almost all major divisions of alethinophidian snakes and proposing a new terminology for these bundles. This terminology will be followed here. It differs from the one generally used by previous authors as follows: the muscles adductor mandibulae externus superficialis and levator anguli oris retain the same names; the M. adductor mandibulae externus medialis of Lakjer (1926) is named M. adductor mandibulae externus profundus; the M. adductor mandibulae externus profundus of Lakjer (1926) is named M. adductor mandibulae externus medialis pars posterior. The anilioids and booids show a distinct lateral muscular bundle that I called M. adductor mandibulae externus medialis pars anterior which is absent (secondarily lost) in the Tropidopheoidea and Caenophidia (Zaher, 1994b,c).

The terminology for the remaining adductor musculature is characterized as in Haas (1973), Kardong (1980) and Cundall (1986). Intermandibularis muscle terminology follows Langebartel (1968), Groombridge (1979) and Cundall (1986). The terminology of the cephalic glands follows Taub (1966), Kochva (1978) and McDowell (1986), of cranial nerves follows that presented by Auen & Langebartel (1977).

Results

Description of the cephalic glands and muscles of *Clelia plumbea* (Figs. 1, 2).
    Cephalic glands (Figs. 1, 2, 5, 9, 10, 11):
    The single **premaxillary gland**, with its triangular shape, lies beneath the rostral scale, superficial to the premaxillary bone.
    The **nasal glands** fit into a depression delimited by the prefrontal, nasal bones, and the nasal capsule and partially cover the septomaxillary process. They show an inverted "L" shaped pattern due to an expansion of their posteroventral region.
    The **Harderian glands** are almost covered by the M. adductor mandibulae externus superficialis, the exposed part lying on the lateral surface of the head just behind the eye. They fit in a cavity, posteromedially to the postorbital bone and lateral to Mm. levator pterygoidei and pseudotemporalis. Passing medially to the postorbital, they extend anteriorly into the orbit to surround the eye on its medial surface.
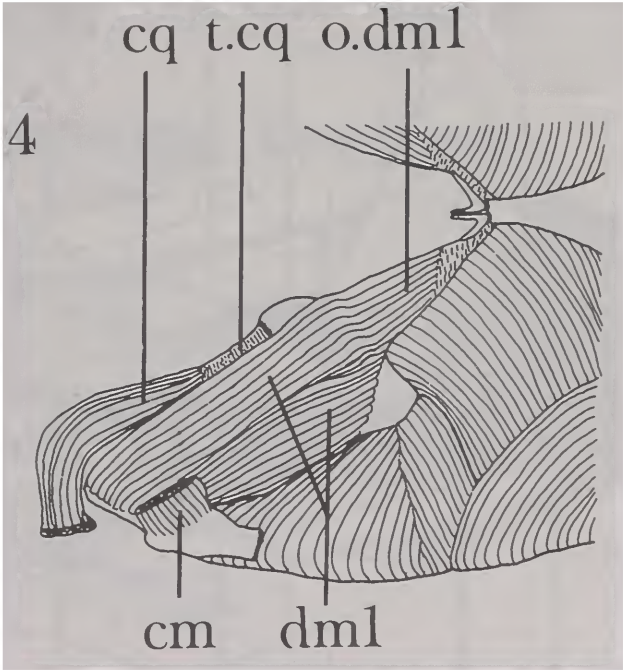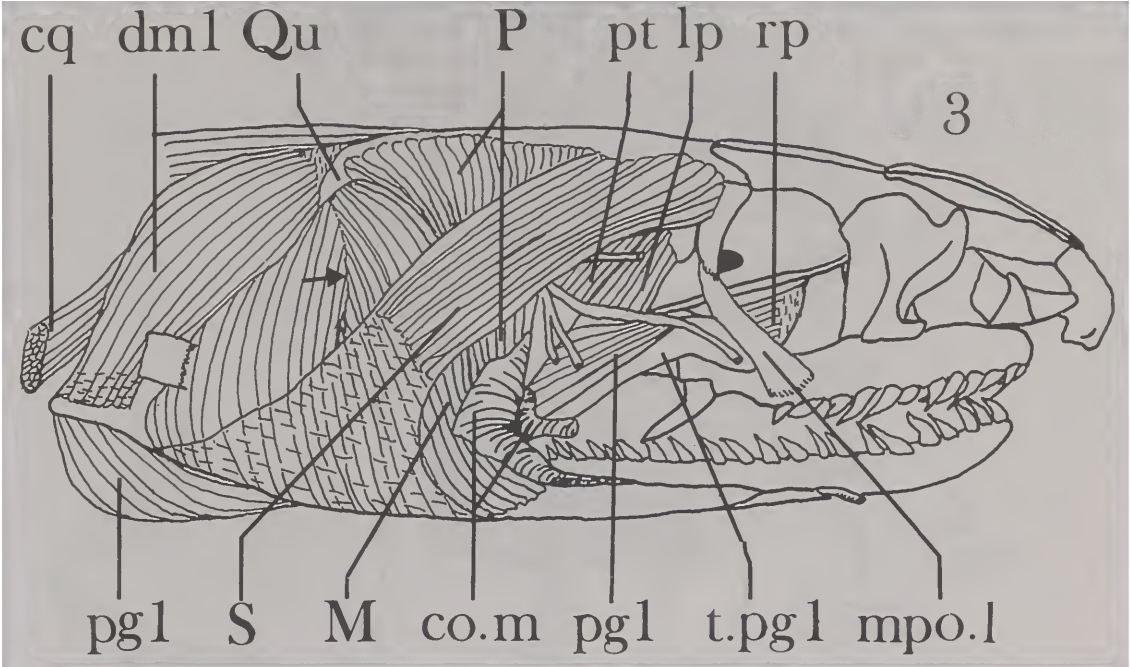   The **supralabial glands** lie beneath the supralabial scales. Passing laterally to the maxillary bone and, posteriorly, reaching the Mm. adductores externi, they end just after the posterior fibers of the M. adductor mandibulae externus superficialis at the corner of the mouth.
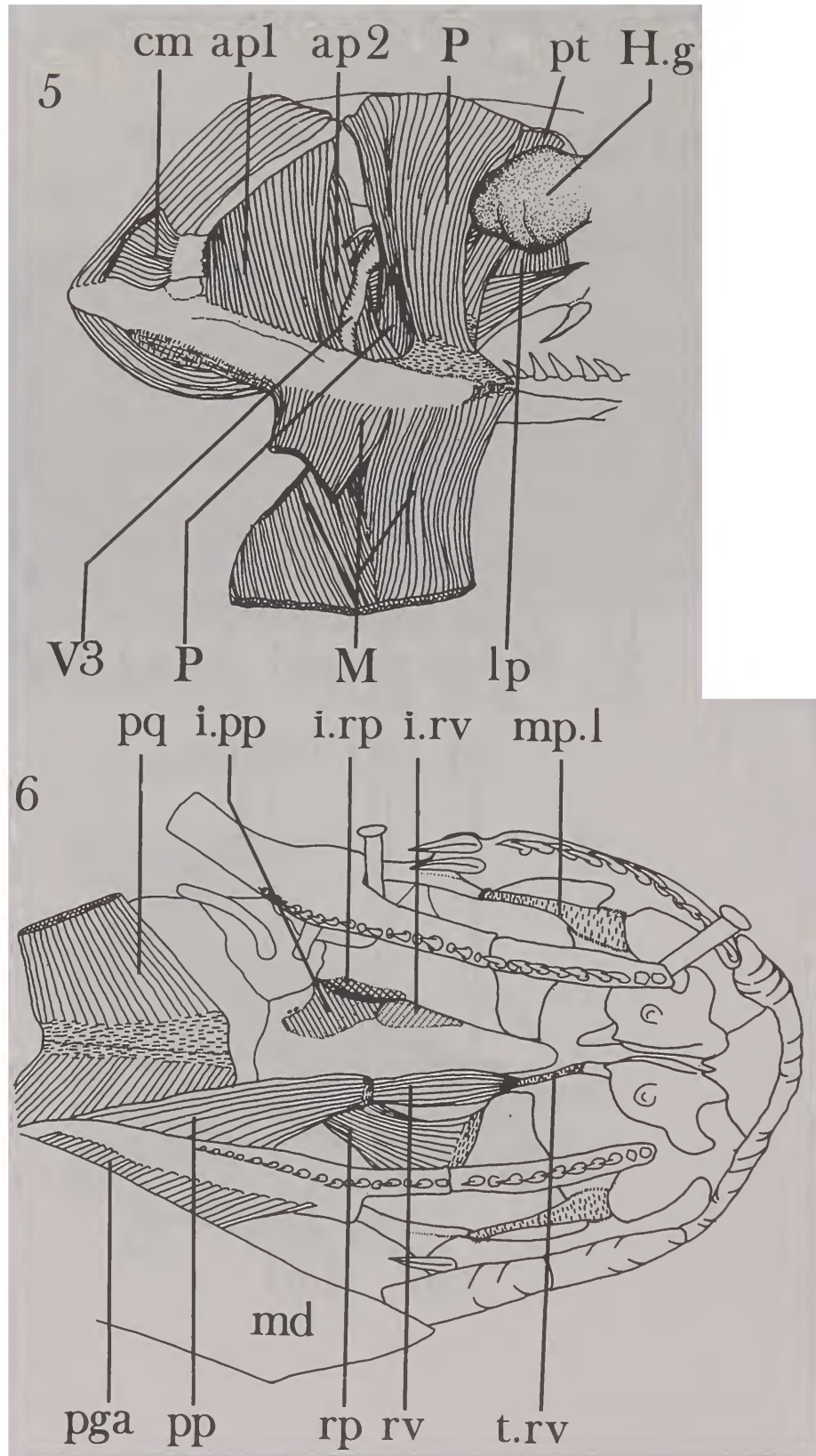   The **Duvernoy's glands** overlap to the upper posterior part of the supralabial glands. They lie behind the eye and present a convex upper surface. These glands are recognizable by their distinctly lobed body and creamy, yellow color; they are darker than the supralabial glands.
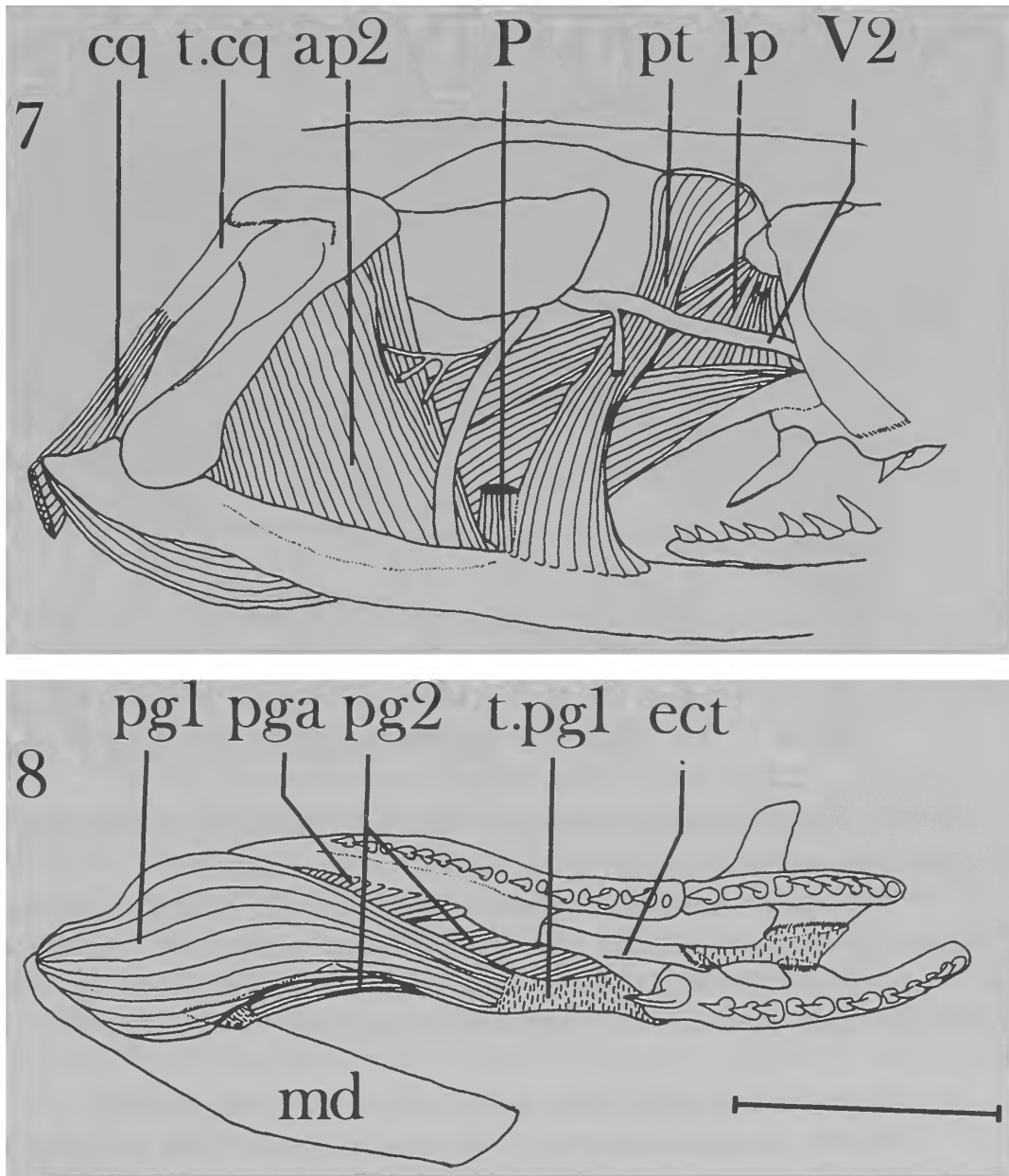   The **infralabial glands** lie beneath the infralabial scales. Extending from the anterior tip of the mandible, they pass alongside the lateral surface of the dentary and compound bones to end near the corner of the mouth, lateral to the Mm. adductores externi.
    The **rictal glands** ["glande temporale antérieure" of Phisalix (1922); "anterior temporal gland" of Smith and Bellairs (1947) and Gabe & Saint Girons (1969); "posterior gland" of Taub (1966) and Kochva (1978)], recently redescribed and analyzed by McDowell (1986) in various lineages of colubroid snakes, are present in *Clelia plumbea*. They lie in a depression of the wall of the M. adductor mandibulae externus superficialis, superficial to it and medial to the quadrato-maxillary ligament which hides them. These small glands are distinct from the corner of the mouth and the supralabial glands.They are round-shaped and flattened laterally, presenting a floccular surface (group VI of McDowell, 1986: 361). Histological sections of the rictal gland show a single duct, lined by secretory cells, opening at the corner of the mouth, and a body similar to a sero-mucous gland (pers. obs.).

