

SKELETON OF CYPRINOID FISHES IN RELATION TO PHYLOGENETIC STUDIES.

III. THE SKULL AND OTHER SKELETAL STRUCTURES OF HOMALOPTERID FISHES.

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INTRODUCTION.

In a comparative account of the skull of a few Homalopterid species and of a Gastromyzonid example given by me (Ramaswami, 1948), it was pointed out that the phylogeny of the Homalopteridae including the Gastromyzonidae could not be discussed as I had not examined the Cyprinid and Cobitid genera which are the probable progenitors of the two groups.

Subsequently a number of Homalopterid and Gastromyzonid genera was made available to me by Dr. S. L. Hora, Director, Zoological Survey of India, Calcutta, and I thank him for the generous gift of the material. I propose to examine four genera of Homalopteridae (*sen. stric.*) and place on record their cranial and other osteological characters with a view to elicit their origin and affinities.

Segemehl (1891) examined one species of *Homaloptera (ocellata* C.V.) and while pointing out its Cyprinid and Cobitid affinities, he cautiously refrained from coming to any conclusions with regard to the relationships of the Homalopteridae as the examination of a single species would not warrant any generalizations. In this connexion, it may also be mentioned that Regan (1929) considered the Homalopteridae widely different from the Cobitidae. More recently Berg (1947) described the family Homalopteridae as comprising the Homalopterini and Gastromyzonini. But Hora (1950) established by an examination of external characters that the original Homalopteridae including Gastromyzonidae should be split up into two independent families,—the Homalopteridae and Gastromyzonidae, as was envisaged by him previously (Hora, 1932). Among the Homalopteridae according to Hora

ERRATA

Skeleton of Cyprinoid Fishes in relation to Phylogenetic Studies. I. The systematic position of the Genus *Gyrinocheilus* Vaillant by L. S. Ramaswami. *Proc. Nat. Inst. Sci.*, Vol. XVIII, No. 2, pp. 125-140, and II. The systematic position of *Psilorhynchus* McClelland by L. S. Ramaswami. *Proc. Nat. Inst. Sci.*, Vol. XVIII, No. 2, pp. 141-150.

Page 126, footnote: *Instead of* All figures have been drawn at a magnification of $\times 17$ (approx.) except Figs. 10-12a, *read*: Figures have been drawn at a magnification of $\times 17$; 10-12a are not reduced; figs. 3 and 4 are reduced to $1/3$ approx. and the rest to $\frac{1}{2}$ approx.

„ 136, 7th line from bottom: *read* lacrimal for laerimal.

„ 142, Figure 2: delete typewritten abbreviation 'tf'.

„ 144, 28th line from top: *read* Homa-lopteridae for Homal-opteridae.

(*op. cit.*), the genus *Homaloptera* is generalised and formed the 'starting point for the different and ultimate evolution of the other genera'. By a study of the scale structure, Law (1950) however, pointed out that *Homaloptera* was probably a heterogeneous assemblage of forms and that 'different forms of *Homaloptera* seem to have given rise to various types of Homalopterine genera'.

MATERIAL.

The following species have been studied by me:

Homaloptera zollingeri Bleeker; *H. amphisquamata* W. & de B.; *H. leonardi* Hora & Tweedie; *H. rupicola* Prashad & Mukherji; *Balitora brucei* Gray; *Balitora brucei* var. *mysorensis* Hora; *Bhavana australis* Jerdon; *Lep-
turichthys nicholsi* Hora.

OBSERVATIONS.

The ethmoid region.—In the genera of Homalopteridae examined, the supraethmoid portion of the ethmoid is broad and is firmly articulated with the frontals (figs. 1a–4a, 3c fr) posteriorly as in the cyprinids. There is a median anterior prolongation of it as in *Psilorhynchus* (Ramaswami, 1952b) which may be pointed as in *Balitora* (figs. 1a, 1b p) or expanded as in *Homaloptera* and *Lep-
turichthys* (figs. 2a, 3a, 3c, 4a p). This pointed or expanded prolongation is also seen in the ventral aspect (figs. 1b–4b p); the ethmoid is also noticed on the same aspect (figs. 1b–4b et) with whose lateral surface the palatine (*pal*) articulates in *Balitora*, *Lep-
turichthys*, *Homaloptera zollingeri*, *H. leonardi* and *Bhavana*. In *H. amphisquamata* peculiarly the palatine (figs. 3a, 3b *pal*) does not articulate with the ethmoid since the anterior preethmoid (*pet*) is elongated and thus keeps out the ethmoid. Moreover, in the same species, the supraethmoid is not broad enough so that the articulation of the elongated preethmoid with the ethmoid is clearly visible on the dorsal aspect. Sagemehl (1891) delineated an elongated second preethmoid (septomaxilla, according to him) in *Homaloptera ocellata* (fig. 1, Plate 18). Further, unlike the Gastromyzonidae, not a single species of Homalopteridae shows a slender supraethmoid portion which is therefore uniformly broad in all the genera examined.

