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CONTRIBUTIONS TO THE CRANIAL OSTEOLOGY OF THE  
FISHES.\*

No. II.

THE MAXILLAE IN THE EELS AND THE IDENTIFICATION OF THESE BONES  
IN THE FISHES GENERALLY.

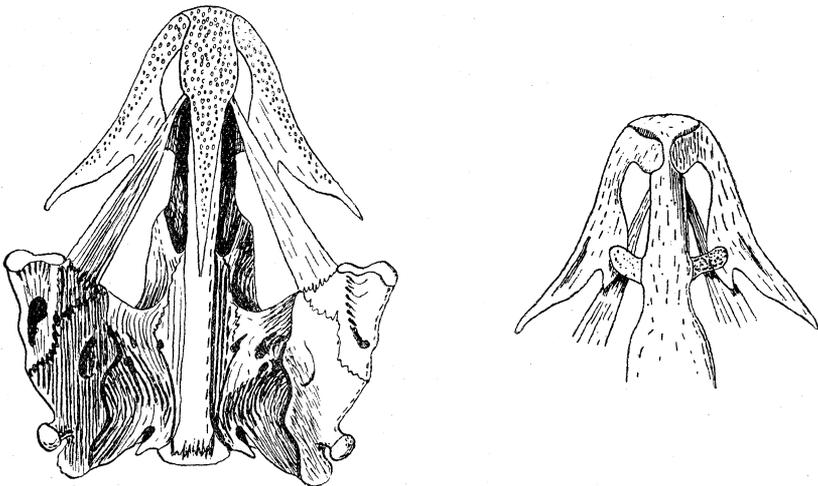
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(Figures 1-8.)

The apode fishes present us with a palate and upper jaw which is of exceeding interest when interpreted aright. The number of bones in the jaw and palatal arch is reduced to four, including the quadrate and hyomandibular, on each side. Of these, the last two are identifiable at sight (Figures 1 and 2).



Figs. 1. and 2. *Anguilla*.

C. Tate Regan, in a paper<sup>1</sup> on the osteology and classification of the Apodes, thus describes the bones we are interested in "Præmaxillaries not developed as distinct elements; maxillaries bordering the mouth, separated anteriorly by the ethmoid; hyo-palatine bones reduced to 2 or

\*For No. 2 see "Records" vol. xiv, no. 4, p. 271.

<sup>1</sup>Tate Regan—Ann. Mag. Nat. Hist., (8), x, 1912, p. 378.

3, hyomandibular, quadrate and palatopterygoid, the last sometimes absent."

The quadrate and hyomandibular being identified we are left with two bones in front of these, instead of the six usually present in this situation in other fishes. Of the teeth-bearing bones situated on either side of the ethmoid and bounding the gape, Boulenger<sup>2</sup> wrote, "Cuvier regarded the lateral bones of the upper jaw as præmaxillaries, Owen and Richardson as palatines (at least in *Muraenas*), whilst Peters and most recent authors have identified them throughout the order as maxillaries." Gill<sup>3</sup> in a series of papers dealing with the osteological characteristics of the families of the Apodes consistently designates them maxillaries. Continuing, Boulenger wrote<sup>4</sup> "The conclusion I have come to from the examination of numerous skulls belonging to various genera, is that the præmaxillaries have disappeared in all, whilst the maxillaries have persisted in the true eels (*Anguillidae*) and disappeared in the *Muraenidae*, their place being taken by the fused palato-ectopterygoids, which may even join the mandibular suspensorium. The vestigial bone, regarded by Jacoby as the pterygoid in *Muraena helena*, may be identified as the metapterygoid, and therefore does not disprove the homology, here suggested, of the other elements of the palate." This conclusion is quite unsupported by any illustrations or further discussion. The brief descriptions given by Gill in the series of papers already quoted do not disclose any divergent features presented by the bone as it is found in the five families of the Apodes he describes, beyond slight differences in the relation of its forward end to the mesethmoid. Tate Regan<sup>5</sup> discusses Boulenger's conclusion in a foot-note. He states:—"I find that in all their relations these bones are the same in the *Muraenidae* as in the other families; distally they are external to the mandibles; moreover the true palatopterygoids are present in the usual place, but reduced to mere threads of bone."

From my own observations I am prepared to endorse Tate Regan's conclusion; whatever be the true designation of this tooth-bearing bone it is the same bone throughout the Apodes.