cq dm1 Qu   P   pt lp rp   3

pg1 S M co.m pg1 t.pg1 mpo.l

cq t.cq o.dm1   4

cm dm1

5

cm apl ap2 P pt H.g

V3 P M lp

6

pq i.pp i.rp i.rv mp.l

md

pga pp rp rv t.rv
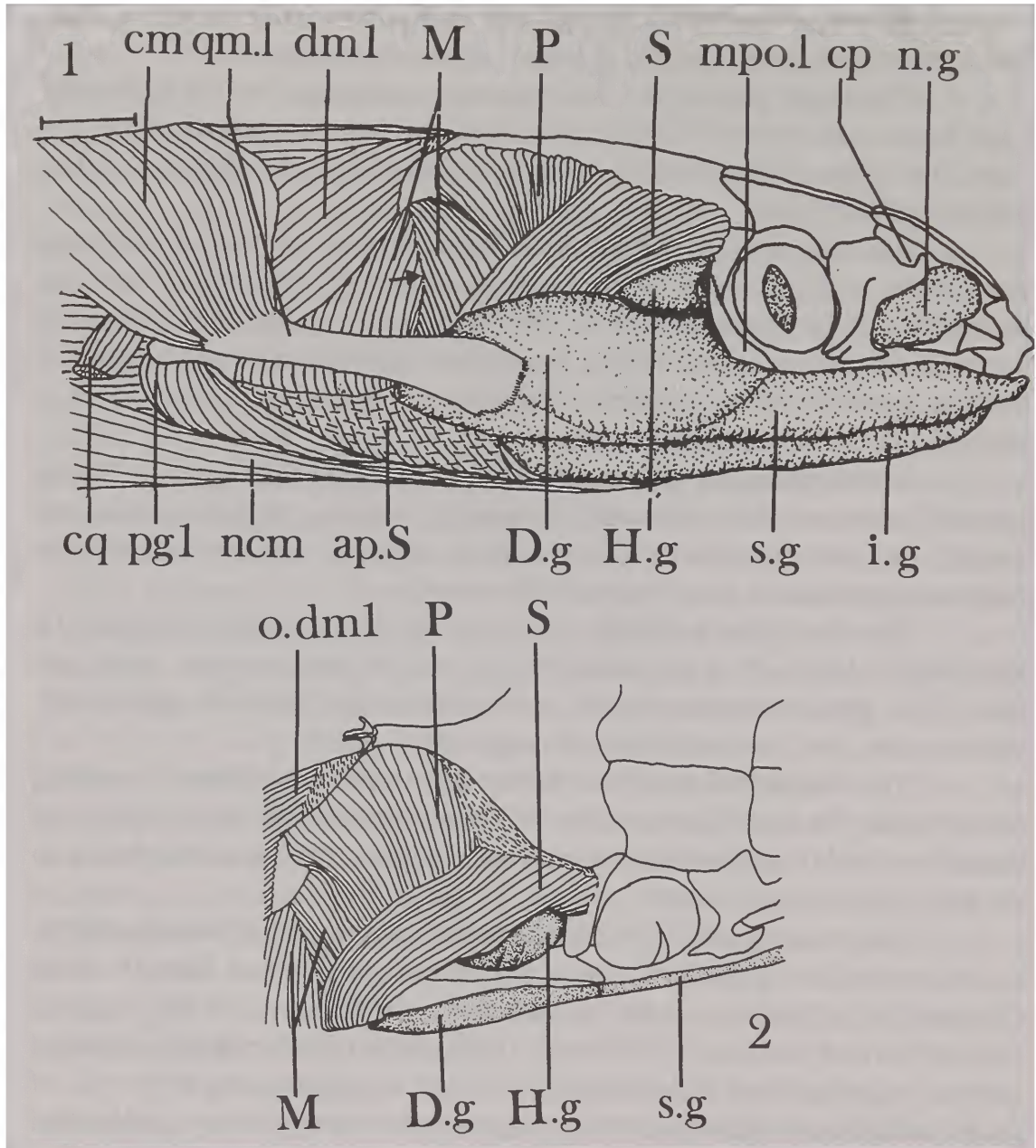
Figures 1 to 8. *Clelia plumbea*. Cephalic muscles and glands. 1 to 4, right lateral view of the head showing progressively more medial bundles of the adductor externus musculature; 5-6, dorsal view of the right side of the head showing the superficial adductor muscles and the M. depressor mandibulae; 7, ventral view of the head showing the constrictor internus dorsalis musculature and its area of origin; 8, ventral view of the left palato-maxillary arch and mandible showing the pterygoideus musculature.
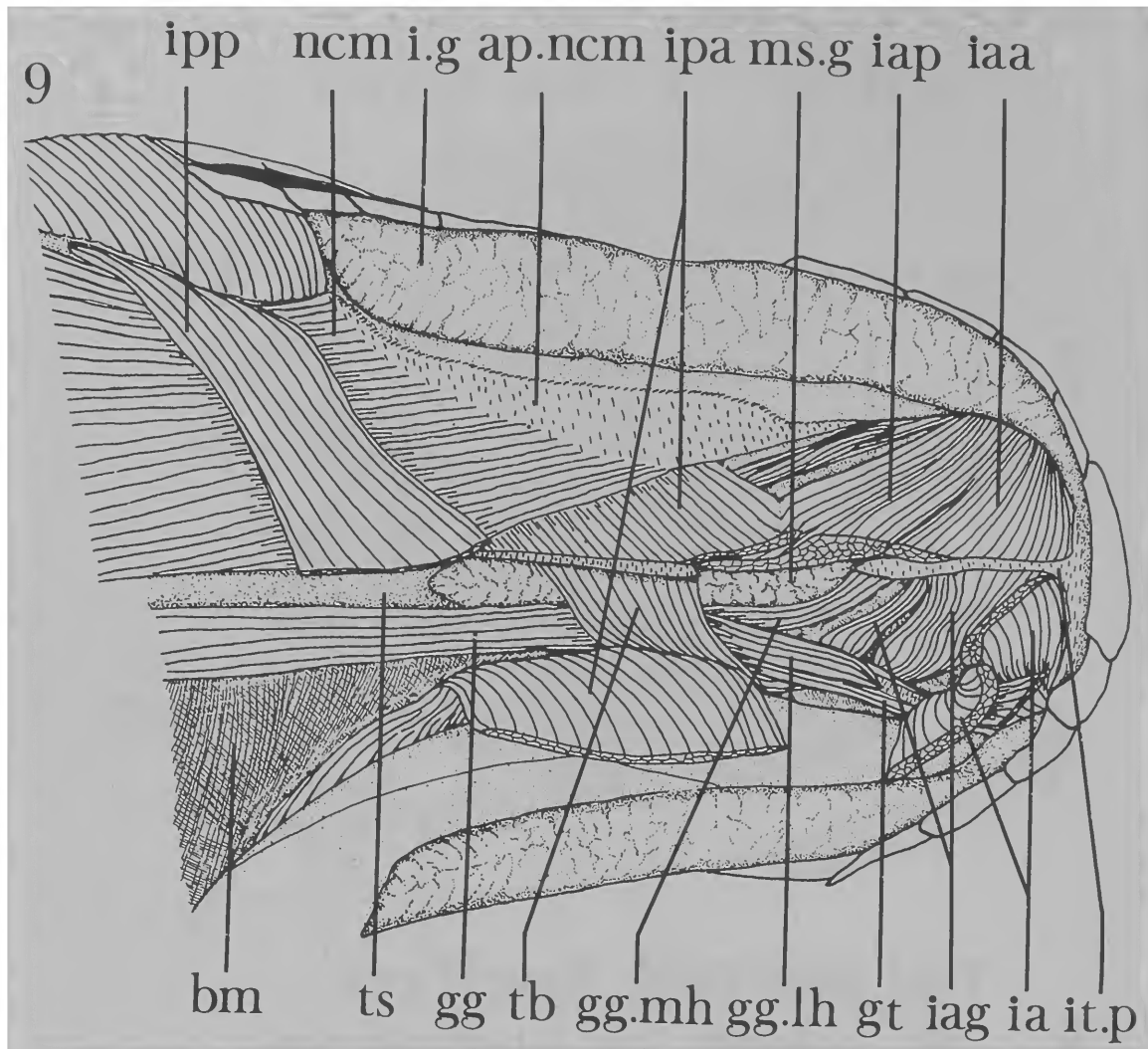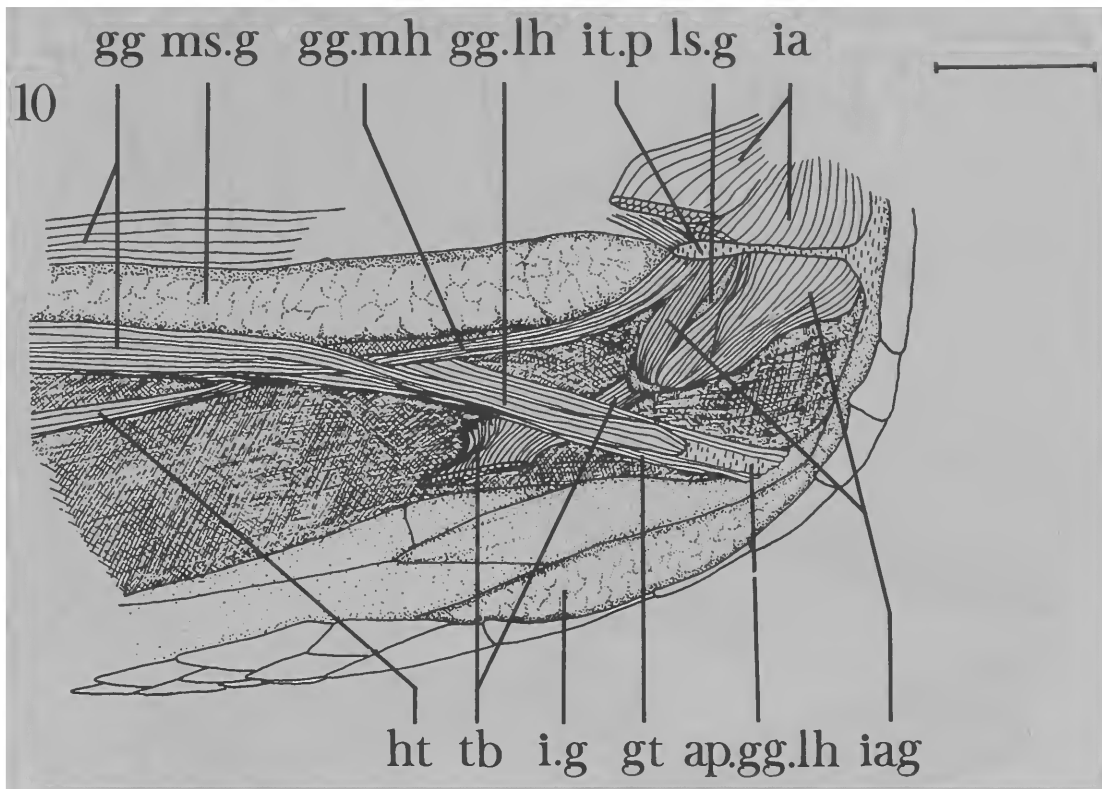
The single **median sublingual gland** lies ventrally to the tongue, attached in its anterior portion to the connective tissue sheath.

The **lateral sublingual glands** insert into the buccal membrane, dorsolaterally to the interramal pad, and are almost surrounded ventrally by the M. intermandibularis anterior pars glandularis. The M. transversus branchialis pars glandularis originates on the posterior tip of the glands.

*Muscles innervated by the facial nerve (VII)* (Figs. 1, 3, 4):

The **M. constrictor colli** is a very thin muscular sheet, covering the lateral and ventral surfaces of the neck, that arises mostly from the lateral surface of the dorsal head of the quadrate and from the epimysium of the M. adductor mandibulae externus medialis pars posterior. It inserts on the skin, posteriorly or posteroventrally to the corner of the mouth. This muscular sheet is innervated by a ramus of the facial nerve emerging between the anteroventral fibers of the M. depressor mandibulae and the quadrate (not figured in Fig. 1, but same as for *C. rustica*, Fig. 33). The muscular bundle here termed con-

strictor colli is the homologue of the bundle described in *Waglerophis merremi* by Anthony & Serra (1949; their muscle 12, "petit pinceau musculaire croisant superficiellement le cervico-maxillaire") and Romano & Hoge (1972; their muscle 5, "feixe muscular que se insere na pele").

The **M. depressor mandibulae** comprises a superficial and a deep part, separated by the tendon of the M. cervicoquadratus. The pars superficialis covers the external face of the quadrate. Anteriorly, it originates at the level of the anterodorsal surface of the quadrate (quadrate head). Posteriorly, the fibers cover the posterodorsal region of the quadrate, originating on the supraoccipital crest via an aponeurosis that covers part of the posteromedial fibers of the M. adductor mandibulae externus profundus. The fibers of the occipital head do not reach the supraoccipital crest. The two heads meet below the dorsal head of the quadrate to form an unique pars superficialis which inserts into the dorsolateral surface of the retroarticular process. The pars profundus origi-nates on the posteromedial border of the quadrate and inserts on the dorsomedial surface of the retroarticular process, behind the tendinous insertion of the M. protractor quadrati. This deep sheet is subdivided into an anterior and a poste-rior muscular unit, by a gap containing an arteriole.

The **M. cervicomandibularis** is a thin muscle which takes its origin on the epimysium of the spinalis-semispinalis musculature, from vertebrae 4 through 9. Extending anteroventrally, it passes laterally to the cervicoquadratus
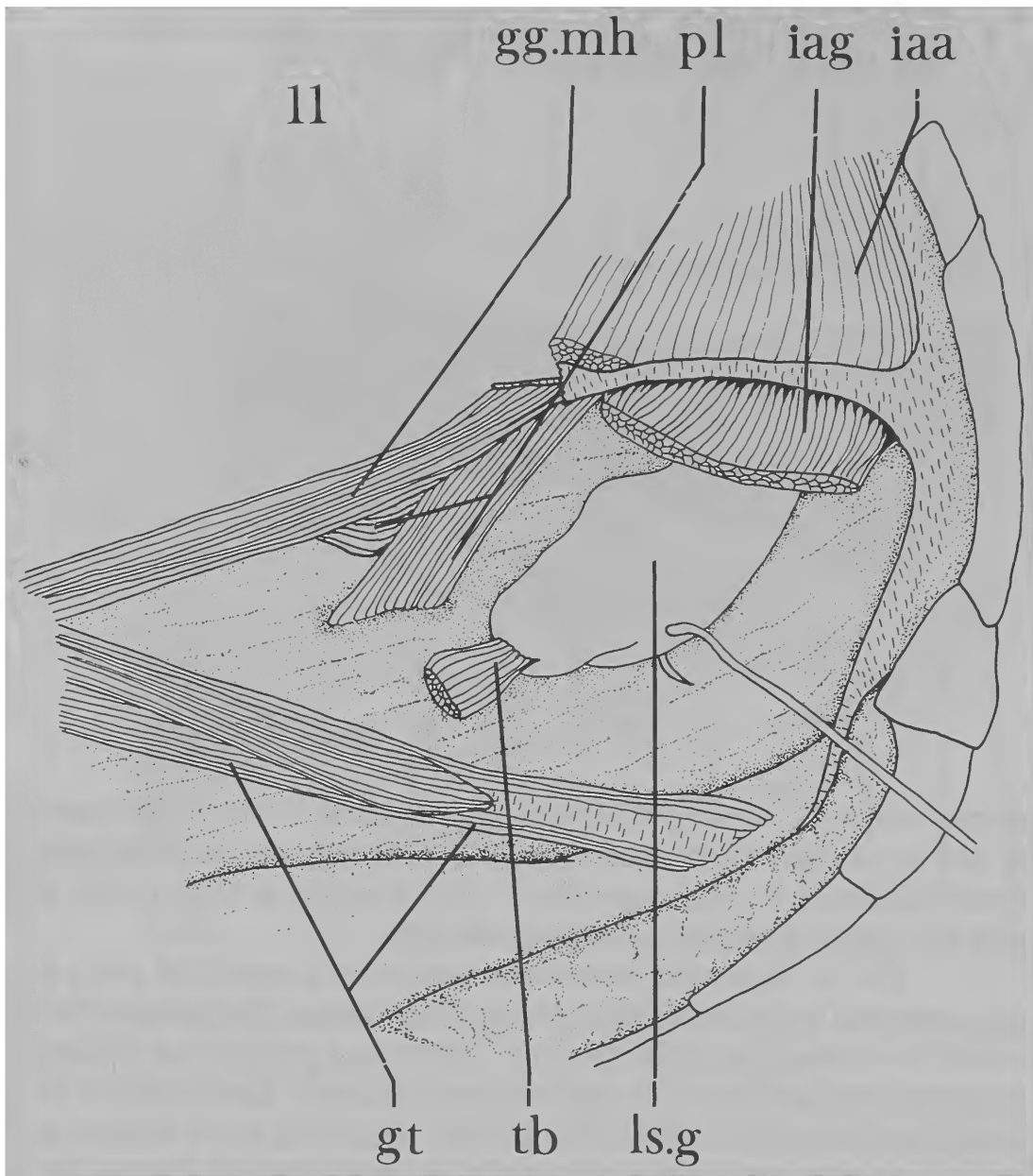
and inserts on the epicondylar zone of the quadrate at the posterior end of the quadrato-maxillary ligament.

Muscle innervated by spinal nerves (Figs. 1, 4):

The small **M. cervicoquadratus** is the only muscle of the head innervated by spinal nerves. It arises, posteroventrally to the retroarticular process, from the fascia covering the M. neurocostomandibularis and from the skin of the neck. Extending anterodorsally, its fibers pass between the pars superficialis and pars profundus of the M. depressor mandibulae and converge on a tendon which inserts on the posterodorsal tip of the quadrate.
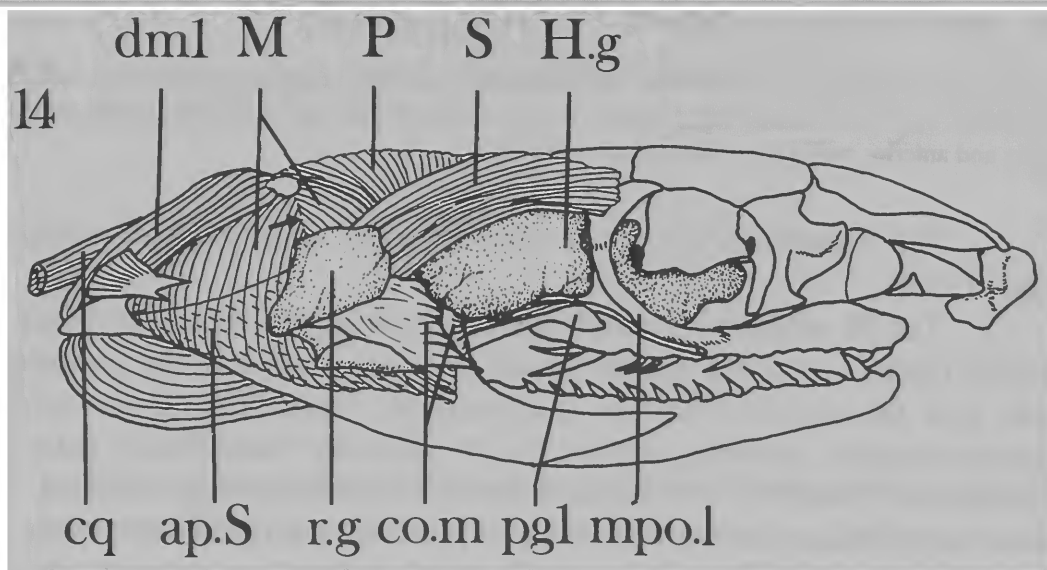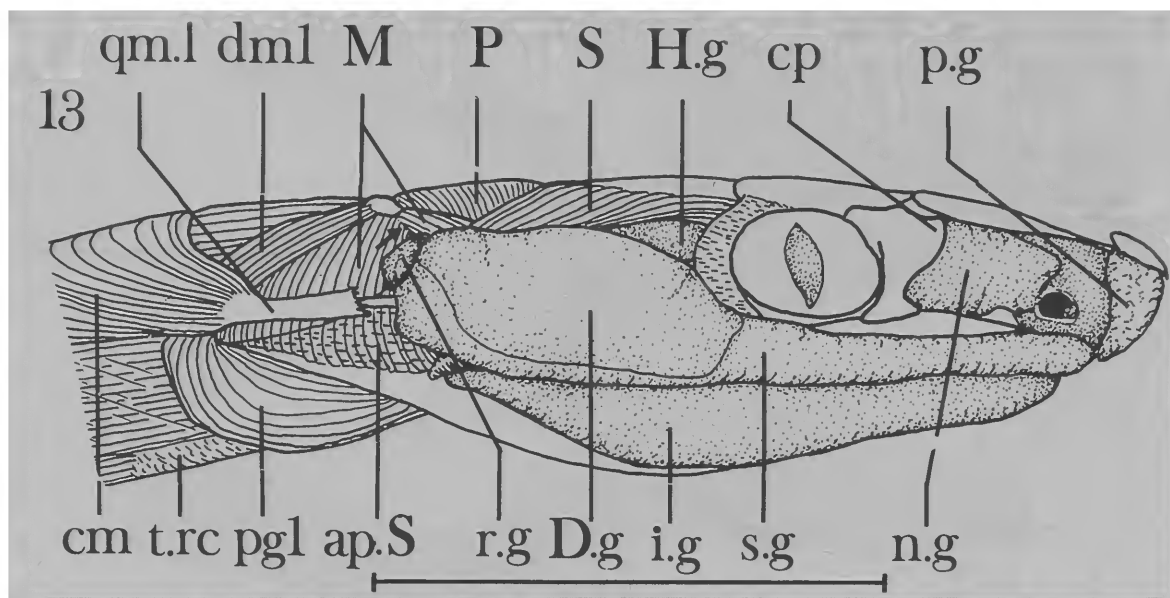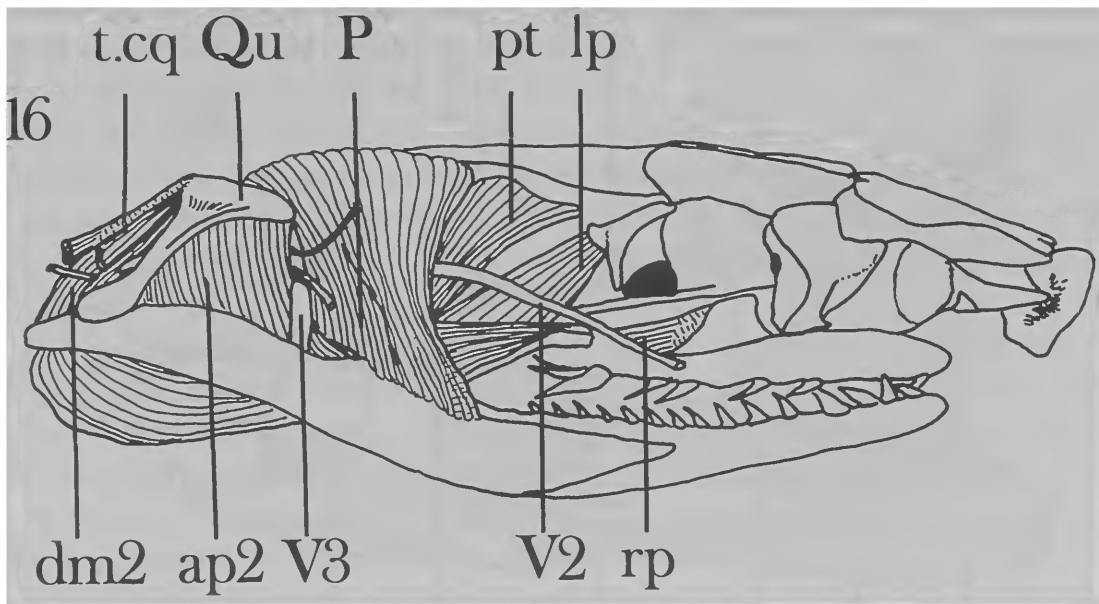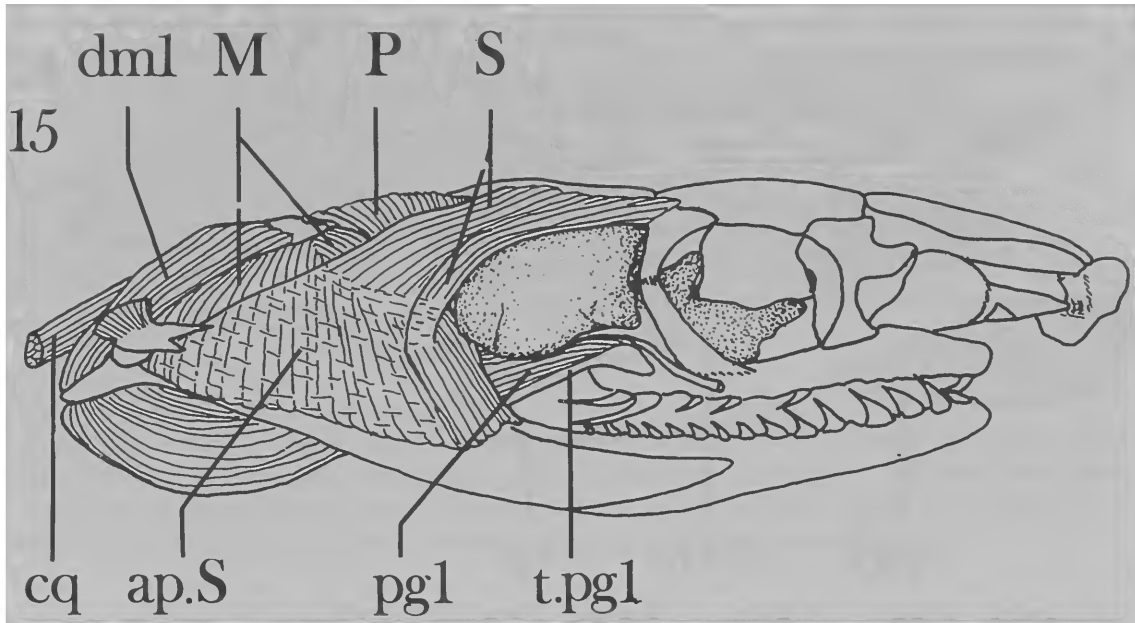
ht gt tr dl sl pl gg.mh   bm