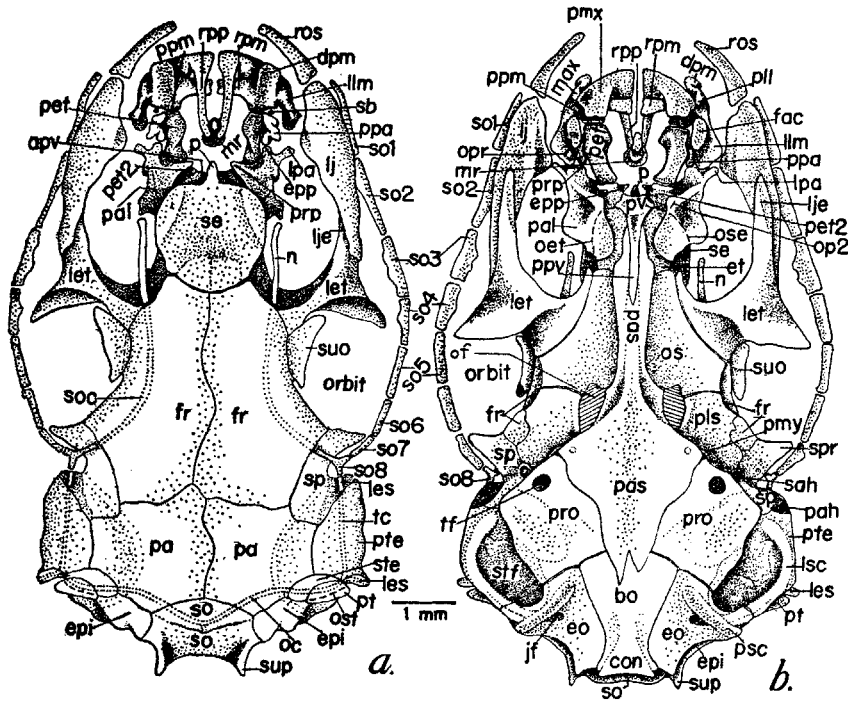
Articulating with the ethmoid and prevomer laterally in the Homalopteridae, there is a small rounded bone which has been called by previous authors like Sagemehl (1891) and Regan (1911) a 'septomaxillary'. Having taken into account the inappropriateness of the term for the bone, I labelled it as the anterior process of the ethmoid in my previous paper on the Homalopterid skull (Ramaswami, 1948). Regan (1911) describing the occurrence of this bone in Cypriniformes, noted that it was firmly united with the prevomer and that it articulated, directly or otherwise, with the maxilla anteriorly. Later Starks (1926) in describing the ethmoid region of fish skull employed the term 'preethmoid' for describing this nodule of bone in forms like *Misgurnus* etc.; in the Indian cyprinids examined by me, the bone occurs prominently and further, I have already used the term in describing the bone in *Gyrinocheilus* (Ramaswami, 1952a) and *Psilorhynchus* (Ramaswami, 1952b).

In the Homalopteridae, as in the Cobitidae examined by me, the preethmoid not only gives articulation laterally to the palatine but also to a rod of bone in front [called 'submaxillary' by Sagemehl (1891) and Regan (1911)] which connects it with the maxilla anteriorly. In my previous paper (Ramaswami, 1948) I labelled this rod of bone the preethmoid as it was disposed in front of the 'anterior process' of the ethmoid.

A study of the skull characters of the Cobitidae has enabled me now to speculate upon the possible origin of the preethmoids. It is noticed that in the Cobitidae like *Acanthopthalmus*, *Misgurnus*, *Somileptes* etc., there is an elongated

preethmoid intercalated, articulating with the maxilla anteriorly by a facet and posteriorly by facets with the prevomer ventrally, and the palatine dorsally. If this bone splitted horizontally, it would give rise dorsally to a bone situated between and articulating anteriorly with the maxilla and posteriorly with the palatine, called by me prepalatine in the present paper, and ventrally to one which articulates anteriorly with the maxilla and posteriorly with the prevomer projection; this will be the new preethmoid. Such a condition is met with in *Botia*, one of the cobitidid examples where a prepalatine and a preethmoid are noticed. Sagemehl (1891) however, described similar bones in the cobitid forms studied by him as 'submaxillaries'.