Now as to their correct designation. It will be shown that they are correctly termed maxillae, and by that is meant that they are homologous with those bones which have in the past been termed palatines. Among past observers Owen and Richardson, *vide* Boulenger, alone were correct in the identification of these bones. To this conclusion I am led by the relation of the bones to the mesethmoid and their situation inside the lips. An examination of the head of any fish having the maxillary and premaxillary labial bones will reveal the fact that these two bones are situated in the substance of the lip. When the mouth is shut they fit one behind the other in folds of the lip, the mandibular teeth are in contact

<sup>2</sup>Boulenger—Cambridge Natural History (Fishes), 1904, p. 599.

<sup>3</sup>Gill—Proc. U.S. National Museum, xiii, 1890 (1891).

<sup>4</sup>Boulenger—Loc. cit. p. 600.

<sup>5</sup>Tate Regan—Loc. cit., p. 378.

with the maxillary teeth (i.e. those borne on the bones that have heretofore been termed vomer and palatine), and the labial bones and their teeth are lateral to and outside those of the mandible. When the mouth is opened these labial bones are pulled down and are found in the lips at the free edge of the cheek (Figure 3).

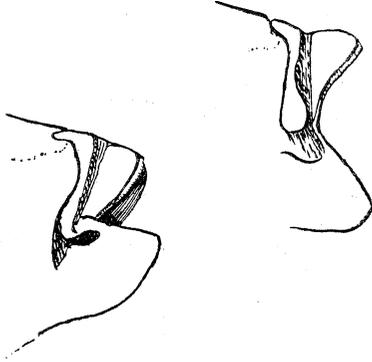


Fig. 3. *Girella tricuspidata*, Quoy and Gaimard. Showing the labial folds enclosing the labial bones. Mouth wide open and nearly shut. The outlines of the bones accentuated.

Comparing now an eel head with such an one as above described, first with the mouth shut, it will be observed that full well developed lips are present in both, but that in the eel there is no fold formed by the overlapping of the labial bones; next with the mouth open, the teeth in the upper jaw are situated *within* the cheek and lips just as are those on the maxilla (palatine) of other fishes, and the teeth on the premaxilla (vomer) are bounded in front by a lip and buccal sulcus in the same manner as those on the premaxilla of other fishes are bounded in front, but that in these other fishes the lip has, imbedded in its substance, the premaxillary and maxillary labial bones. Now closing the jaws slowly, the two sets of teeth, upper and lower, will be found to come directly into contact.

The teeth-bearing bones of the eels are clearly not mobile labial bones; to that extent then they do not appear to be homologous with either of the labial bones.

Let us turn our attention next to the relation of these bones to the mesethmoid. The labial bones are attached by fibrous union in front of the mesethmoid and supported by a labial supporting spur of a bone which is firmly attached, at times sutured to the mesethmoid on either side just behind its fore end, and which itself bears teeth. The last portion of the last paragraph holds our attention at once. The bones we are discussing are firmly attached to the mesethmoid on either side just behind its fore end, and themselves bear teeth. The verity of this statement and actual identity of the maxilla of the eel with the so called palatines, true maxillae, of other fishes, become apparent when specimens

in which the maxillae and premaxillae are so closely related anteriorly as to present a continuous sweep around the front, *e.g.*, *Esox lucius*.

The labial bones are developed in membranous stroma, perhaps in relation to the evanescent labial cartilages in front of the mesethmoid. The maxilla is developed as an ossification of, or on the anterior end of the suborbital cartilaginous arch in close proximity to its attachment to the mesethmoid. If this tooth-bearing bone be not the maxilla then in the eels the suborbital arch has failed to develop a bone anteriorly, and a bone, developed in other teleosts anteriorly to the mesethmoid, has come to occupy its place. The development of the bones then, as known in other teleosts, supports the contention that this is the maxilla. In fact a critical survey of the bone in its relation to soft structures, to the other bones both of the upper and lower jaws, and the developmental evidence, discovers no single reason for the old identification of the bone as the maxillary labial. The designation palatopterygoid, applied to the remaining undetermined bone in the palate conveys nothing, except it be an expression of faith in its development from, or in relation to the palate quadrate cartilage; nowhere else in the vertebrate skull do we find a palatopterygoid bone. The term is either a confession of ignorance or a subterfuge. This bone can only be palatine or quadrato-jugal, there is no evidence of any fusion of bones here. Of these two bones the quadrato-jugal sometimes extends forward medial to the hinder end of the maxilla, but usually stops short when it reaches that bone. The palatine commonly extends far forward medial to the maxilla, sometimes actually finding attachment to the palatine plate of the premaxilla. It may be concluded that the so called palatopterygoid is really the palatine; there is no evidence to the contrary.