12
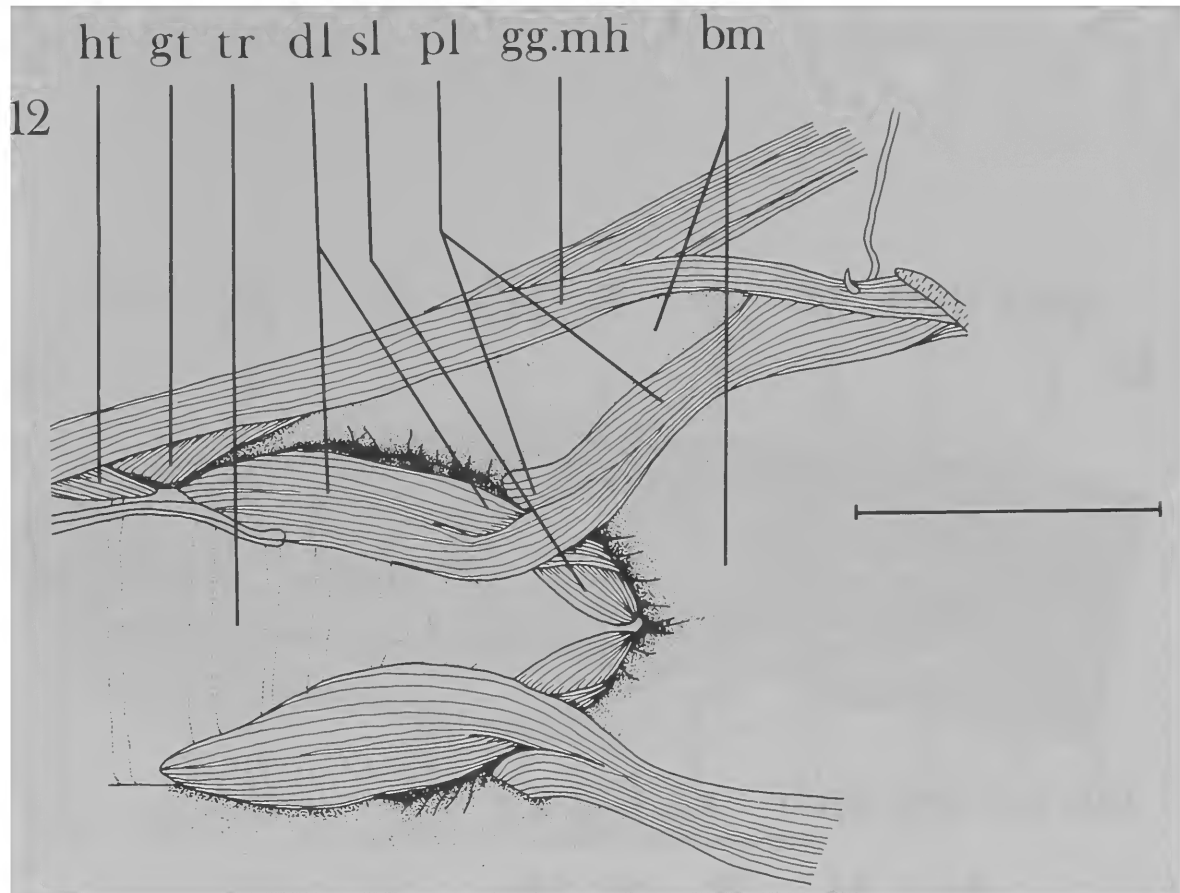
Figures 9 to 12. *Clelia plumbea*. Ventral view of the head showing the intermandibularis musculature and glands. 9, general view; 10-11, anterior region of the left side; 12, intrinsic musculature of the larynx and anterior end of the trachea in a ventral view.
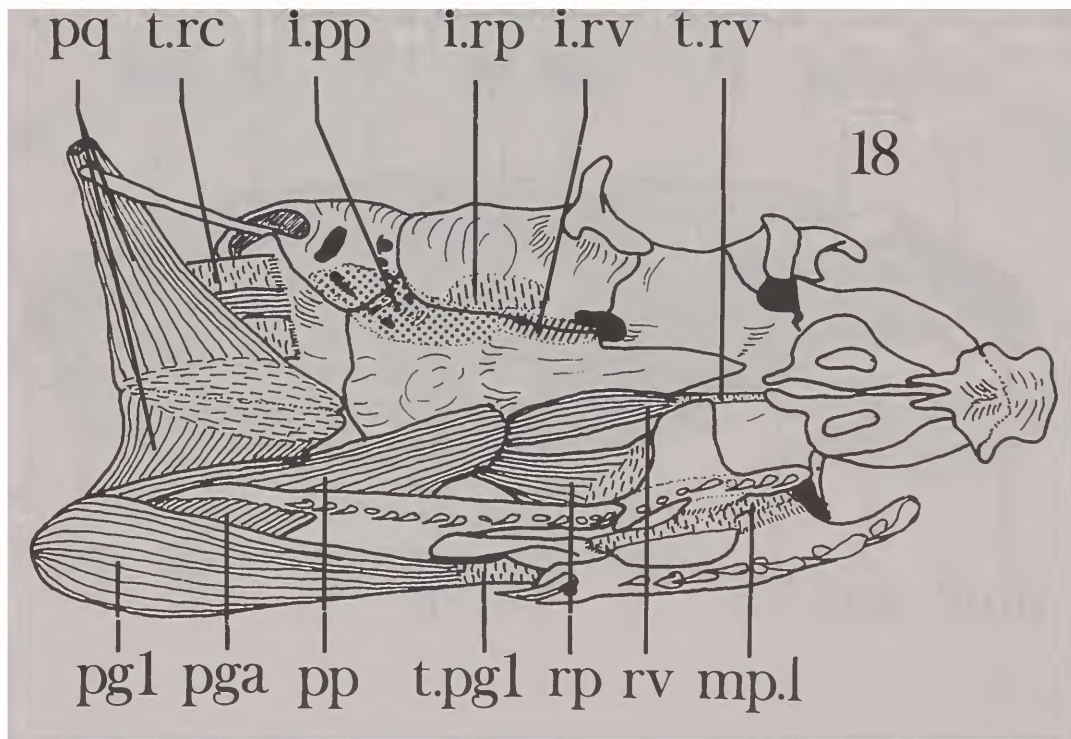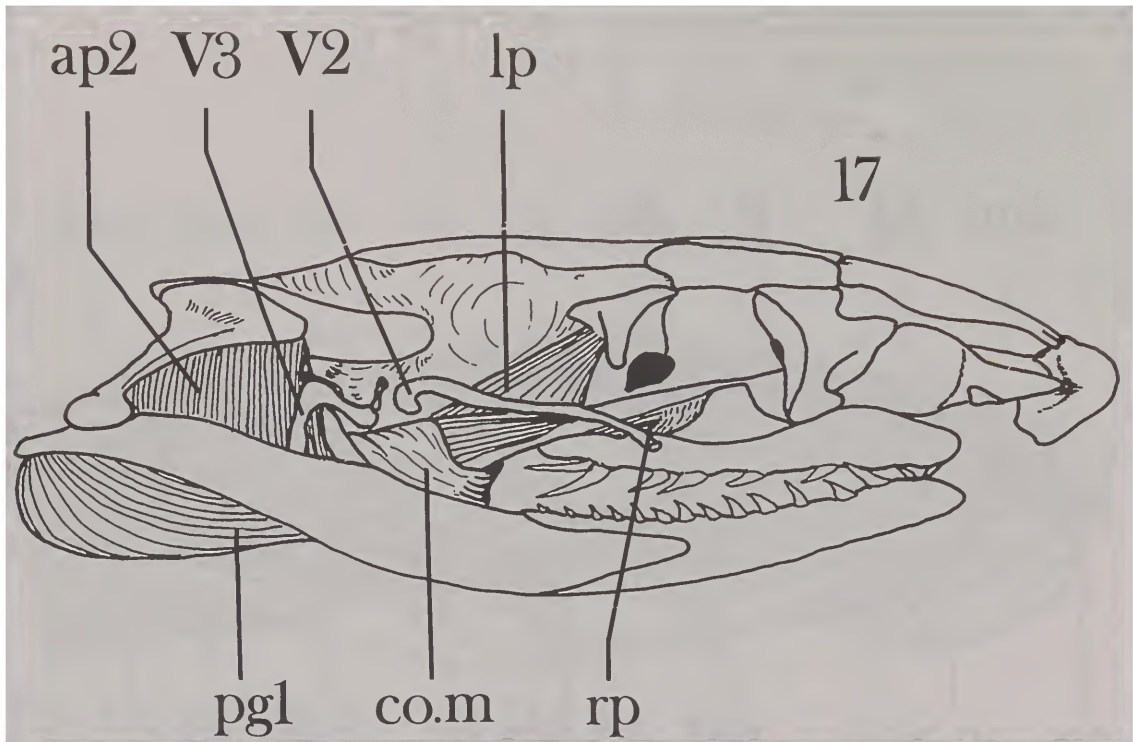
The mandibular adductors (innervated by the trigeminal nerve, V) (Figs. 1 to 8):
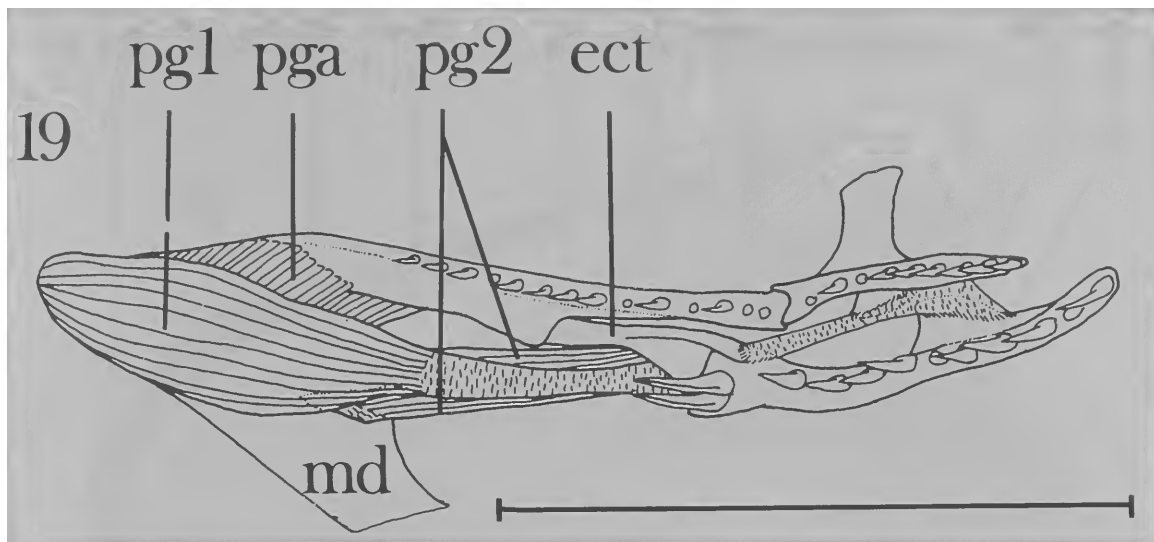
The **M. adductor mandibulae externus superficialis**, composed of parallel fibers, originates directly on the proximal surface of the postorbital bone and the anterior half of the temporal crest. The fibers extend posteroventrally, covering part of the M. adductor mandibulae externus profundus, to insert via a broad aponeurosis on the epimysium of the M. adductor mandibulae externus medialis pars posterior and the ventrolateral surface of the compound bone. It is a single muscle without any anterior subdivision of fibers attached on the rictal fold [which indicates the absence in *Clelia plumbea* of an anterior head of this muscle or a fully formed levator anguli oris <u>sensu</u> Zaher, 1994b].

The **M. adductor mandibulae externus profundus** originates on the posterior half of the supratemporal crest, its deep fibers attaching loosely to the region situated between the crest and the supratemporal bone. From the origin the fibers converge as they pass anteroventrally. This muscle is subdi-

13
qm.l dm1 M P S H.g cp p.g

cm t.rc pgl ap.S r.g D.g i.g s.g n.g

14
dm1 M P S H.g

cq ap.S r.g co.m pgl mpo.l

15

dml M   P   S

cq   ap.S   pg1   t.pg1

16

t.cq Qu   P   pt lp

dm2 ap2 V3   V2 rp

Figures 13 to 19. *Pseudoboa nigra*. Cephalic muscles and glands. 13 to 17, right lateral view of the head showing progressively more medial bundles of the adductor musculature; 18, ventral view of the head showing the constrictor internus dorsalis musculature and its area of origin; 19, ventral view of the left palato-maxillary arch and mandible showing the pterygoideus musculature.

vided into two parts that can be demonstrated by a slight cut on the posteromedial surface, the subdivision being complete only on its ventral region. The superficial part inserts on the mandible between the dentary and the mandibular fossa, the anterior fibers inserting via a tendon on the tip of the posterodorsal process of the dentary. The deep part, on the other hand, attaches to the anterior edge of the prearticular crest. At their insertion, the anterior fibers of the deep part are intermingled with the posterior fibers of the M. pseudotemporalis (Fig. 7).
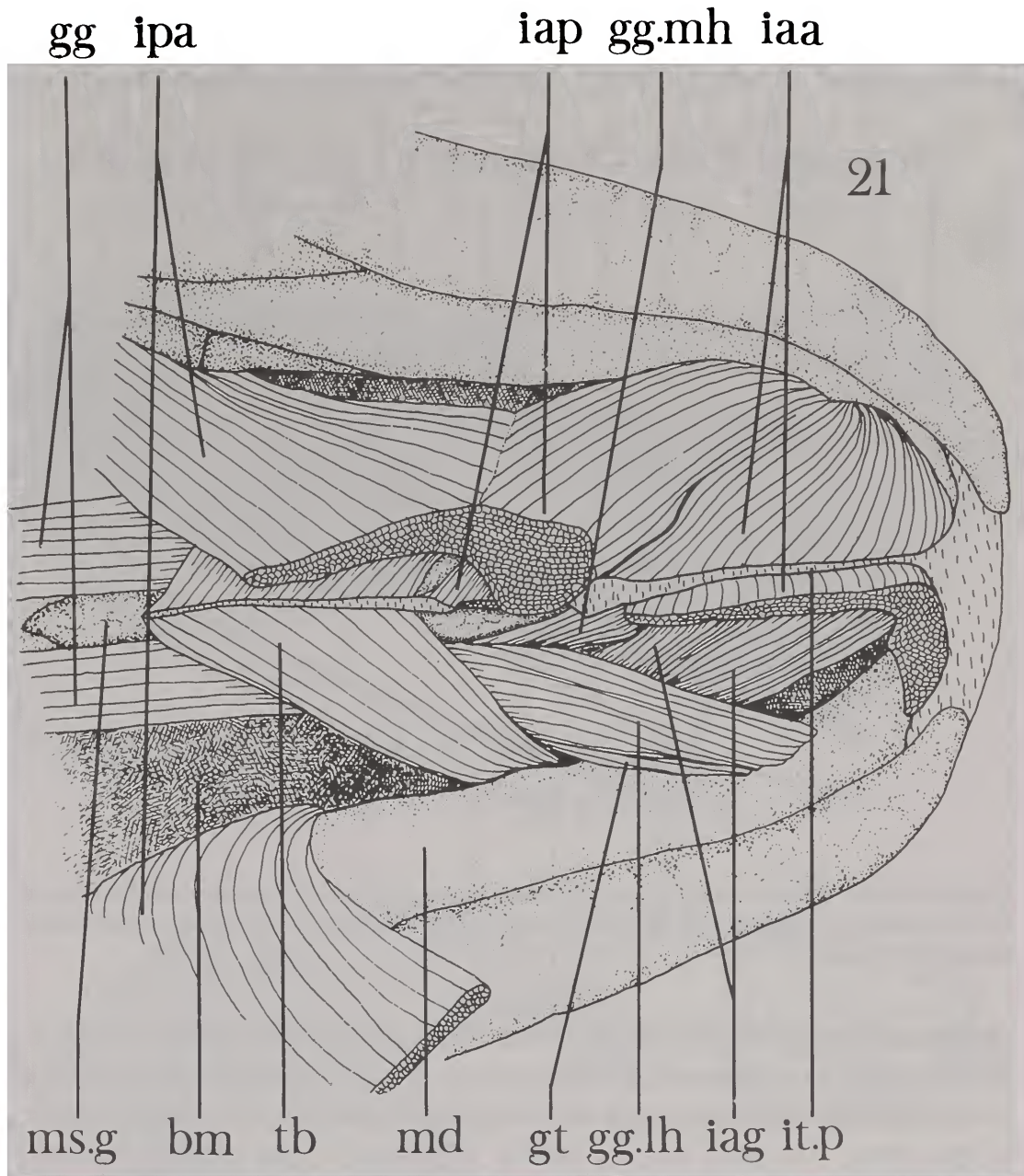
The **M. adductor mandibulae externus medialis, pars posterior,** is a triangular muscle which originates along the anterolateral edge of the quadrate, from the anterodorsal corner of this bone through the lateral epicondyle. It inserts on the lateral surface of the compound bone, from the articular through the posterior foramen of the surangular. The superficial fibers of this muscle have a pinnate configuration due to the quadrate aponeurosis which arises from the lateral corner of the proximal end of the quadrate and divides the muscle in two distinct anterodorsal wedges (from which the superficial fibers originate). Medially and ventrally the aponeurosis disappears and the fibers become parallel.