In the Homalopteridae it is very likely that the bones labelled by me prepalatine and preethmoid have arisen in the same way as in the Cobitidae. If so,



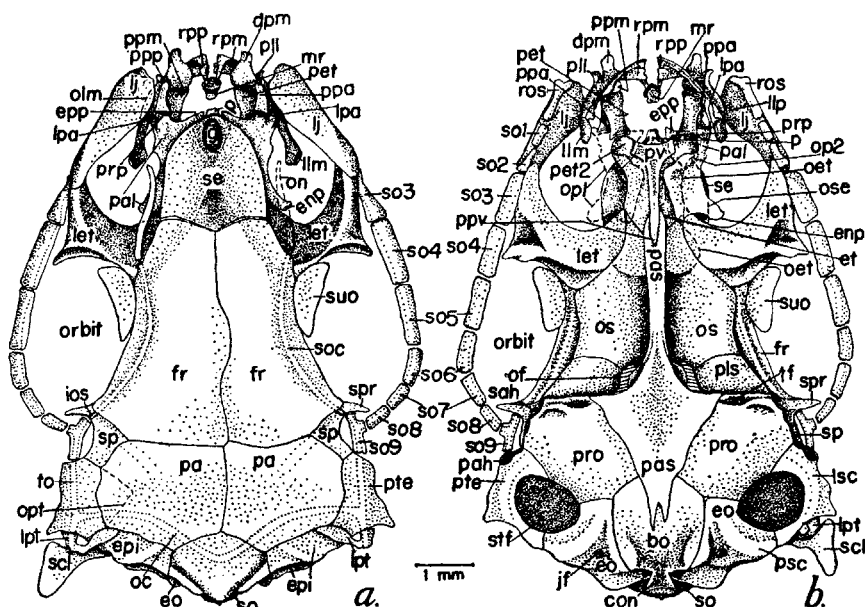
TEXT FIG. 1a, 1b. Dorsal and ventral views respectively of the skull of *Balitora brucei* var. *mysorensis* Hora; in fig. 1a the maxillae are gently pulled apart.

the Cobitidae and the Homalopteridae having taken their origin from a cyprinoid ancestor have evolved on parallel lines. Thus it may be that the first formed preethmoid of the early Cobitidae and of the Homalopteridae elongated and then gave rise to the prepalatine and preethmoid bones.

Probably to increase the mobility of the anterior region, some ancestral cobitids and homalopterids developed a second preethmoid as an apophysis of the antero-lateral ethmoid region (sometimes the anterior extension of the prevomer also taking part with the latter) with which the first preethmoid i.e. the preethmoid formed by the splitting of the bone referred to in *Acanthophthalmus*, etc., commenced to articulate. The preethmoid of the cyprinids therefore, may be homologous with the elongated first preethmoid and not with the second preethmoid of the

present day Cobitidae and Homalopteridae, though, at first sight, the latter appears topographically comparable with that in the Cyprinidae.

It must be pointed out here that the bones labelled by me (Ramaswami, 1948) as the lateral rostral and the preethmoid in the Homalopteridae and the Gastro-myzonidae correspond to the 'submaxillaries' of Sagemehl (1891); Regan (1911) and Gregory (1933) also referred to them in the cypriniform examples described by them retaining the same nomenclature as Sagemehl. I avoided the term 'submaxillary' since topographically the bones are not disposed ventrally to the maxilla and therefore, the term 'submaxillary' was not justifiable. I have therefore ventured to designate in my present paper the bone articulating with the antero-lateral corner of the ethmoid and of the prevomerine projection as the second preethmoid (figs. 1a-4a, 1b-4b, 3c *pet*2) and that in front of it, as the first preethmoid (*pet*). The other bone sitting on the first preethmoid and articulating with the palatine facet, which was labelled 'lateral rostral' on purely topographical grounds



TEXT FIG. 2a, 2b. Dorsal and ventral views respectively of the skull of *Homaloptera zollingeri* Bleeker; the supraclithrum is shown on one side only.

by me (Ramaswami, 1948), I now describe as the prepalatine (figs. 1a-4a, 1b-4b, 3c *ppa*), a term which has already been employed by Starks (1926) for describing a bone in similar location in *Siganus* studied by him.