Let us now turn our attention to the broader question indicated in the title of this communication. In 1921<sup>6</sup> I postulated a fish jaw in which the labial bones were absent, supporting my postulate by reference to the fact that "in the muraenid eels maxillae and premaxillae are not developed," using those terms in the sense of their old application to the labial bones. When making that statement I assumed that Boulenger was right (*vide antea*). I had no suspicion that the tooth-bearing bone in the eels was in verity a maxilla as demonstrated above. Having now learned that the postulate was unnecessary, that the actuality might have been cited, it appears to me that the question of the serial homology of the piscine and tetrapod premaxillary and maxillary bones might again be profitably reviewed.

The *raison d'être* of the old designation may be summed up very briefly. These two bones are the most anterior in the upper jaw, therefore they *must* be premaxilla and maxilla; that being so the more anterior must be premaxilla, the other the maxilla. There is absolutely no other evidence in support of this practice.

I have contended<sup>7</sup> that the labial bones of the bony fishes are homologous with the labial cartilages of the sharks and rays. In many of these

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<sup>6</sup>Kesteven—*Journ. Anat.*, lvi, 1922.

<sup>7</sup>Kesteven—*Loc. cit.*, p. 315.

forms the mouth is overhung by a hood which at first sight appears to be the lip. It is, however, lined both on the inside and on the outside by typical shagreened skin, and covers the true lip; this is lined on the outside like the hood but is lined on the inside by mucous membrane. Within the substance of the lip are the two labial cartilages one behind

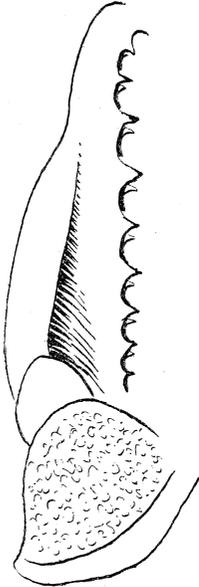


Fig. 4. *Squatina australis*. Half upper jaw from within showing buccal groove.

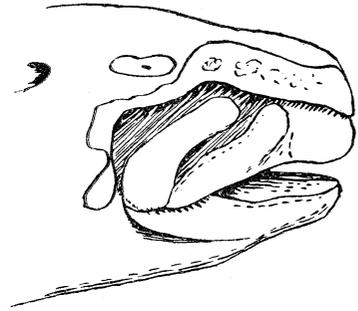


Fig. 5. *Squatina australis* from the side showing the folds enclosing the labial cartilages. The flap covering the mouth above has been cut away.

the other. The situation of these cartilages is best demonstrated in those elasmobranchs in which the mouth is terminal in front, as in the majority of the teleosts. The three drawings of *Squatina australis* show the situation of the true lip with its contained cartilages (Figs. 4, 5 and 6). In *Orectolobus maculatus* (Fig. 7) the cartilages lie in the lip, in very nearly the same situation as the labial bones in *Girella*; they do not, however, extend forward to meet in the mid line. Together they occupy a well formed lip, showing a sulcus between the cartilages and a deep furrow at their hinder end when the mouth is closed. When the mouth is opened the cartilages are drawn down and occupy the front border of the cheek, again as in *Girella* (Fig. 8); moreover the sulcus between the cartilages is shallowed considerably and the furrow behind almost completely abolished. There can be no question that the two, cartilages and bones, are labial structures, using that term here in a purely descriptive sense. Even so, the term is significant, labial structures are not used in mastication, neither are these. The labial bones are never used in mastication, that is performed between the teeth or plaques on the bones *within* the lips both of the upper and

lower jaws. The labial bones are prehensile devices, functionally they are not jaw bones.

Attention has already been directed to the fact that in *Polyodon* and in *Acipenser* the maxilla is developed in a manner completely different from that of the maxilla in other fishes.<sup>8</sup> In these forms it has developed

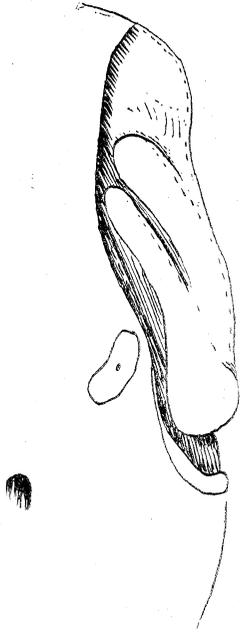


Fig. 6. *Squatina australis*. Half upper jaw from above showing the folds enclosing the labial cartilages.

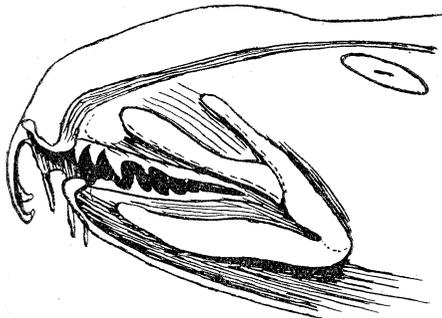


Fig. 7. *Orectolobus maculatus*, showing position of labial cartilages and labial furrow. Mouth closed.