The **M. adductor mandibulae posterior** lies deep to the M. adductor mandibulae externus medialis pars posterior. It is easily separated from the former by the ramus mandibularis of the trigeminal nerve which passes lateral

hy bm ts   M   md ipa i.g   bm iap

20

gg ncm ipp ap.ncm tb   iaa it.p
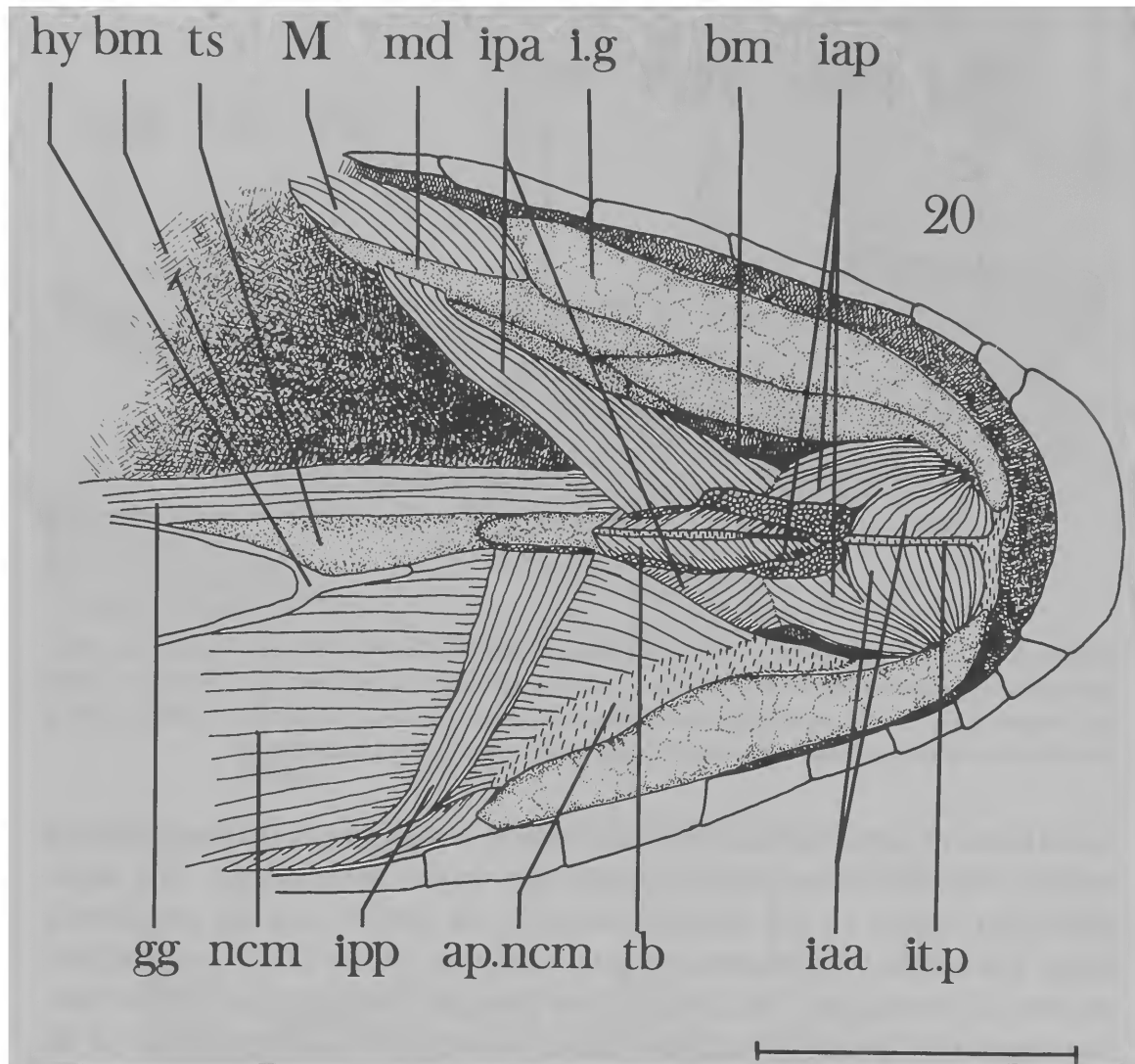
to the pars profundus (lateral and medial divisions of Kardong, 1980) and by a small ramus of the same nerve which passes between the pars superficialis (pars minimus of Kardong, 1980) and the M. adductor mandibulae externus medialis pars posterior. The pars minimus originates on the anteromedial border of the quadrate from the lateral condyle to the anterodorsal tip of the quadrate. It inserts on the lateral border of the surangular crest, from the articular to the level of the mandibular ramus of the trigeminal nerve. The pars profundus originates on the anteromedial border and the internal surface of the quadrate, its superficial fibers inserting into the mandibular fossa whereas its deep fibers attach to the medial surface of the prearticular crest. All the fibers forming this muscle have a parallel setting.

The **M. pseudotemporalis** is made up of parallel fibers that pass posteroventrally and lie medial to the maxillary ramus of the trigeminal nerve. The muscle originates just ventral to the parietal crest, in a depression of the

gg ipa   iap gg.mh iaa

ms.g   bm   tb   md   gt gg.lh iag it.p

parietal wall, lying almost entirely under the posteromedial part of the M. adductor mandibulae externus superficialis (only the posterior end lies under the M. adductor mandibulae externus profundus). The pseudotemporalis inserts, medially to the fibers of the M. adductor mandibulae externus profundus and anteriorly to the deep division of this muscle, onto the anterodorsal border of the surangular crest and anterior to the mandibular fossa. The rictal fold also attaches on the epimysium surrounding the anterior fibers.
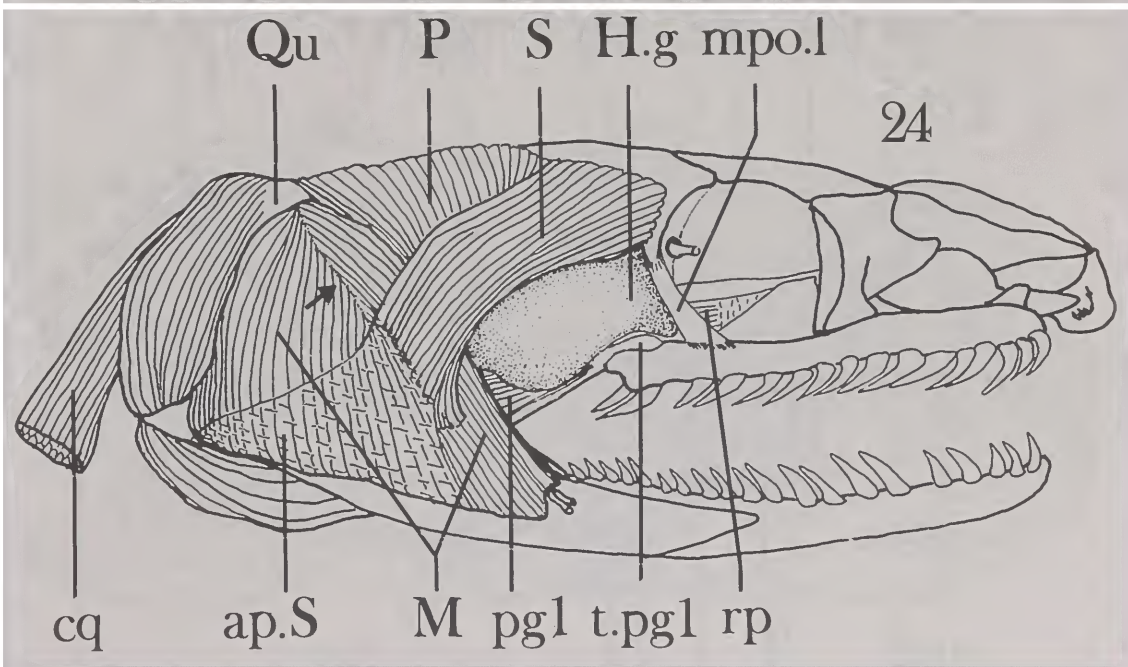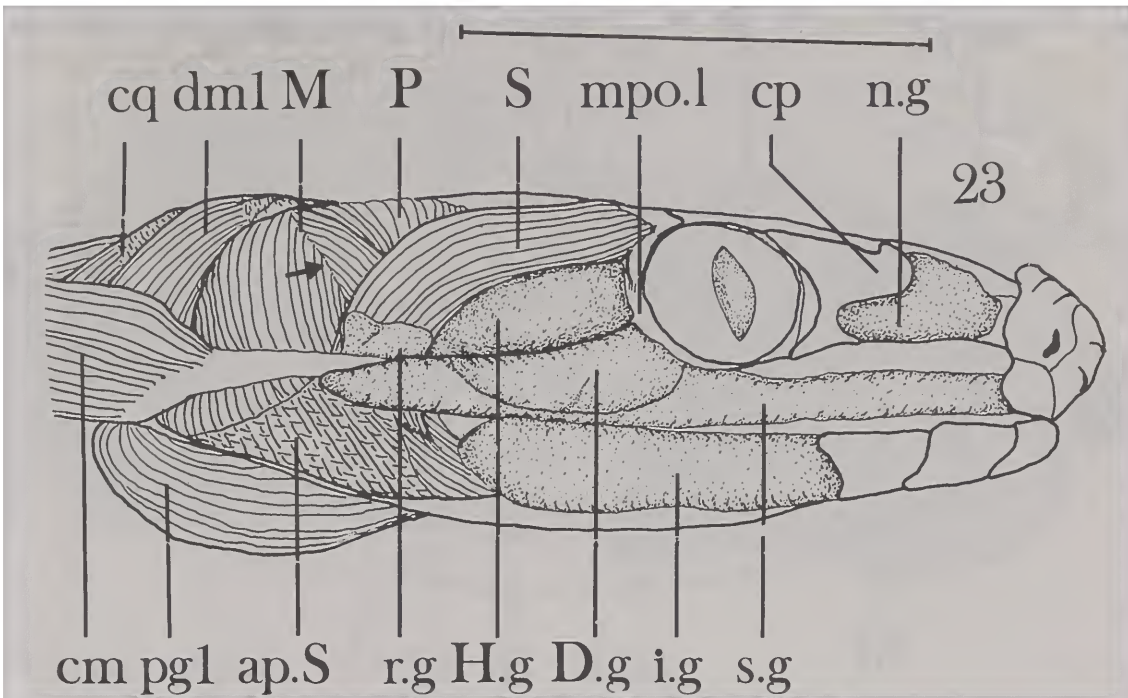
The **M. pterygoideus superficialis** is composed of two distinct parts, a minor and a major one (McDowell, 1986). The pars minor ("part b" of Haas, 1931b) arises, via an aponeurosis, mainly from the medioventral surface of the
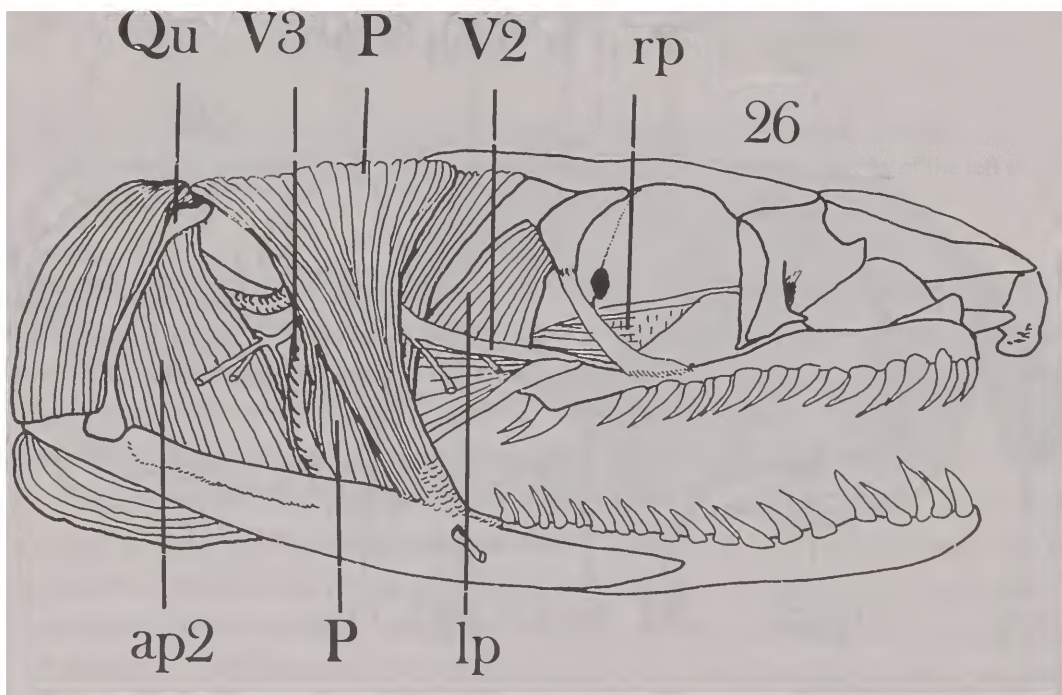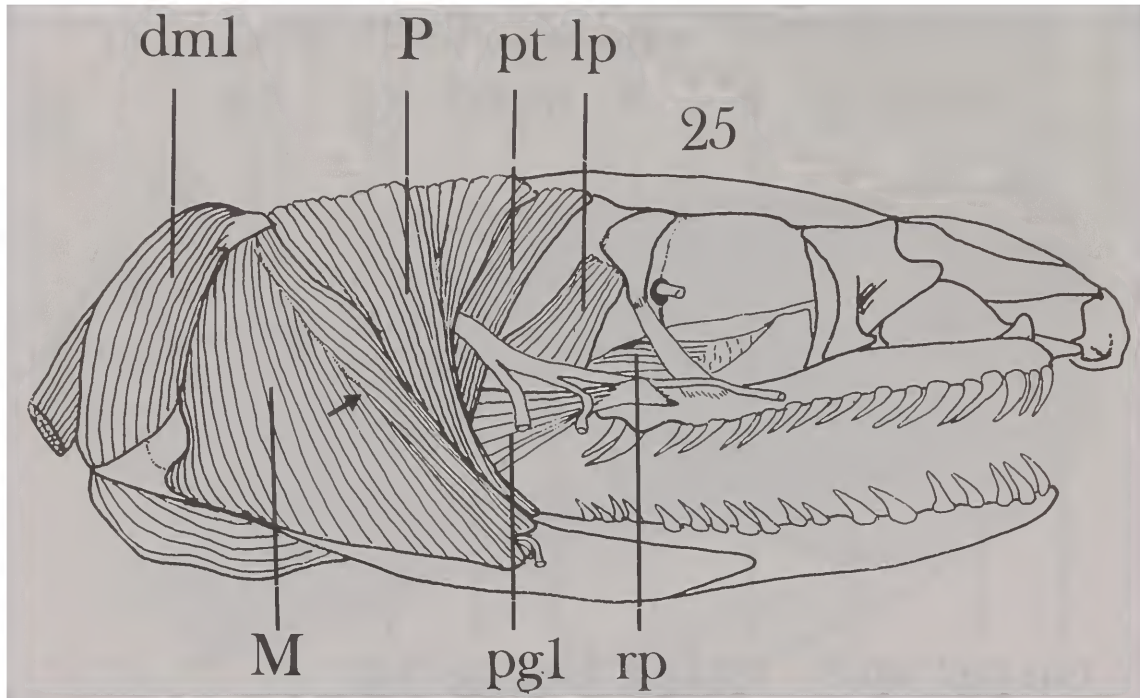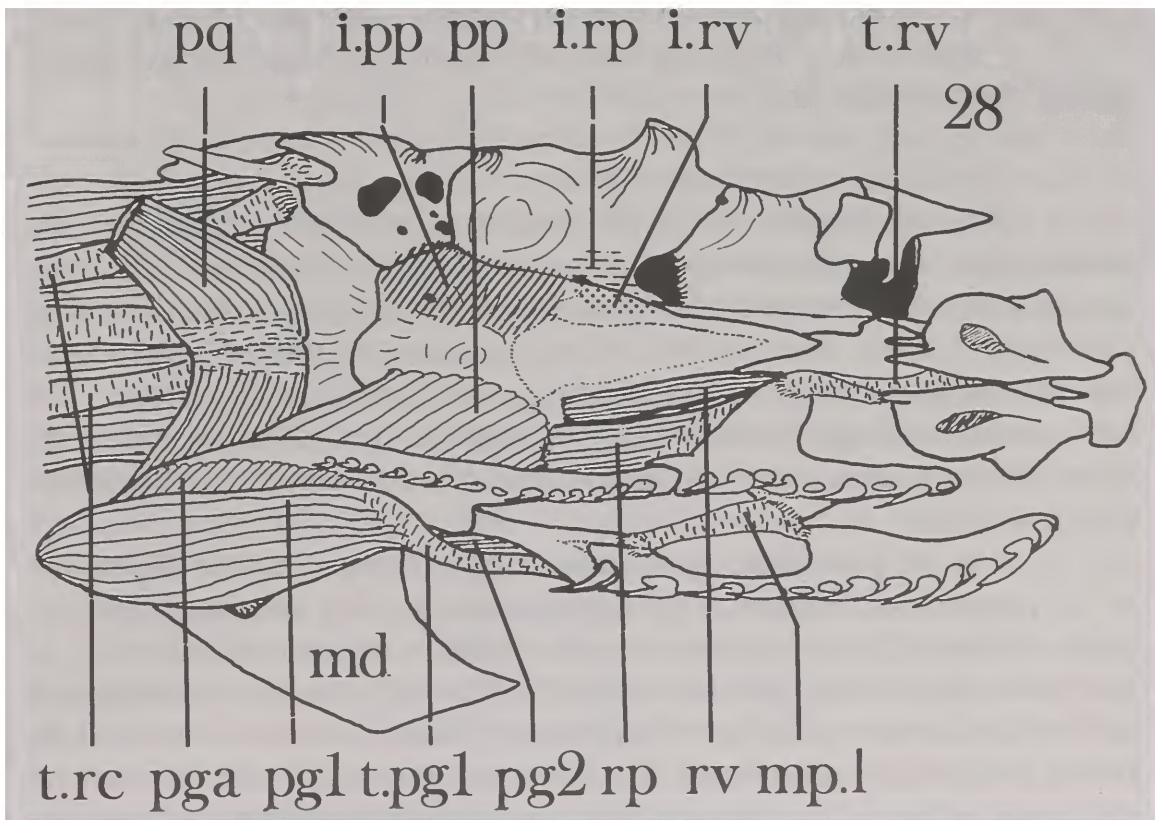
ht gt gg.lh dl tb gg.mh pl ls.g iag it.p iaa

22
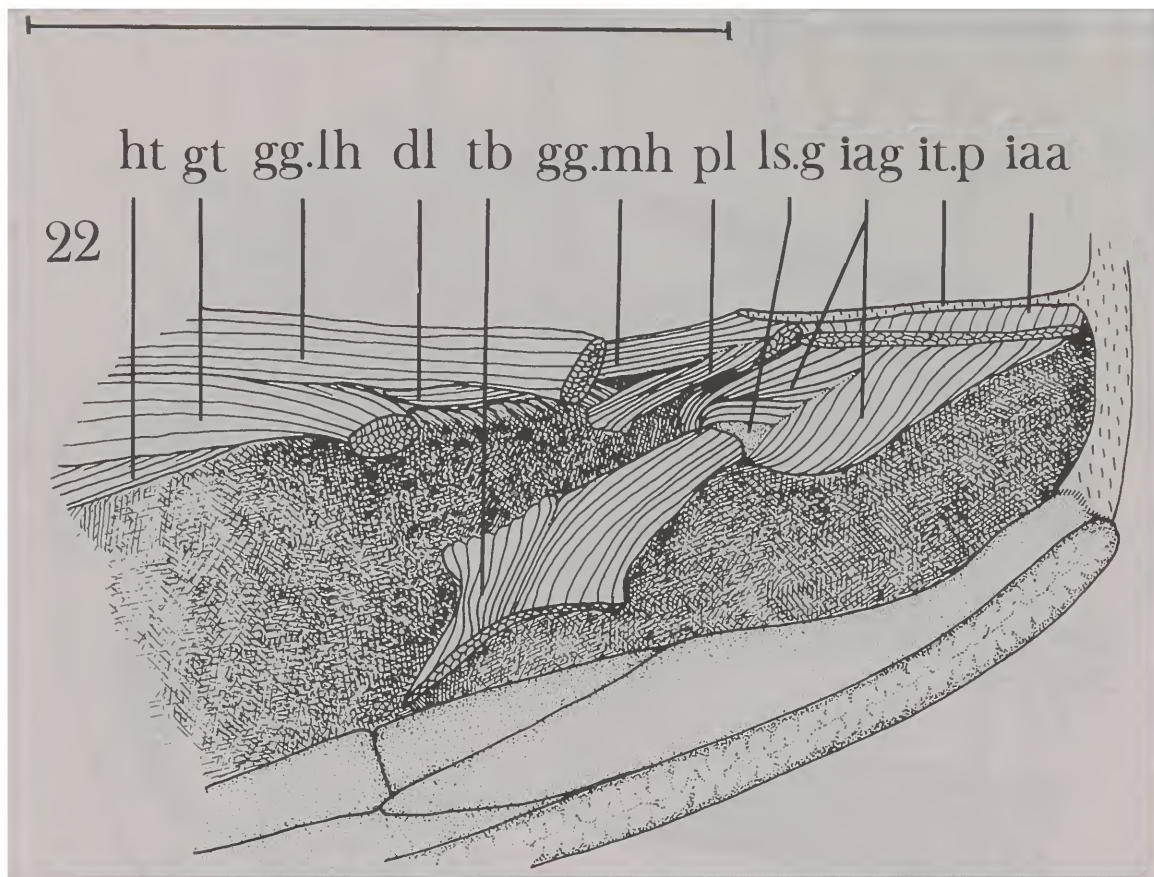
Figures 20 to 22. *Pseudoboa nigra.* Ventral view of the head showing the intermandibularis musculature and glands. 20, general view; 21, anterior region; 22, more enlarged ventral view of the left side of the anterior region.

compound bone (although the posterior fibers arise from the dorsal surface of the principal muscular unit, the pars major). It inserts directly on the dorsolateral surface of the ectopterygoid, not extending backward to the posterior quarter of this bone. The pars major ("part a" of Haas, 1931b) originates from an aponeurosis attached to the posteroventral surface of the retroarticular process. The fibers of this part pass anteroventrally to the mandible; then they converge toward a prominent tendon which merges at the anterior part of the muscle and attaches on the anterodorsal end of the ectopterygoid, just above the ectopterygoid-maxillary articulation. This muscle do not act functionally as an adductor but intervenes in the retraction of the maxillary bone, providing an anteroposterior movement that rotates the maxillary tooth row medially and depresses the rear end of the maxilla (Cundall & Gans, 1979).