There is usually a ligament passing from the prepalatine to the facet (figs. 2a, 3a *ppp*) of the maxilla where the prepalatine articulates. In *Balitora brucei* var. *mysorensis* there is a small sesamoid bone (fig. 1a *sb*) in front of the prepalatine (*ppa*).

The premaxilla of the Homalopteridae (figs. 1a-4a, 1b-4b, 3c *pmx*) resembles that in the Cyprinidae. There is a dorsal rostral process (*rpp*) disposed dorsally to the median rostral (*mr*). In *H. amphisqueamata* the rostral process (figs. 3a, 3b *rpp*) extends beyond the median rostral (*mr*) and in *H. rupicola* (fig. 3c *rpp*) it rests on the anterior end of the supraethmoid. The lateral process may be short and expanded as in *Balitora* (fig. 1b *lpa*) or may be elongated as in *Homaloptera* (figs. 2b, 3b, *llp*), *Lepturichthys* (fig. 4b. *llp*) and *Bhavana*.

The homalopterid maxilla shows all the processes noticed in that of the cyprinid, viz., the dorsal premaxillary process (figs. 1a-4a, 1b-4b, 3c *dpm*), the ventral rostral process (*rpm*), the lateral process for the ligament of the adductor mandibulae muscle (*pll*) and posteriorly the prominent projections for the articulation of the prepalatine (*ppa*) and the first preethmoid (*pet*). However, in the cyprinids, the maxilla on the posterior face shows one or two facets; one of them is directed towards the preethmoid and the other towards the palatine. In *Lepturichthys*, the dorsal premaxillary process (figs. 4a, 4b *dpm*) is very prominent and mesially to it there is a large prominence (*pr*) whose posterior edge articulates with the first preethmoid (*pet*). In the ventral view of the skull the anterior portion of this prominence is visible as a small projection (fig. 4b *pr*) mesially to the dorsal premaxillary process (*dpm*).

The prevomer (figs. 1b-4b *pv*) is noticed ventrally as underlying the ethmoid (*et*) and parasphenoid (*pas*) bones. Anterolaterally, the prevomer articulates with the second preethmoid (*pet2*); in *H. amphisquamata* alone it is broad (fig. 3b *pv*) and the posteromedial limb is also short.

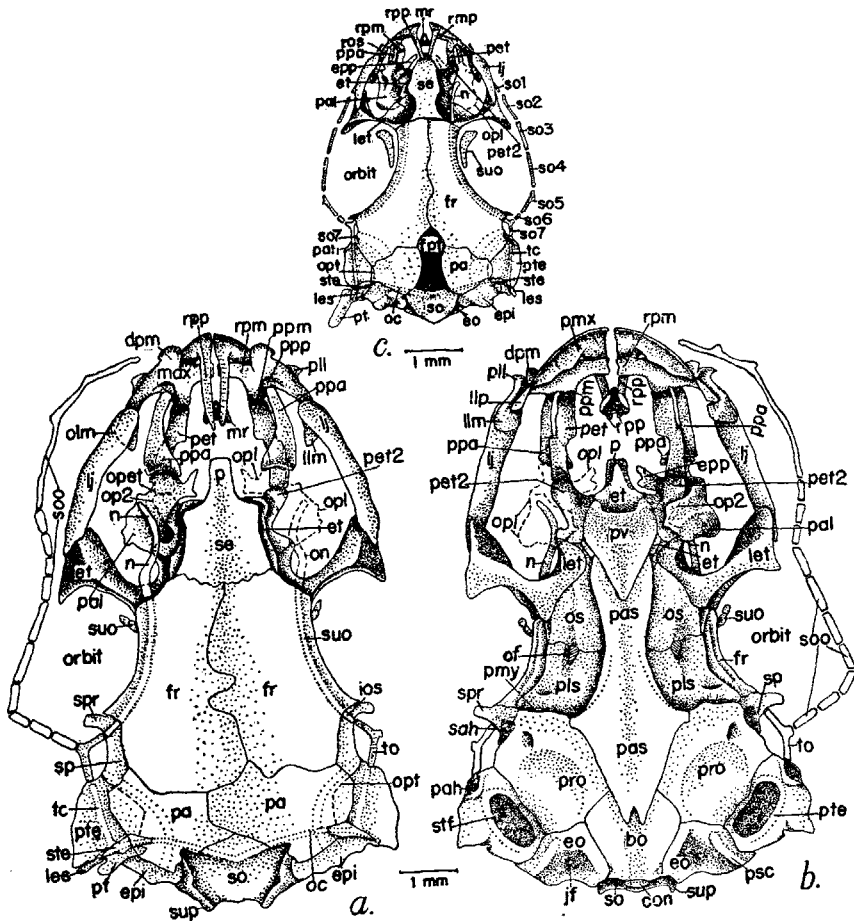
The lacrimojugal of the Homalopteridae while agreeing topographically with the lacrimal of Cyprinidae, is comparatively longer, probably formed by the fusion of a lacrimal and a posterior jugal and hence the term lacrimal is not used here. The bone (figs. 1a-4a, 1b-4b, 3c *lj*) is very large and in *Balitora* and *Lepturichthys*, and there is in front of it one (figs. 1a, 1b, 3c *ros*) or more sensory canal bones. In the latter example, I have labelled a bone (figs. 4a, 4b *ros*) as corresponding to the rostral of *Balitora* and associated with it mesially, there are two other sensory canal bones, probably also rostral derivatives. In *H. amphisquamata*, and *H. leonardi* the long lacrimojugal (figs. 3a, 3b *lj*) is not so closely associated with the canal bones as in *H. zollingeri*, so much so, it is difficult to say of the exact extension of the rostral if the latter exists at all in front of the lacrimojugal.