<sup>8</sup>Kesteven—*Loc. cit.*, p. 314.

in relation to the palatopterygoid cartilage, in the majority of other fishes it is the so called palatine that develops in this situation. It is of significant interest to note that in these forms, as in the majority, if not all of the elasmobranchs, the palatopterygoid cartilages of either side meet in front, whereas in, I believe, all other teleosts, the palatopterygoid cartilages do not meet anteriorly but are attached on either side of the fore end of the ethmoid. There is every reason to believe that the bone is correctly named in the two ganoids, but if so then it cannot be in the forms in which the so called palatine develops in relation to the ethmoid and suborbital cartilaginous arch. It may be argued that

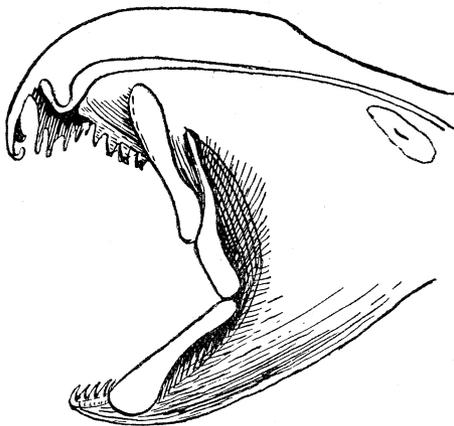


Fig. 8. *Orectolobus maculatus*, showing labial cartilages. Mouth open and labial furrows opened out.

my whole contention lacks force because in a very large proportion of the tetrapods the maxilla develops entirely independently of the subocular cartilaginous arch. On the other hand if my interpretation be correct, the true jaw bones developed first on the primitive cartilaginous masticatory framework; later when that framework acquired an attachment to the axial craniovisceral skeleton anteriorly, the jaw bones acquired a new relationship to that later skeleton also, later still the greater part of the primary cartilaginous arch was dropped altogether, and the jaw bones retained their new relationship.

It is a fact that in certain of the teleosts the premaxilla is directly related to the forward end of the mesethmoid and the bone below it. Thus Huxley<sup>9</sup> describes the position in *Esox* "The anterior pair of preoral bones, small, and beset with teeth upon their under surface, are connected with the vomer and the termination of the cartilaginous rostrum formed by the internasal septum. They obviously answer to the human pre-

<sup>9</sup>Huxley—Elements of Comparative Anatomy, 1864.

maxillae." Before proceeding further it should be noted that *Esox* presents features in this respect which are to a large extent peculiar. Parker<sup>10</sup> has shown that in *Salmo* they are not developed in relation to either of the structures mentioned above, and Swinnerton<sup>11</sup> has given a like demonstration in *Gasterosteus*. Huxley's homology fails also by reason of the fact that the so called vomer is not the vomer of the higher vertebrates. Continuing Huxley wrote:—"An elongated bone, which bears no teeth, is connected anteriorly with the maxilla, and *lying external to the other bones, forms the boundary of the gape*. Its homology with the maxilla of man appears unquestionable." This homologisation rests upon the correct identification of the premaxilla, and the situation of the bones in the gape.

The table which follows is interesting; it is based on the old designation of the preoral bones in the teleosts.

	Palato- pterygoid	Situation of Functional Jaw	Position of Maxilla and Premaxilla	Maxilla and Premaxilla Developed
Elasmobranchs	present	p.q.		
<i>Polyodon</i> and <i>Acipenser</i>	present	p.q.	on p.q.	on p.q.
Apodes	present?	p.q.?	on p.q.	on p.q.
Teleosts generally	present	p.q.	in front of p.q.	in front of p.q.
Amphibians	present	p.q.	on p.q.	on p.q.

As will be seen in this table the teleosts are quite unique in two respects if the old interpretation be adopted.

It is concluded that the old interpretation is not correct, and the terms premaxillary and maxillary labial are proposed for the two bones in the upper lip of the teleostean fishes which have heretofore been termed premaxilla and maxilla respectively.

It is further concluded that the true maxilla in the teleosts, homologous with that of the tetrapods, is the bone which has heretofore been designated palatine.

These conclusions are in conformity with those of a former contribution.

<sup>10</sup>Parker—Phil. Trans., clxiii, 1873 (1874), p. 95.

<sup>11</sup>Swinnerton—Q. Journ. Micro. Sci., xlv, 1902, p. 503.

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