The **M. pterygoideus accessorius** originates on the ventral surface of the pterygoid, never reaching the posteromedial border of this bone. The fibers pass medial to the tooth row, arising directly from the posterior tip of the

cq dm1 M P S mpo.l cp n.g

23

cm pg1 ap.S r.g H.g D.g i.g s.g

Qu P S H.g mpo.l

24

cq ap.S M pg1 t.pg1 rp

t.cq   V3   V2   lp   27

dm2   ap2   fa pt

pq   i.pp pp   i.rp i.rv   t.rv

28

md.

t.rc pga pg1 t.pg1 pg2 rp rv mp.l
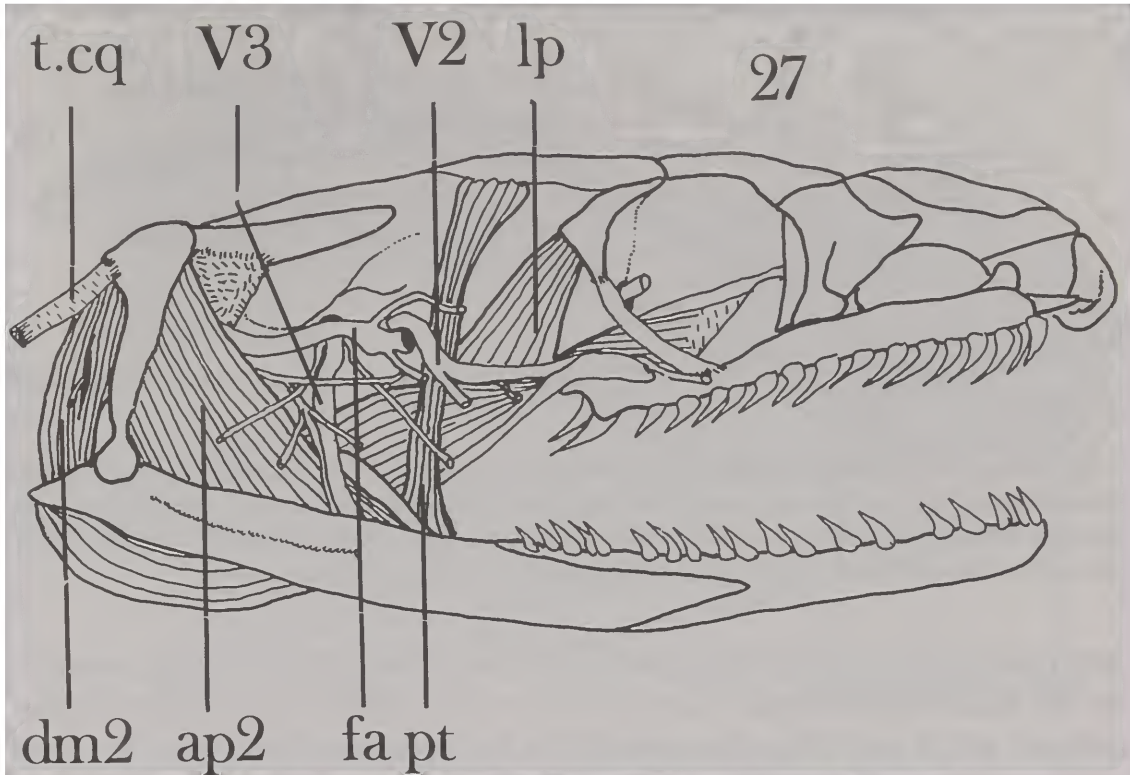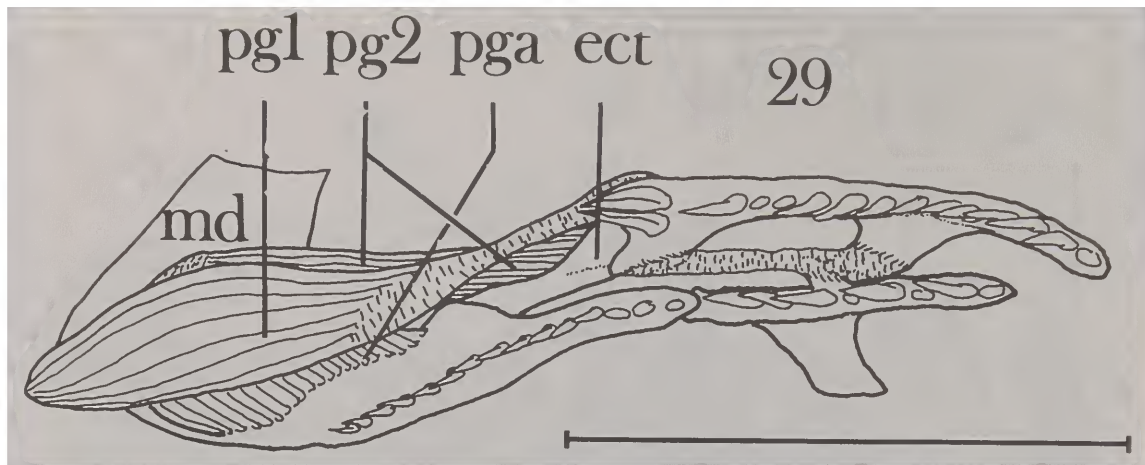
Figures 23 to 29. *Oxyrhopus petola*. Cephalic muscles and glands. 23 to 27, right lateral view of the head showing progressively more medial bundles of the adductor musculature; 28, ventral view of the head showing the constrictor internus dorsalis musculature and its area of origin; 29, ventral view of the right palato-maxillary arch and mandible showing the pterygoideus musculature.

pterygoid to the ectopterygoid-pterygoid articulation (not extending ventrally to the latter). This muscle inserts on the ventral surface of the retroarticular process which extends anteroventrally on the compound bone up to the level of the anterior fibers of the M. pterygoideus superficialis and dorsally to it. At this level, some of the fibers of the latter are intermingled with fibers of the M. pterygoideus accessorius.

The dorsal constrictors (Fig. 6):

The two bundles of the **M. protractor quadrati** originate on the basioccipital crest and on an aponeurosis at the midventral surface of the anterior neck muscles. Almost all the fibers arise from this aponeurosis along with their contralaterals, from the level of the basioccipital crest up to the region between the epistropheus and the hypapophyse of the following vertebra. The two bundles converge posterolaterally to insert on the medial surface of the retroarticular process, ventral to the insertion of the M. depressor mandibulae pars profundus.

The **M. protractor pterygoidei** originates on a shallow depression of the posterolateral region of the basisphenoid. Arising anteriorly from the posterior edge of the M. retractor vomeris, its fibers extend posterolaterally to the prootic-parietal-basisphenoid contact (bordering the parietal-basisphenoid contact) and posteromedially to the posterior Vidian foramen and cerebral foramen (without covering them). The fibers run posteroventrally to insert on the dorsal surface of the pterygoid from the ectopterygoid-pterygoid articulation to the caudal tip of the bone. This muscle becomes fusiform on its point of

ncm ipp   M ap.ncm i.g gg ipa   bm md iap it.p

30

hy   ts   tb   iap gg.mh   iaa
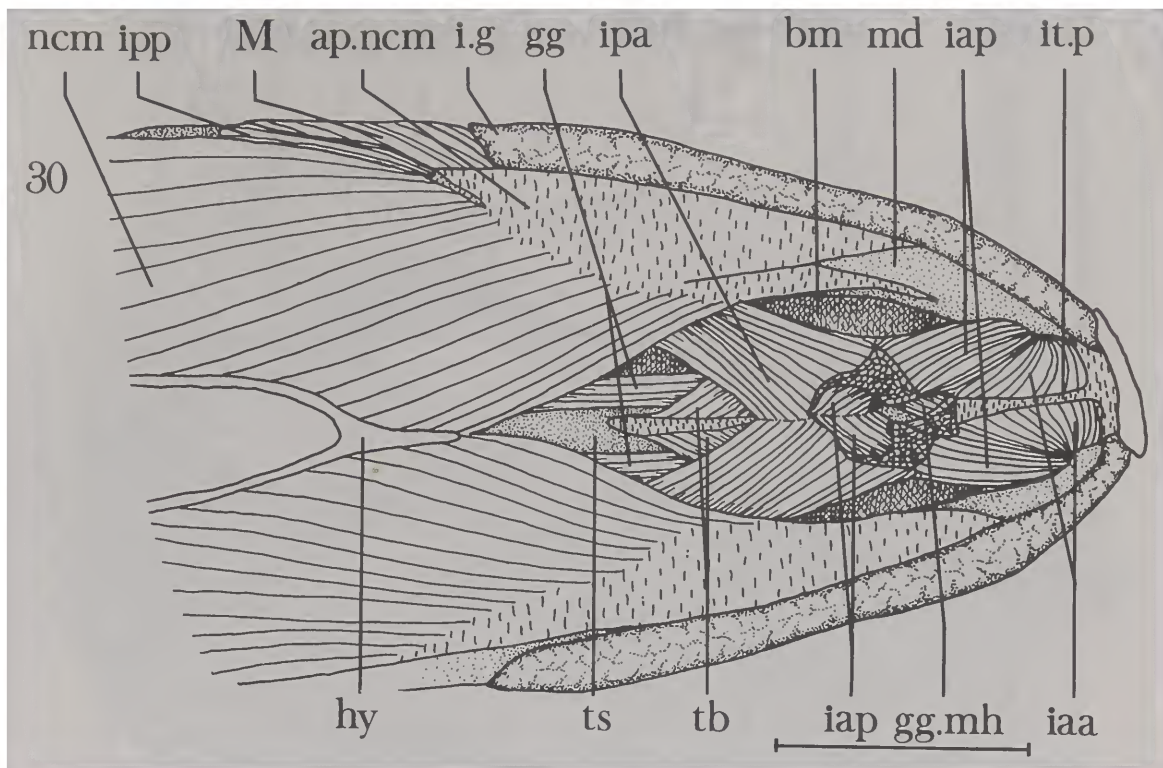
insertion, providing a particularly firm attachment on the posterior tip of the pterygoid.

The posteroventral surface of the postorbital process of the parietal forms a depression from which the fibers of the **M. levator pterygoidei** originate. The muscle courses posteroventrally from the point of origin to insert on the dorsal surface of the pterygoid, mainly on the anterolateral border of that bone and the posterodorsal surface of the ectopterygoid. Some of the posterodorsal fibers of the M. levator pterygoidei attach on the ventral epimysium of the M. protractor pterygoidei.

The **M. retractor pterygoidei** originates on the posteroventral surface of the parietal, medially bordering the para- basisphenoid between the secondary anterior Vidian foramen (lying between the parietal and parabasisphenoid walls) and the prootic-parietal-basisphenoid contact. It inserts anterolaterally, via an aponeurosis, on the dorsal surface of the choanal process of the palatine and on the ectopterygoid-pterygoid articulation.

The **M. retractor vomeris** originates on the lateral border of the parabasisphenoid, just anterior to the M. protractor pterygoidei and overlapping the secondary anterior Vidian foramen. The fibers are directed anteriorly along the ventral border of the parietal to converge on a tendon which inserts on the posterodorsal process of the vomer.

ts gg   ipa gg.mh ms.g iap pl iaa

31

ht gt tr   bm tb md i.g gg.lh iag ls.g ap.gg.lh
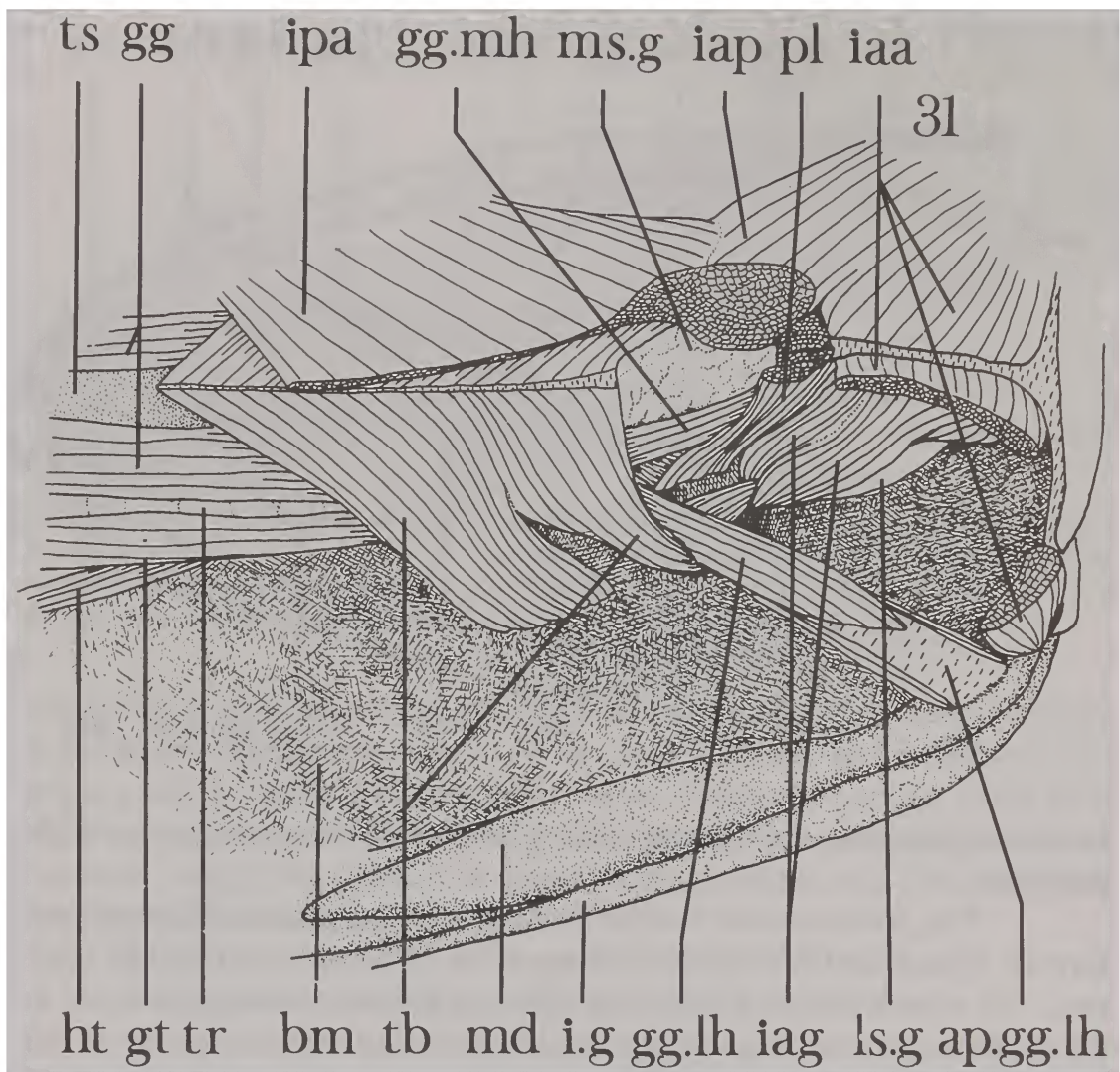
The ventral constrictors (Figs. 9, 10, 11):

The **M. intermandibularis anterior** includes three heads: the pars anterior, the pars posterior and the pars glandularis. The pars anterior and posterior are difficult to differentiate anatomically because of the fusion of their bundles. Nevertheless, the sites of insertion indicate the presence of two different parts. The pars anterior originates at the tip of the mandible. Almost all fibers diverging from that point insert on the interramal pad. The most posterior ones insert on the skin at the level of the anterior tip of the mental groove. The pars posterior originates just behind the pars anterior and inserts on the skin at the level of the anterolateral margin of the mental groove. The most posterodorsal fibers of the pars posterior insert on their contralateral counterparts via a midventral raphe (ie., the extension of the midventral raphe uniting the two bundles of the M. transversus branchialis), just anterior to the insertion of the M. transversus branchialis. The posteroventral fibers are fused
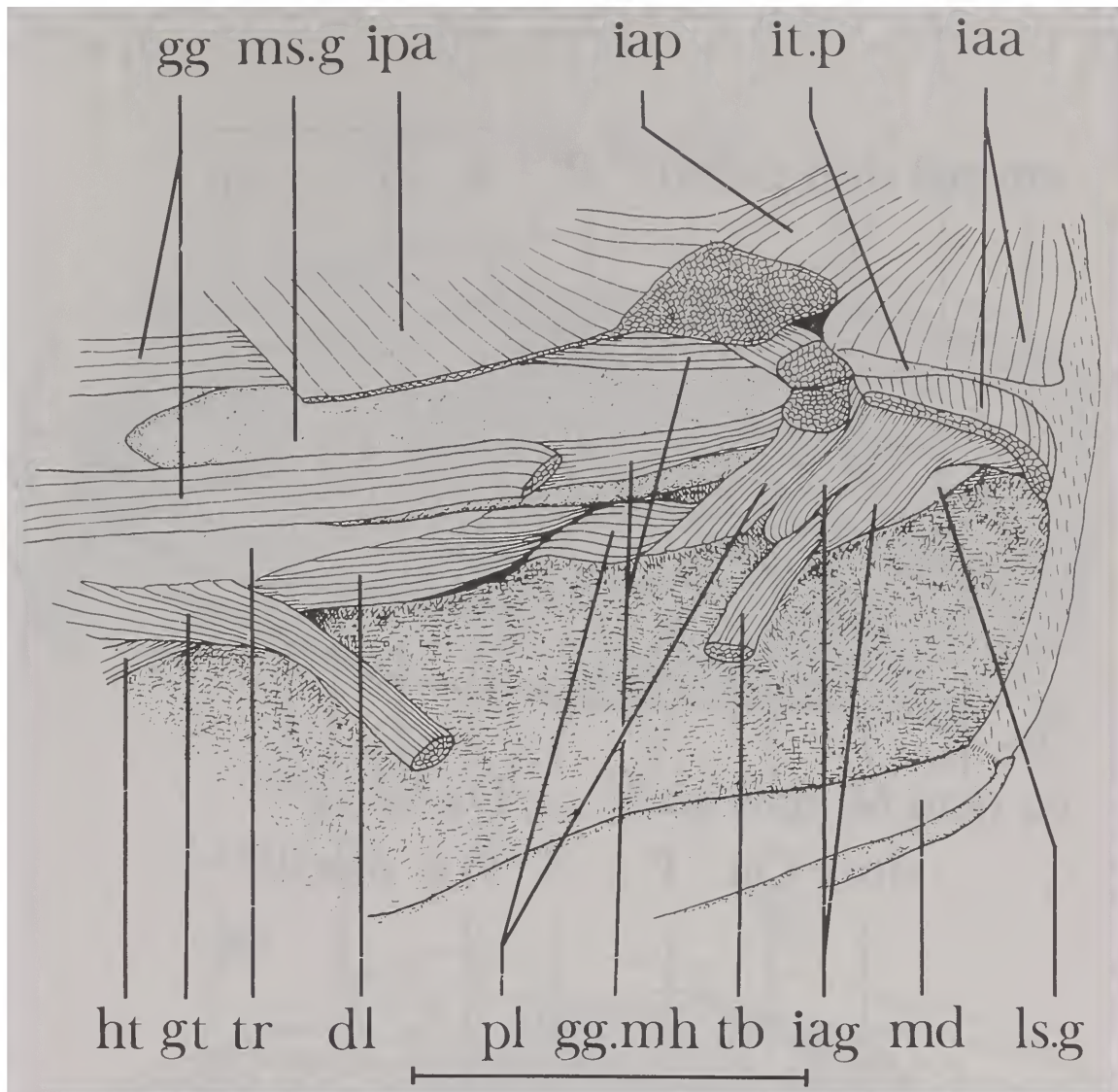
Figures 30 to 32. *Oxyrhopus petola*. Ventral view of the head showing the intermandibularis musculature and glands. 30, general view; 31-32, more enlarged ventral view of the left side of the anterior region.

with the more anterior fibers of the M. intermandibularis posterior pars anterior [forming the "X-shaped figure" (McDowell, 1972), more precisely termed the intermandibular chiasma by the same author]. The pars glandularis is formed of two distinct heads that surround the ventral surface of the lateral sublingual gland. Two conditions were observed for the origin site: 1) the two heads originate on the ventrolateral and ventral surfaces at the posterior end of the lateral sublingual gland and anteriorly to the M. transversus branchialis pars glandularis which takes it origin on the posterior tip of the gland (Fig. 10); 2) the two heads originate on the posterior tip of the lateral sublingual gland, surrounding the origin of the M. transversus branchialis pars glandularis. The

cm pgl dml o.dml P S cc cp

33

cq ncm M qm.l ap.S r.g D.g i.g s.g

dml Qu P S H.g mpo.l

34

cq pgl ap.S M co.m pgl t.pgl

P   pt   lp V2

35

ap2 V3   P   pg1 rp

t.cq Qu   P

36

dm2 ap2
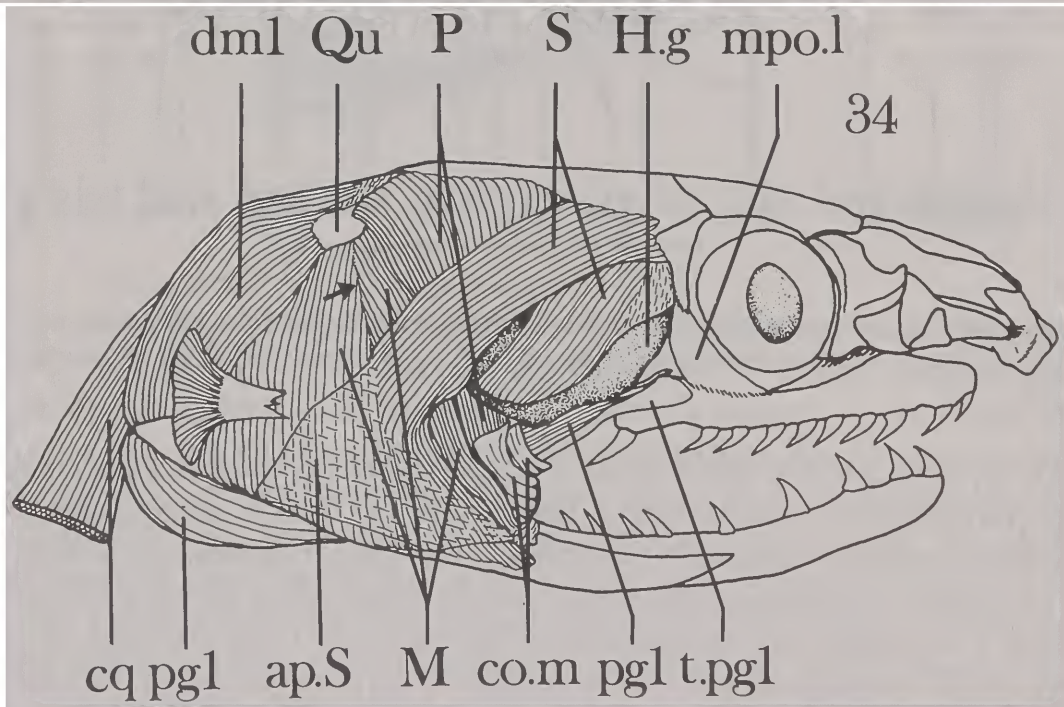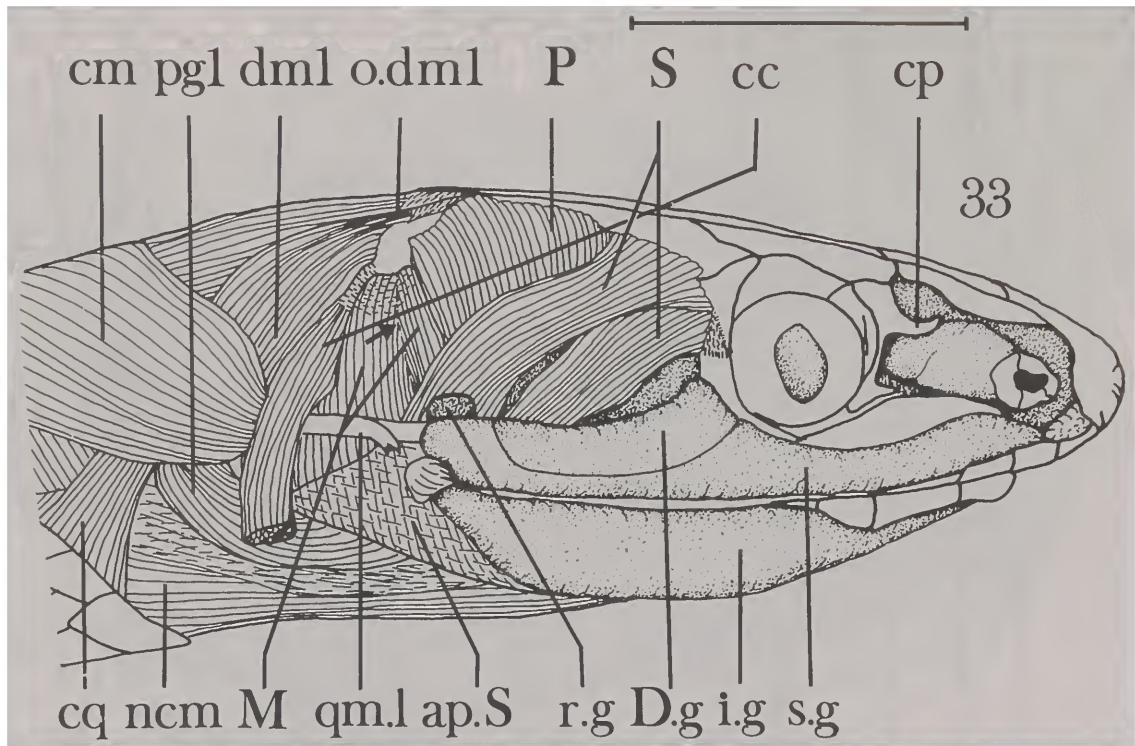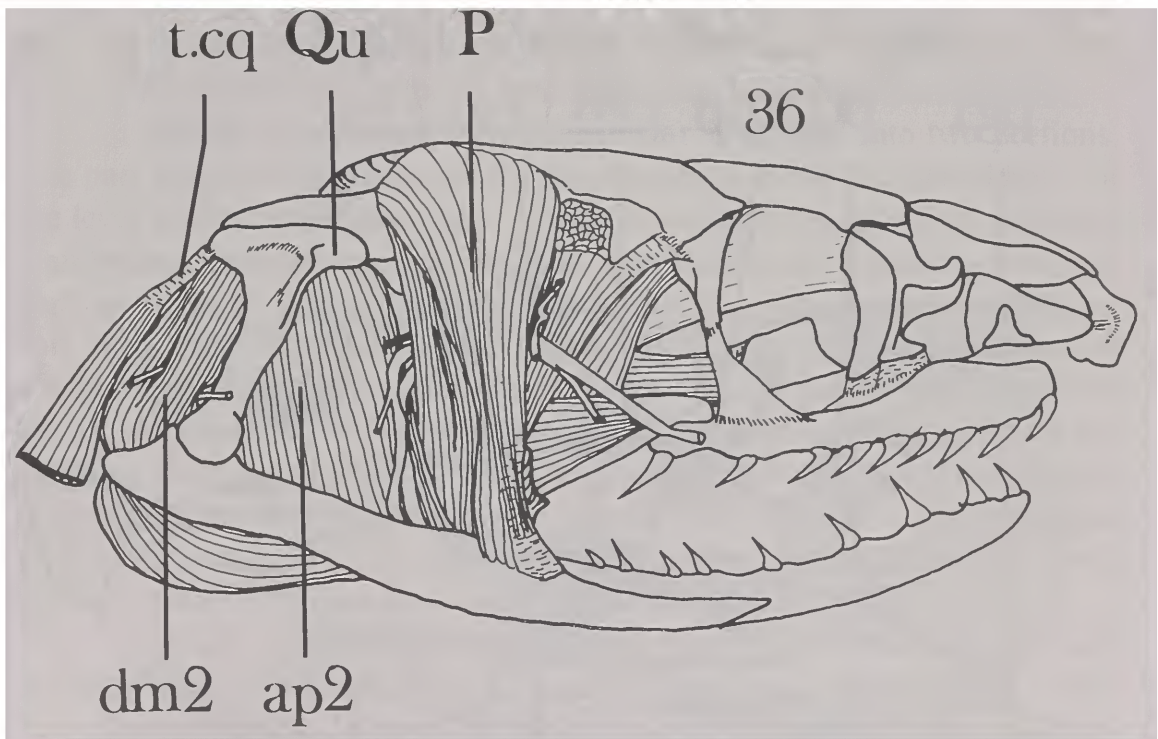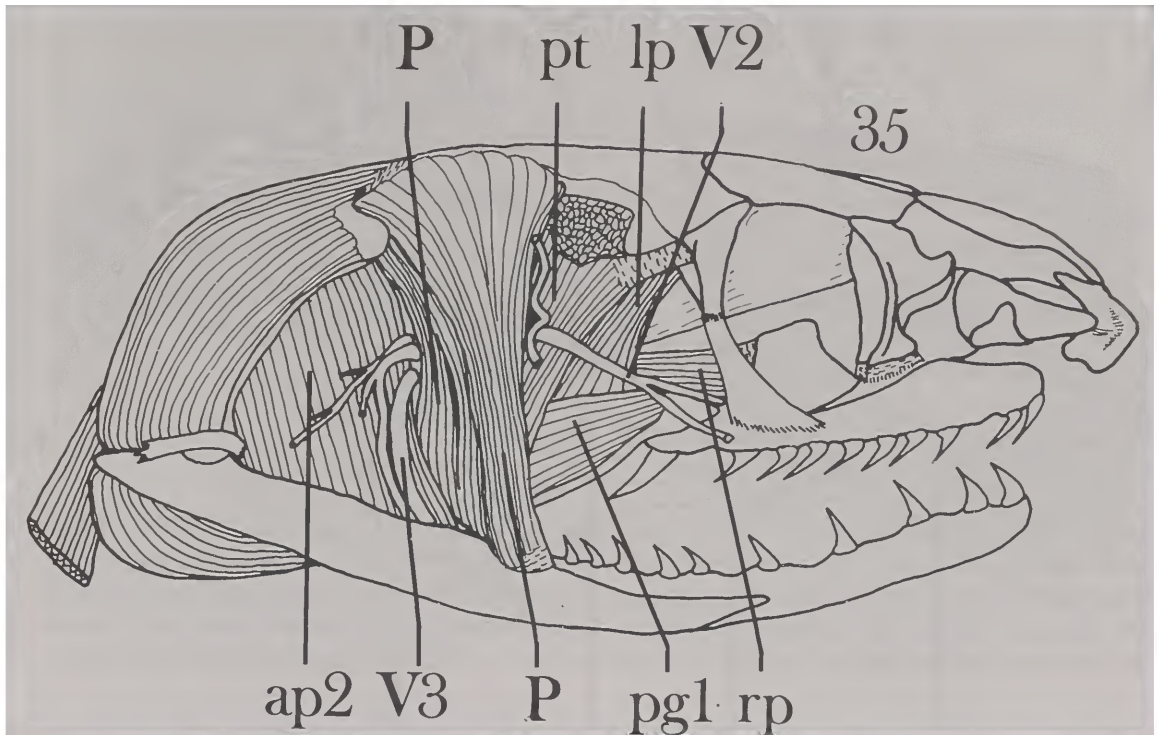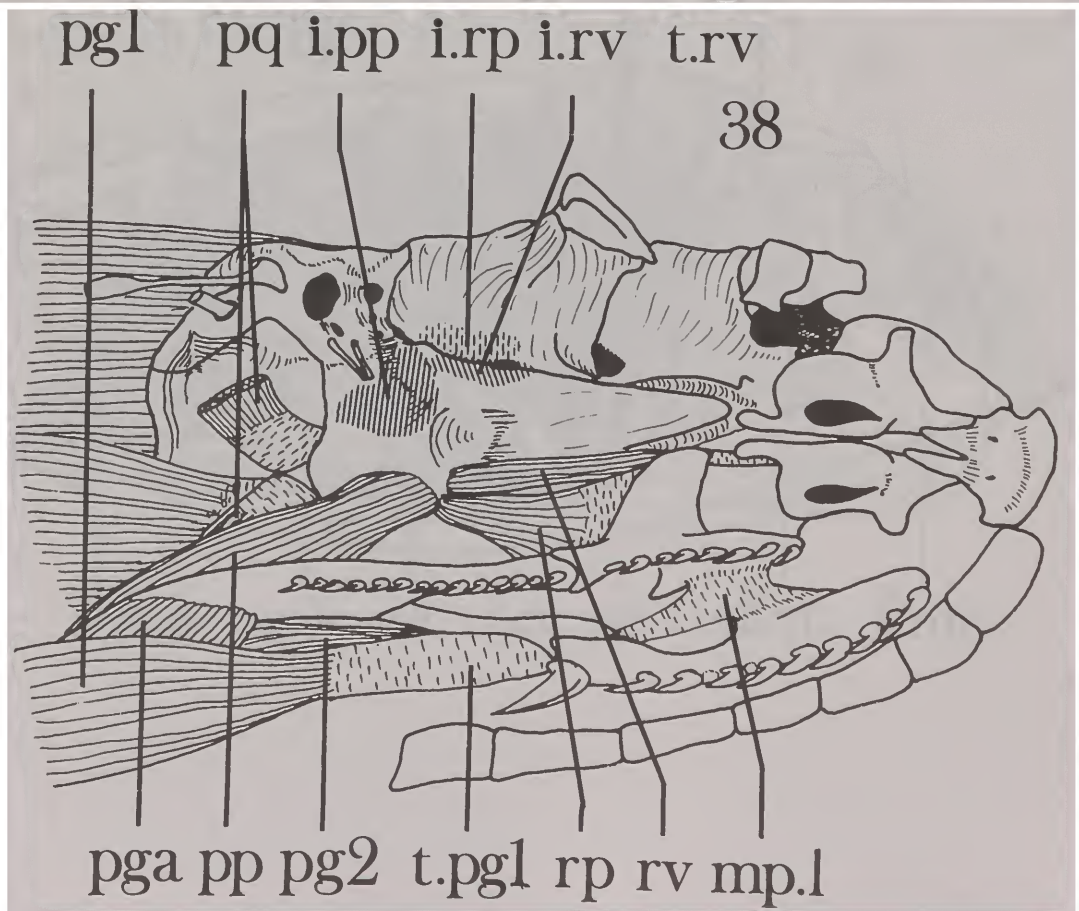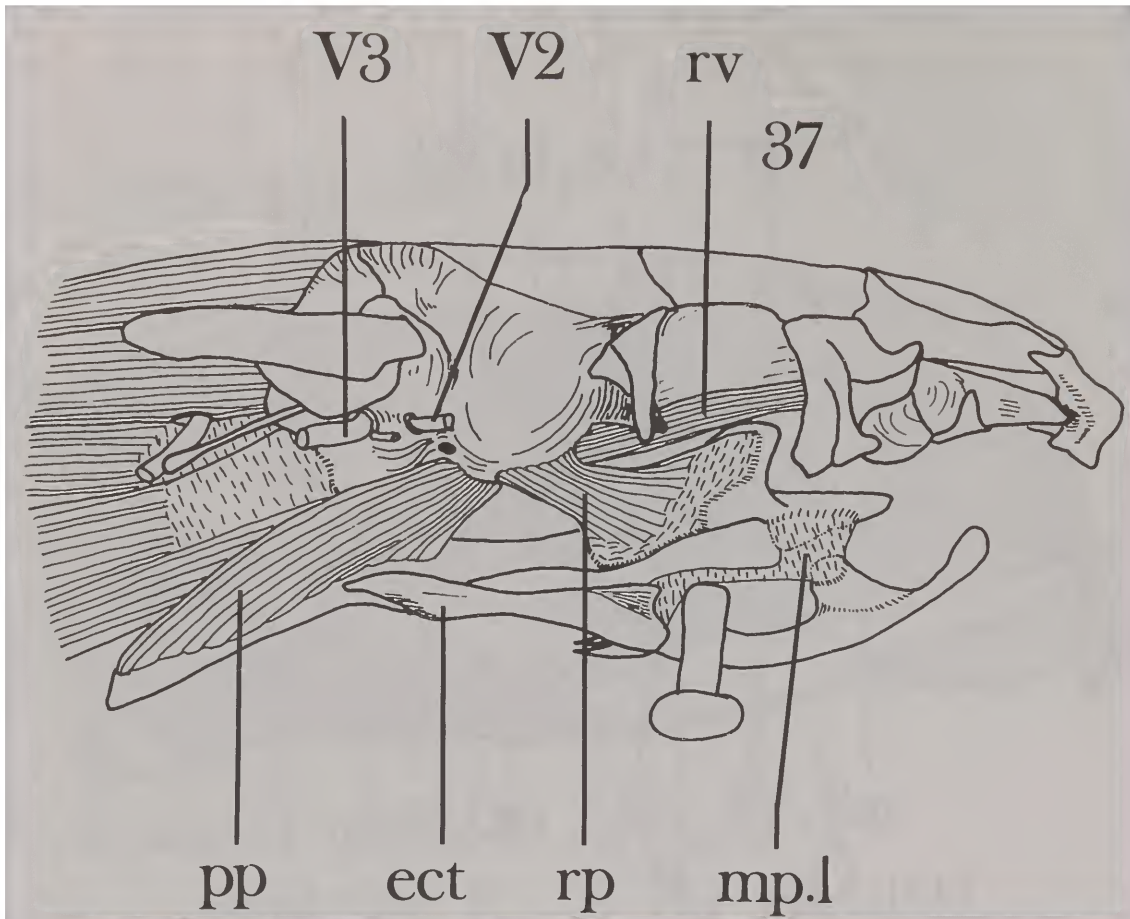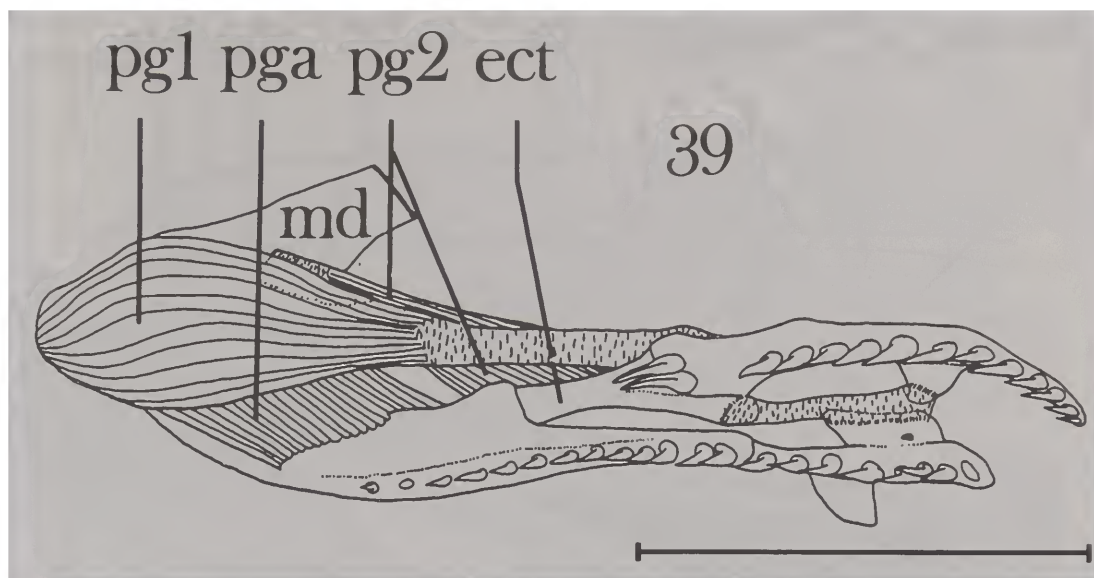
Figures 33 to 39. *Clelia rustica.* Cephalic muscles and glands. 33 to 36, right lateral view of the head showing progressively more medial bundles of the adductor musculature; 37, right lateral view of the head, the quadrate has been removed and the palato-maxillary arch refleted ventrolaterally; 38, ventral view of the head showing the constrictor internus dorsalis musculature and its area of origin; 39, ventral view of the right palato-maxillary arch and mandible showing the pterygoideus musculature.

fibers of the two heads always run anteromedially to insert on the interramal pad dorsal to the origin of the M. intermandibularis anterior pars anterior.

The **M. intermandibularis posterior** is divided into two portions. The pars posterior originates on the lateral surface of the compound bone, at the level of the mandibular fossa, ventral to the insertion of the M. adductor mandibulae externus superficialis. It is a thin muscle that passes forward, superficial to the M. neurocostomandibularis, and joins its contralateral counterpart at the ventral midline where they are attached to the skin at the level of the posterior fibers of the pars anterior. The pars anterior is also a thin muscle taking its origin on the ventromedial surface of the mandible between the posterior process of the angular and the posteroventral surface of the splenial. Extending forwards, medial to the neurocostomandibularis, it inserts almost exclusively on the skin (surrounding part of the mental groove). Only the most posterior fibers attach on their contralateral counterparts.

The **M. transversus branchialis** is composed of two heads (the pars mucosalis and pars glandularis) the posterior half of which is entirely fused. Some fibers originate from the mucosa at mid-distance from dentary and trachea; this facilitates recognition of the pars mucosalis. At that level, most of the fibers composing the muscle and forming the pars glandularis turn ventroposteriorly around the more medial Mm. geniotrachealis and genioglossus
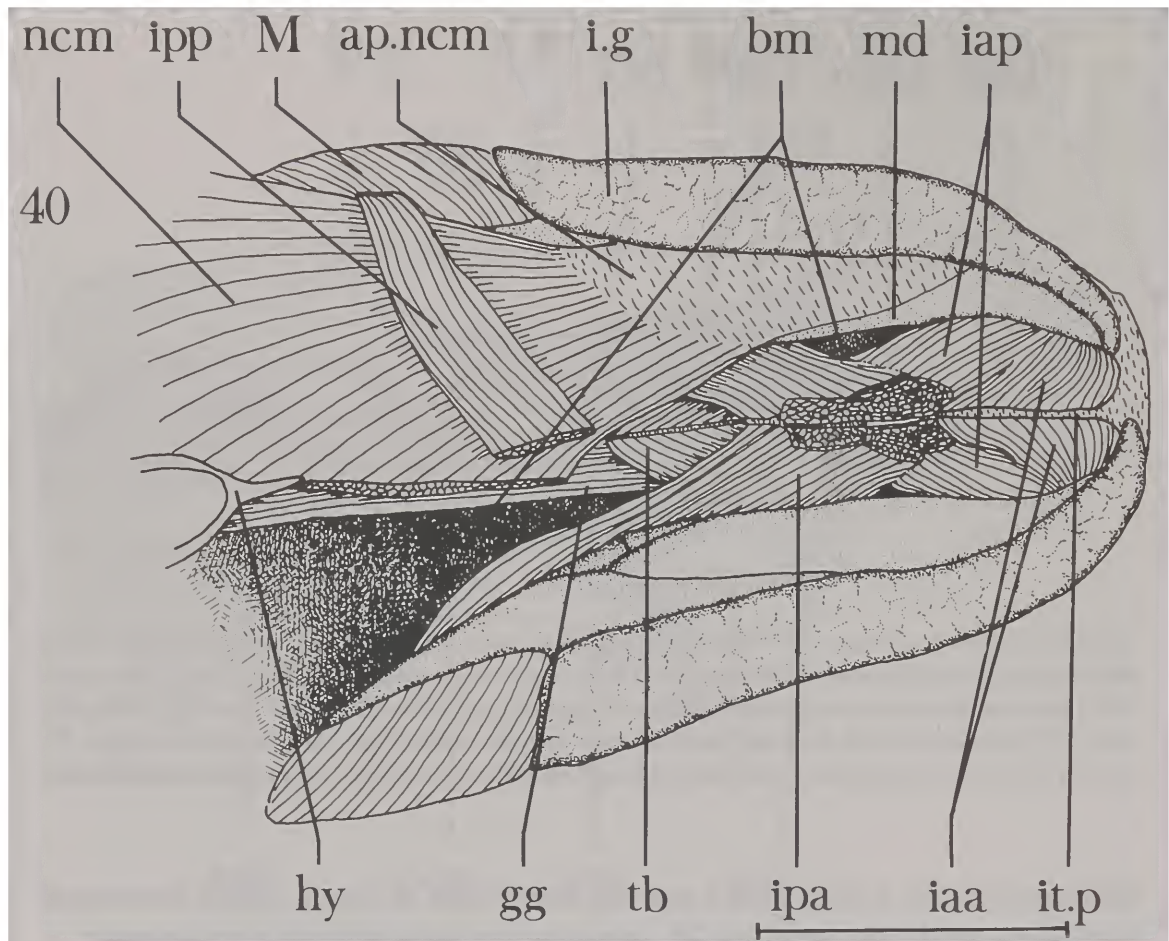
(pars lateralis) and fuse with the fibers of the pars mucosalis. The pars glandularis originates at the posteroventral tip of the lateral sublingual gland. The fused heads insert via a midventral raphe on its contralateral, dorsally to the M. intermandibularis posterior pars anterior. These two muscles are sometimes firmly attached to each other by their midventral raphe.

Posterior branchial and hypobranchial muscles (Figs. 9, 10, 11):

The **M. genioglossus** shows two heads anteriorly. The lateral one originates via a thin aponeurosis from the medioventral surface of the dentary, ventrally to the origin of the M. geniotrachealis and dorsally to the posterior fibers of the M. intermandibularis anterior pars posterior. The medial head originates almost from the posterior edge of the interramal pad. The lateral head passes posteromedially, dorsally to the M. intermandibularis anterior pars posterior and ventrally to the M. geniotrachealis. The medial head passes posteriorly, dorsally to the M. intermandibularis anterior pars posterior's insertion. The two heads join each other at the level of M. transversus branchialis' insertion, dorsal to its posterior fibers. From that point the joined fibers run laterally and side by side to the tongue sheath and insert on the utmost poste-

rior perpendicular musculature (sensu Smith & McKay, 1990), at the level of the 9th ventral scale (the ramus of the hypoglossal nerve which runs anteriorly and inside the tongue musculature enters the tongue complex just posterior to the level of the last perpendicular fibers and the insertion of the M. genioglossus).
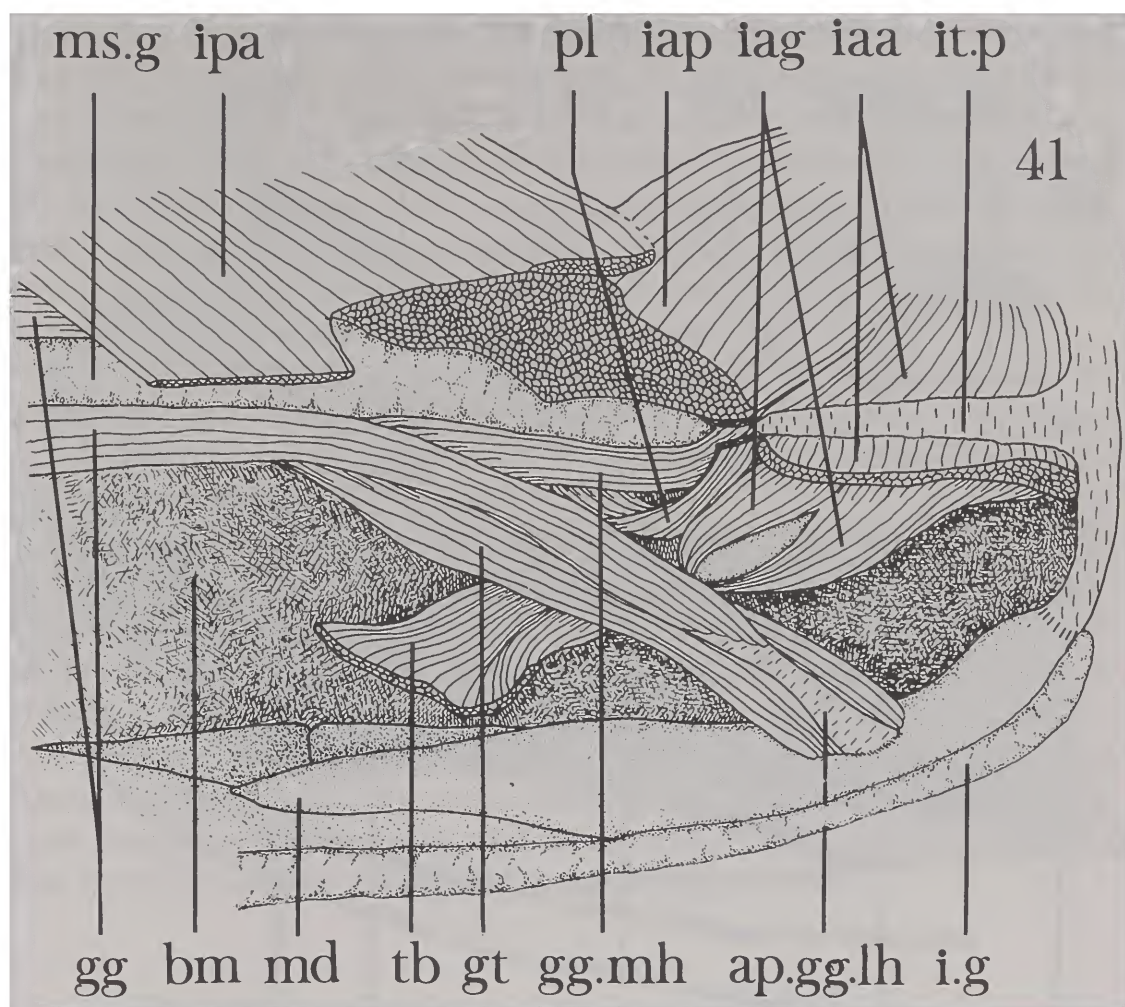
The **M. geniotrachealis** originates on the ventromedial surface of the dentary, just dorsal to the origin of the lateral head of the M. genioglossus and the posterior fibers of the M. intermandibularis anterior pars posterior. It runs posteromedially, passing ventrally to the anterior portion of the M. transversus branchialis and dorsally to the M. genioglossus, to insert along the side of the trachea between cartilages 5-6 to 10-11. A dorsal bundle diverges from the main one at the level of the 2nd to 3rd tracheal cartilages, passes dorsally to the posterior region of the M. dilator laryngeus and anterior fibers of M. hyotrachealis, to insert side by side at the level of cartilages 3 to 5.

The **M. hyoglossus** arises at the posterior tip of each ceratobranchial cartilage, at the level of the 21st to 25th ventral scale. The two bundles extend
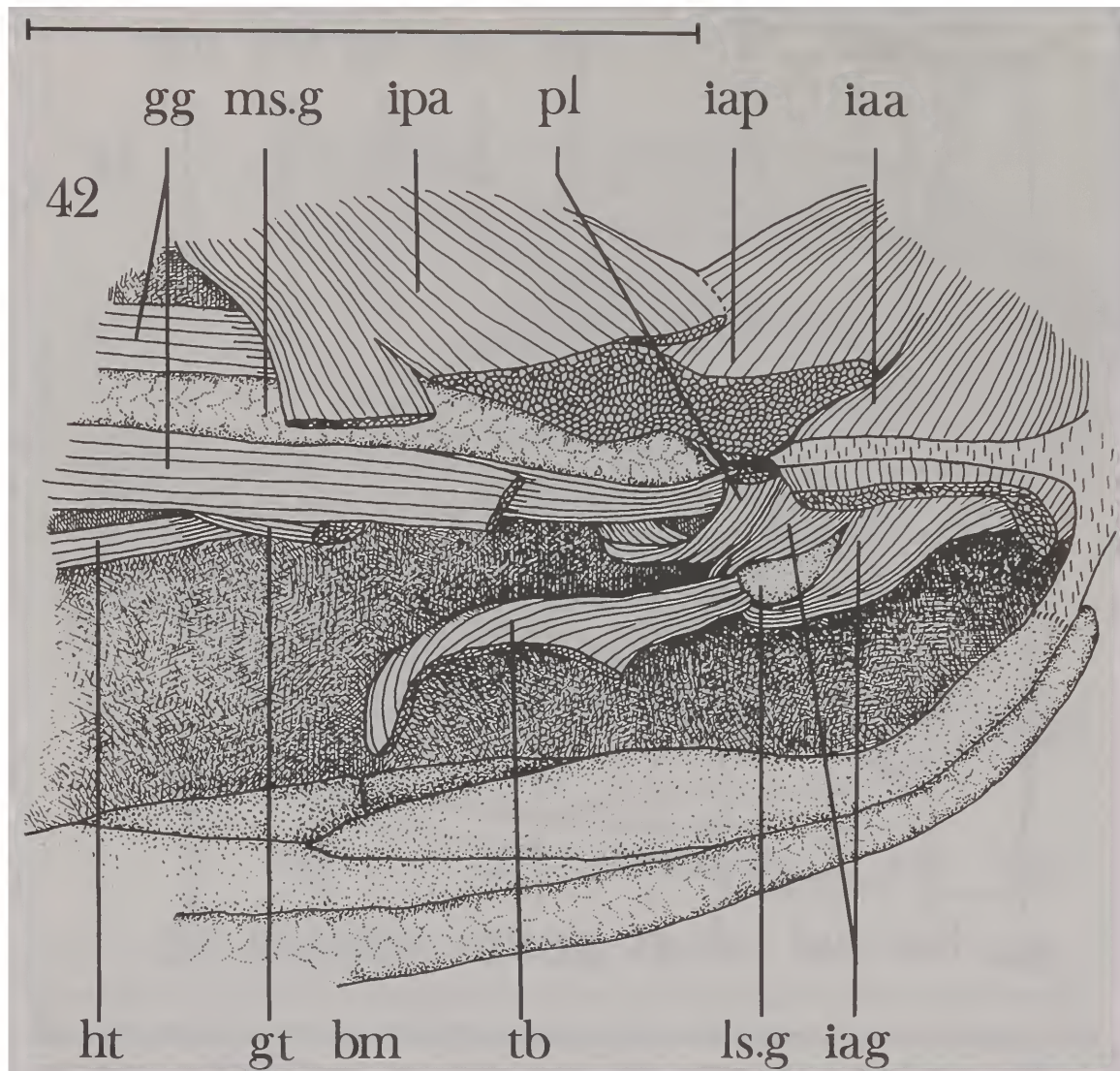
Figures 40 to 42. *Clelia rustica.* Ventral view of the head showing the intermandibularis musculature and glands. 40, general view; 41-42, more enlarged ventral view of the left side of the anterior region.

parallel to each other as far as the 7th to 9th ventral scale; here they are surrounded by the perpendicular musculature and become intrinsic muscular bundles of the tongue, except some of the most external fibers which insert on the connective tissue surrounding this region. The other fibers extend to the tongue tip.

The **M. neurocostomandibularis** is formed by the fusion of three heads. The more dorsal one (vertebral head) originates on the fascia of the spinalis-semispinalis musculature, lateral to vertebrae 9 to 11. It passes under the M. cervicoquadratus and over the axial musculature, downward and forward along the side of the body. Ventrally, the vertebral head is joined by fibers

originating from the distal ends (including the costal cartilages) of the first four ribs (costal head) and, more anteriorly, by fibers originating from the tip and lateral edges of the basihyal and hyoid cornua [second ceratobranchials of Langebartel (1968) and Cundall (1986); posterior extensions of the basihyal of List (1966), McDowell (1972) and Rieppel (1981)] (hyoid head). The fused fibers insert on the lateral surface of the mandible, via an aponeurosis, between the posterior tip of the posterodorsal process of the dentary and the anterior tip of the lateral process of the compound bone.

The narrow **M. hyotrachealis** arises from the lateral surface of the second ceratobranchial at the level of the third ventral scale, and passes anteromedially to insert on the laterodorsal wall of the trachea between the cartilaginous rings 4 and 5.

The **M. protractor laryngeus** extends from the dorsolateral region of the interramal pad and the anterodorsal fibers of the M. genioglossus medial head to the buccal membrane at the level of the posteromedial region of the lateral sublingual gland, and dorsally to it. At this point, the fibers curve posteromedially to insert on the intrinsic musculature of the larynx, fusing with the more ventral fibers of the M. dilator laryngeus. Some of the more lateral fibers insert directly on the buccal membrane. In one specimen the more posterolateral fibers of the left bundle arise directly from the skin and pass laterally to the M. genioglossus medial head.

The intrinsic musculature of the larynx (Fig. 12):

The **M. dilator laryngeus** surrounds laterally and dorsally the anteriormost region of the trachea from the larynx through the 3rd-4th tracheal cartilages. The dorsal fibers insert on the lateral rim of the arytenoid cartilage, the more ventral ones overlap dorsally the M. sphinctor laryngis to insert on the anterior tip of the arytenoid.

The **M. sphinctor laryngis** arises on the sides of the superior median process of the larynx and courses anterodorsally, over the arytenoid cartilage, to insert mainly on the ventrolateral surface of the processus epiglotticus. The deep fibers of the M. sphinctor laryngis insert along the lateral rim of the arytenoid cartilage.

DISCUSSION

This section provides a comparative analysis of the cephalic muscles and glands of *Clelia plumbea*, *Clelia rustica*, *Pseudoboa nigra*, and *Oxyrhopus petola*. It follows the arrangement used in the preceding section for the de-

scription of the cephalic muscles and glands of *C. plumbea*. The descriptive section of *C. plumbea* was also used as a basis for the analysis of the same structures in *C. rustica*, *P. nigra* and *O. petola*. Various cephalic muscles show intraspecific variations (concerning their point of origin, insertion and, to some extent, their mass). These are discussed in this section. Intraspecific muscle variations shown in the present study reflect the same general tendency described for other colubrid genera (see Cundall, 1986).

Head glands and ligaments

When present, the rictal gland is always floccular and distinct from the corner of the mouth and supralabial gland. *Pseudoboa nigra* (Fig. 14) has the most developed rictal gland, in comparison to the other species, lying against the lateral surface of the M. adductor mandibulae externus superficialis and sometimes overlapping the anterior region of the adductor mandibulae externus medialis pars posterior. This condition contrasts with the one found in *Clelia plumbea*, *C. rustica* and *Oxyrhopus petola* in which a small sized rictal gland lies always against the lateral surface of the M. adductor mandibulae externus superficialis. *Oxyrhopus petola* has a very peculiar longitudinally elongated rictal gland (Fig. 23).

The Duvernoy's gland is always present and clearly differentiated from the supralabial gland. However, in *Pseudoboa nigra* and *Clelia plumbea* the Duvernoy's gland is well developed (Figs. 1, 13), presenting a convex dorsal edge instead of a concave one as in *Oxyrhopus petola* and *Clelia rustica* (Figs. 23, 33). In *O. petola*, this gland is greatly reduced.

The posteroventral region of the nasal gland is always elongate posteriorly (in contrast with the more or less ovoid shape generally observed among colubrids). However, the length (from the lateral lamina to the anterior edge of the prefrontal bone) and the height (from the dorsal edge of the maxilla to the ventral edge of the lateral lamina of the prefrontal) of the posteroventral region varies significantly. In *Clelia plumbea*, *C. rustica* and *Pseudoboa nigra* the length of the posteroventral region do not exceed twice its height. In *Oxyrhopus petola*, the length always exceed twice its height (generally three times its height).

The lateral part of the quadrato-maxillary ligament (inserting on the skin medial to the last supralabial scale) is large in *Clelia plumbea* and *Pseudoboa nigra*. In *Oxyrhopus petola* and *C. rustica* this ligament is thin (Figs. 1, 13, 23, 33).

Head muscles

The constrictor colli arises on the lateral surface of the supratemporal

head of the quadrate or between the Mm. adductor mandibulae externus medialis pars posterior and depressor mandibulae along the lateral edge of the quadrate. When present, it inserts posteriorly or posteroventrally to the corner of the mouth (Fig. 33). The M. constrictor colli seems to be variable in many ophidian taxa (Anthony & Serra, 1949; Romano & Hoge,1972; Varkey, 1979). This is also true for *Clelia plumbea* and the other taxa examined in this study. However, these species always lack a muscular sheet, termed constrictor colli, by many authors and which originates on the fascia lying over the spinal musculature of the neck region.

The occipital head of the M. depressor mandibulae is absent or poorly developed in *Pseudoboa nigra* and *Clelia plumbea*, the medial fibers originating directly from the posterodorsal surface of the quadrate or from the parietosupratemporal ligament (but not reaching the supraoccipital crest) (Figs. 2, 4). In *Oxyrhopus petola* and *Clelia rustica* the occipital head is well developed, with its fibers reaching the supraoccipital crest.

The M. cervicomandibularis inserts always in the quadrato-maxillary ligament laterally to the lateral condyle of the quadrate. However, its origin, although being always on the epimysium of the spinalis-semispinalis musculature (at the middorsal line), varies intraspecifically in regard to the length of the site, which lies: in *C. plumbea* from vertebrae 4 through 9, in *Pseudoboa nigra* from 3 through 10, in *Oxyrhopus petola* from 4 through 7 and in *Clelia rustica* from 4 through 8.

The M. cervicoquadratus always originates in the skin of the neck and fascia covering the M. neurocostomandibularis and inserts in the posterodorsal tip of the quadrate, via a tendon. The origin of this muscle always passes between the pars superficialis and pars profundus of the M. depressor mandibulae.

The M. adductor mandibulae externus superficialis of *Pseudoboa nigra* shows a distinct anterior bundle which inserts loosely by its lateral surface on the rictal plate (Fig. 15). *Oxyrhopus petola* and *Clelia rustica* show a similar subdivision, but in those species the anterior bundle is much less differentiated and does not insert on the rictal plate. *Clelia plumbea* does not have a subdivided M. adductor mandibulae externus superficialis (Fig. 3). Figures 33 and 34 show an anomalous condition observed only on the right side of one specimen of *C. rustica* (MNHN 1990-4301) on which a distinct bundle of the M. adductor mandibulae externus superficialis originates on the laterodorsal surface of the Harderian gland.

In *Clelia rustica, Oxyrhopus petola* and *Pseudoboa nigra* the deep part of the M. adductor mandibulae externus profundus is longer than in *Clelia plumbea*, the insertion being extended more posteriorly in the edge of the

prearticular crest (Figs. 16, 26, 36).

The M. adductor mandibulae externus medialis pars posterior of the four species shows a pinnate arrangement of its anterodorsal fibers, arising mostly from a quadrate aponeurosis (Figs. 3, 14, 24, 34).

The M. adductor mandibulae posterior shows a distinct pars superficialis [pars minimus of Kardong (1980)] in all four species. In *Clelia rustica, Oxyrhopus petola* and *Pseudoboa nigra* the deep part belonging to the pars profundus of this muscle, inserts on the mandibular surface, medially to the prearticular crest. In *C. plumbea*, the site of insertion does not extend ventrally on the mandibular surface.

The M. pseudotemporalis has the same origin and insertion in the four species, although in *Clelia plumbea* the insertion is more lateral in the compound bone (Fig. 7). In one specimen of *Clelia rustica* the M. pseudotemporalis arises almost from the mediodorsal fibers of the M. adductor mandibulae externus superficialis (Figs. 35, 36).

The specimens of *Clelia plumbea* and *Pseudoboa nigra* show a M. protractor pterygoidei which covers the posterior part of the origin of the M. retractor pterygoidei in its origin instead of arising posteriorly to the latter (Figs. 6, 18). *Oxyrhopus petola* and *Clelia rustica* show the two conditions (only the second condition is presented in Figs. 28 and 38 for these two species). When the second condition is present, the M. retractor vomeris does not contact the M. protractor pterygoidei at their origins, and this seems to indicate that the variation observed here in *O. petola* and *C. rustica* is due to an anteromedial extension of the origin of the M. protractor pterygoidei.

The fibers forming the pars minor of the M. pterygoideus superficialis insert only on the anterodorsal surface of the ectopterygoid bone in *Pseudoboa nigra* (Fig. 19) instead of the totality of the surface as in the other three species (Figs. 8, 29, 39).

In the four species, almost all fibers of the M. protractor quadrati arise via an aponeurosis from the fascia at the midventral line of the anterior ventral neck muscles. The more anterior fibers of this muscle always take their origin on the basioccipital crest, via the same aponeurosis. In one specimen of *C. rustica* the two bundles of the M. protractor quadrati take their origin directly from the basioccipital crest instead of arising from a midventral aponeurosis, along with it contralateral (Fig. 38). The insertion is always on the medial surface of the retroarticular process.

The M. intermandibularis anterior pars anterior is almost identical in the four species dissected, although in one specimen of *Pseudoboa nigra* and in *Clelia plumbea* the most posterior fibers insert directly on the skin of the throat instead of being attached to the interramal pad (Figs. 9, 10, 11).

In all the species the M. intermandibularis anterior pars posterior inserts almost on the skin lateral to the mental groove, along with the M. intermandibularis posterior pars anterior with which the posteroventral fibers of the former intermingle with the anterior fibers of the latter (Figs. 9, 20, 30, 40). In *C. plumbea, C. rustica* and *P. nigra* the pars posterior has some of the most dorsal fibers that meet fibers of the opposite side at a midventral raphe, just anterior to the M. transversus branchialis (Figs. 21, 40). This condition was not found in the specimens of *O. petola.*

In *O. petola, P. nigra* and *C. rustica* the two heads forming the pars glandularis of the M. intermandibularis anterior originate on the posterior tip of the lateral sublingual gland, surrounding the fibers of the M. transversus branchialis pars glandularis (which always take their origin in the posterior tip of the lateral sublingual gland), as the second condition described for *C. plumbea* (Figs. 22, 32, 42). In one specimen of *C. rustica* some of the fibers of the deep part of the pars glandularis insert on the buccal membrane.

In *Oxyrhopus petola, Pseudoboa nigra* and *Clelia rustica* the origin of the M. intermandibularis posterior pars anterior overlaps the posterior tip of the angular to insert on the compound bone.

The M. intermandibularis posterior pars posterior is always very thin and sometimes can be accidentally damaged or partially removed. In *O. petola* this muscle is reduced to a vestigial bundle that inserts more anteriorly on the lateral border of the aponeurosis of the M. neurocostomandibularis (Fig. 30).

In the two species of *Clelia* and in *Pseudoboa nigra,* the M. transversus branchialis has almost all its fibers arising from the posterior tip of the lateral sublingual gland and belonging to the pars glandularis (Figs. 10, 22, 42). In these species a reduced number of fibers arise from the buccal membrane to form the pars mucosalis which fuses directly with the pars glandularis. In *C. rustica* the pars mucosalis is totally absent. Only *Oxyrhopus petola* shows a clearly differentiated pars mucosalis which fuses with the pars glandularis near the point of insertion on the midventral line of the throat and dorsally to the M. intermandibularis posterior pars anterior (Fig. 31). In *O. petola* and *C. rustica* the posterior fibers of the M. transversus branchialis extend posteriorly to the insertion of the two bundles of the M. intermandibularis posterior pars anterior (Figs. 30, 40). In *C. plumbea* the latter muscle overlap all the fibers of the former at their insertion (Fig. 9). In *P. nigra* the two conditions exist.

In all four species, the *M. genioglossus* arises ventrally to the origin of the *M. geniotrachealis* and dorsally to the posterior fibers of the *M. intermandibularis anterior pars posterior* (lateral head) as well as at the posterior tip of the interramal pad (medial head), and it inserts on the utmost

posterior perpendicular musculature (sensu Smith and McKay, 1990). The lateral head of the *M. genioglossus* arises on the medioventral surface of the dentary via an aponeurosis in *Clelia plumbea, C. rustica* and *Oxyrhopus petola* (Figs. 11, 31, 41). In *Pseudoboa nigra* the fibers of the lateral head arise directly from the dentary. In all the species, the *M. genioglossus* medial head arises almost from the interramal pad, except for the most posteroventral fibers which may take their origin directly on the skin, at the level of the anterior tip of the mental groove. In *C. rustica* and *O. petola* those fibers arise, together and medially to the fibers of the *M. protractor* laryngeus, from the skin at the level of the anterior tip of the mental groove (see discussion below for the M. protractor laryngeus).

In all the species dissected, the M. geniotrachealis arises on the medioventral surface of the dentary, dorsally to the M. genioglossus and posterior fibers of the M. intermandibularis anterior pars posterior. It differs among the species only in the length of the insertion which lies between cartilages 4-7 through 10-13. Intraspecific variation of the number of tracheal cartilages involved is as follows: *C. plumbea* = 5-6 to 10-11; *P. nigra* = 7-8 to 12; *C. rustica* = 6-7 to 12-13; *O. petola* = 4-6 to 12-13. In all the species, a very thin sheet of dorsoanterior fibers diverge from the main muscular bundle to insert on the buccal membrane. This thin sheet is somewhat vestigial in one specimen of *P. nigra* where it diverges from the main muscular bundle at the level of the 5th tracheal cartilage and inserts just lateral to it. In the other specimens it diverges at the level of the 4th-5th cartilages to insert between cartilages 6 to 8. In *O. petola* it diverges at the level of the 2nd-3rd tracheal cartilage to insert lateral to the 4th to 5th cartilage. In *C. rustica* it diverges at the level of the 3rd to insert lateral to the 4th to 5th.

In all four species, the Mm. hyoglossi always arise at the tip of the ceratobranchials and course from ventral scales 17-25 to ventral scales 7-9 where they are surrounded by the perpendicular musculature. Intraspecific variation in the lengths of the Mm. hyoglossi are as follows: in *Clelia plumbea* the two bundles arise between the 21st-25th ventral scales and are surrounded by the perpendicular musculature between the 7th-9th ventral scales; in *Pseudoboa nigra* they arise between the 19th-22th ventral scale and extend to the 8th ventral scale; in *Oxyrhopus petola* they arise at the 17th-20th ventral scale and run parallel to each other until the 7th-8th ventral scales; finally, in *Clelia rustica* they arise between the 19th-20th and run parallel to each other until the 8th-9th ventral scale. Cundall (1986) already described two different anomalous conditions involving the course of the left and right hyoglossi in *Opheodrys vernalis* and *O. aestivus*. The same kind of anomaly was observed in *Clelia.* In one specimen of *C. rustica,* the two hyoglossi cross each other, the right passing

ventrally to its partner, to lie in the opposite ceratobranchial at the level of the 17th ventral scale. More anteriorly, the right hyoglossus crosses again over the ventral surface of the left, at the level of the 14th ventral scale. In one specimen of *C. plumbea*, the bundle of the right ceratobranchial courses ventrally to the other between ventral scales 21 to 15 where they turn across each other to run side by side, attached by connective tissue. No variation of the M. hyoglossus was observed in the specimens of *O. petola* and *P. nigra*.

In all four species the M. hyotrachealis always arises on the laterodorsal surface of the second ceratobranchial, at the level of the third ventral scale, to insert on the laterodorsal wall of the trachea at the level of the 3rd to 7th tracheal cartilage (Figs. 10, 22, 31, 42). In one specimen of *Pseudoboa nigra* the insertion is directly on the M. geniotrachealis, meeting with the lateral fibers of that muscle at the level of the 7th tracheal cartilage. Intraspecific variations are as follows: *C. plumbea* = 4th- 5th tracheal cartilage; *P. nigra* = 6th-7th; *C. rustica* = 5th-6th; *O. petola* = 3rd-5th.

In *Clelia rustica* and *Oxyrhopus petola* the M. protractor laryngeus extends its fibers posterodorsally until the buccal membrane with which the epimysium of the lateral wall of the muscle bundle is attached (Figs. 32, 42). In *Clelia plumbea* and *Pseudoboa nigra*, some of the more lateral fibers end at the level of the buccal membrane (Figs. 11, 22). From that point the remaining fibers run posteromedially to insert over the M. dilator laryngeus (e.g., Fig. 12). The latter condition is present in all the species. The origin of the M. protractor laryngeus shows two conditions: 1) almost all the fibers arise from the anterodorsal fibers of the M. genioglossus medial head and from the interramal pad (present in *C. plumbea* and *P. nigra* : Figs. 10, 21), 2) almost all the fibers arise directly from the skin (along with the posteroventral fibers of the M. genioglossus medial head) at the level of the anterior tip of the mental groove and pass laterally to the M. genioglossus medial head (present in *C. rustica* and *O. petola* : Figs. 31, 32, 41, 42). In one specimen of *O. petola* (shown in Figs. 31, 32) the origin of the M. protractor laryngeus is augmented by fibers which arise from the skin at the level of the anterior tip of the mental groove, not having a thin shapped condition but a more diffuse area of origin; this augmented muscle bundle become thin shapped, when passing laterally to the M. genioglossus medial head, to join its point of insertion. In all species the more anterior fibers take their origin on the interramal pad.

The intrinsic musculature of the larynx is essentially the same in all the species dissected (e.g., Fig. 12). Variation occurs in the length of the M. dilator laryngeus' insertion of the most posterior fibers and is as follows: *Clelia plumbea* = 3rd-4th tracheal cartilages; *Pseudoboa nigra* = 6th-7th; *C. rustica* = 4th-5th; *Oxyrhopus petola* = 2nd-4th.

CONCLUSION

This study provides new data on head muscle and gland anatomy of a group of poorly known South American Xenodontinae. From the characters described in this study, the presence of a well developed aponeurotic system (a quadrate aponeurosis and a bodenaponeurosis) associated with the adductor musculature merits some comments. The aponeurotic system is well documented among lizards (Lakjer, 1926; Haas, 1973; Rieppel, 1980a) and anilioid snakes (Lakjer, 1926; Haas, 1973; Rieppel, 1980b; Zaher, 1994b). However, as previously shown by Zaher (1994b) and in the present study, it is erroneously believed that the aponeurotic system is missing in colubroid snakes.

Cundall (1986: 19) observed that "all previous comparative studies [on cephalic muscles of snakes] suggest that shifts from parallel to pinnate fiber arrangements are rare...the data [of his study] are presently consistent with the hypothesis that variation of cephalic muscles in colubroid snakes is limited by selection for parallel fiber array". The ontogenetic transformation provided by the bodenaponeurosis of some Pseudoboini (Zaher, 1994b) are in accordance with Cundall's (1986) functional arguments as it shows a clear ontogenetic sequence on which the bodenaponeurosis, well developed in young specimens, almost disappears in adults. Such ontogenetic pattern also reflects the transition from a generalized (plesiomorphic) to a more restricted (apomorphic) condition regarding the bodenaponeurosis.

The genus *Clelia*, and consequently the genera stated to be closely related to it, are considered to be among the most primitive colubrids (Rabb & Marx, 1973). Among the myological data observed in this study, the presence of a complex aponeurotic system in *Clelia* and related genera may points to a primitive colubrid condition. However, instead of supporting Rabb & Marx's (1973) point of view on the primitive position of the genus *Clelia*, the presence of a widespread aponeurotic system among colubroid taxa suggests an unique reappearance (reversal) of the aponeurotic system in the ancestor of the Colubroidea and subsequent independent loss among various subgroups (Zaher, 1994b).

Intra- and intergeneric variations of the head muscles of the species dissected occur in the shape of the Duvernoy's gland, the size of the rictal gland, the length of the posteroventral region of the nasal gland, the width of the quadrato-maxillary ligament, the presence of an anterior bundle of the M. adductor mandibulae externus superficialis, the size of the insertion site of the deep part of the Mm. adductor mandibulae externus profundus and adductor posterior, the presence and length of an occipital head of the M. depressor mandibulae, the size of the insertion site of the M. intermandibularis posterior

pars anterior, the presence of a pars mucosalis belonging to the M. transversus branchialis, the site of origin of the M. protractor laryngeus and the insertion site of it lateral fibers.

Cephalic muscles and gland morphology of the Pseudoboini species dissected retain the same general pattern shown by the majority of the colubrid taxa. Nevertheless, as shown above, after an analysis of the variability of cephalic glands and muscles, various features belonging to this system can be viewed as characters of systematic value. However, the lack of an explicit phylogenetic framework and our scattered knowledge of the head myology and osteology of the New World xenodontine snakes render useless any attempt, in the present study, to evaluate the phylogenetic content of such characters.

NOTE ON FIGURE CAPTIONS AND LIST OF ABBREVIATIONS

The adductor muscles, constrictores interni dorsalis, and adjacent cephalic glands are shown together for each species and presented in figures 1-8, 13-19, 23-29, and 33-39. Drawings of the intermandibularis musculature and adjacent glands are also presented together in figures 9-12, 20-22, 30-32, and 40-42. Legends are presented accordingly. The arrow shows the position of the quadrate aponeurosis. Bar=1cm.

ap 1- *adductor mandibulae posterior, pars superficialis*
ap 2- *adductor mandibulae posterior, pars profundus*
ap.gg.lh- *aponeurosis* of the *genioglossus, lateral head*

ap.ncm- *aponeurosis* of the *neurocostomandibularis*

ap. S- *aponeurosis* of the *adductor mandibulae externus superficialis*

bm- *buccal membrane*

cc- *constrictor colli*

cm- *cervicomandibularis*

co.m- corner of the mouth

cp- conchal process

cq- *cervico quadratus*

D.g- Duvernoy's gland

dl- *dilator laryngeus*

dm 1- *depressor mandibulae, pars superficialis*

dm 2- *depressor mandibulae, pars profundus*

ect- *ectopterygoid*

fa- facial artery

gg- *genioglossus*

gg.lh- *genioglossus*, lateral head

gg.mh- *genioglossus*, medial head

gt- *geniotrachealis*

H.g- Harderian gland

ht- *hyotrachealis*

hy- *hyoid*

ia- *intermandibularis anterior*

iaa- *intermandibularis anterior, pars anterior*

iag- *intermandibularis anterior, pars glandularis*

iap- *intermandibularis anterior, pars posterior*

ipa- *intermandibularis posterior, pars anterior*

i.g- *infralabial gland*

ipp- *intermandibularis posterior, pars posterior*

i.pp- insertion zone of the *protractor pterygoidei*

i.rp- insertion zone of the *retractor pterygoidei*

i.rv- insertion zone of the *retractor vomeris*

it.p- interramal pad

ls.g- lateral sublingual gland

lp- *levator pterygoidei*

M- *adductor mandibulae externus medialis, pars posterior*

md- mandible

mp.l- maxillo-palatine ligament

mpo.l- maxillo-postorbital ligament

ms.g- medial sublingual gland

ncm- *neurocostomandibularis*

n.g- *nasal gland*

o.dm 1- occipital head of the *depressor mandibulae, pars superficialis*

P- *adductor mandibulae externus profundus*

p.g- premaxillary gland

pg 1- *pterygoideus superficialis, pars major*

pg 2- *pterygoideus superficialis, pars minor*

pga- *pterygoideus accessorius*

pl- *protractor laryngeus*

pp- *protractor pterygoidei*

pq- *protractor quadrati*

pt- *pseudotemporalis*

qm.l- quadrato-maxillary ligament

Qu- quadrate

r.g- rictal gland

rp- *retractor pterygoidei*

rv- *retractor vomeris*

S- *adductor mandibulae externus superficialis*

s.g- supralabial gland

sl- *sphinctor laryngis*

tb- *transversus branchialis*

t.cq- tendon of the *cervicoquadratus*

t.pg 1- tendon of the *pterygoideus accessorius, pars major*

tr- trachea

t.rc- tendon of the *rectus capitus anterior* (*pars dorsalis and ventralis*)

t.rv- tendon of the *retractor vomeris*

ts- tongue sheath

V2- maxillary ramus of the trigeminal nerve

V3- mandibular ramus of the trigeminal nerve

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