The lateral ethmoid (figs. 1a-4a, 1b-4b 3c *let*) separates the anterior olfactory region from the posterior orbital region. Dorsomesially it is in contact with the frontal (*fr*) and ventrally with the ethmoid (*et*), the orbitosphenoid and sometimes with the supraorbital and the second preethmoid. The lateral extension of the bone is in contact with the suborbital sensory canal ossicles and also the lacrimojugal, and projects both anteriorly and posteriorly; in *Lepturichthys* and *Balitora*, the lacrimojugal process of the lateral ethmoid (figs. 4a, 4b *lje*) is very much longer than the posterior process of the same. In *H. amphisquamata* the processes are short and blunt (figs. 3a, 3b) and in *H. zollingeri* (figs. 2a, 2b), *H. rupicola* (fig. 3c) and *Bhavana* the processes are better developed; in *H. leonardi*, they are long and broad. In *H. ocellata* also Sagemehl (1891) showed these processes as well developed.

It may be useful to describe the palatine here though it belongs to the upper jaw. The palatine (figs. 1a-4a, 1b-4b, 3c *pal*) of the Homalopteridae differs from that in the Cyprinidae in a very important feature. While as in the Cyprinidae, the palatine shows a prominent process (either pointed or rounded) (*epp*) towards the anteromesial process of the ethmoid (*et*) and articulates mesially with the second preethmoid (*pet2*) and the ethmoid (*et*) and posteriorly with the entopterygoid (*ept*), there is however, no direct articulation with the maxilla as in the cyprinids. This is because, in the Homalopteridae, the elongated first preethmoid and the prepalatine are intercalated between the maxilla (*ppm*) and the palatine (*pal*).

While in *Lepturichthys*, *Balitora*, *Bhavana* and *H. zollingeri* the prepalatine articular facet of the palatine is small, in *H. amphisquamata* (figs. 3a, 3b) it is comparatively larger. In addition in *Lepturichthys*, *H. zollingeri*, *H. rupicola* and *Balitora* the palatine shows a prominent anterolateral process (figs. 1a-2a, 1b-2b, 4a-4b *lpa*) projecting towards the lacrimojugal (*lj*) which I have therefore, called the lacrimojugal process. In *H. leonardi* peculiarly this lateral lacrimojugal process comes in contact with the lacrimojugal anteriorly and the posterior articulation of the prepalatine is also noticed at this region. Thus a separate prepalatine articular

facet of the palatine is not seen in *H. leonardi*. A lacrimojugal process has also been seen in a few cyprinid genera like *Cirrhina* and *Aspidoparia* studied by me. In all the Homalopterid examples studied by me, it is noticed that there is a ligamentary connexion between the lacrimojugal and the palatine process. In *Bhavana* and *H. amphisquamata* this lacrimojugal process is absent. Peculiarly in *H. amphisquamata* the mesial articulation of the palatine is not with the second preethmoid and the ethmoid as in the other Homalopteridae, but with the elongated



TEXT FIG. 3a, 3b. Dorsal and ventral views respectively of the skull of *Homaloptera amphisquamata* W. & de B.; the supraorbital sensory canal ossicles are shown on one side only and the posttemporal is drawn on the left side of the dorsal view only.
 ,, 3c. Dorsal view of the skull of *Homaloptera rupicola* Prashad and Mukherji; the posttemporal is shown on one side only.

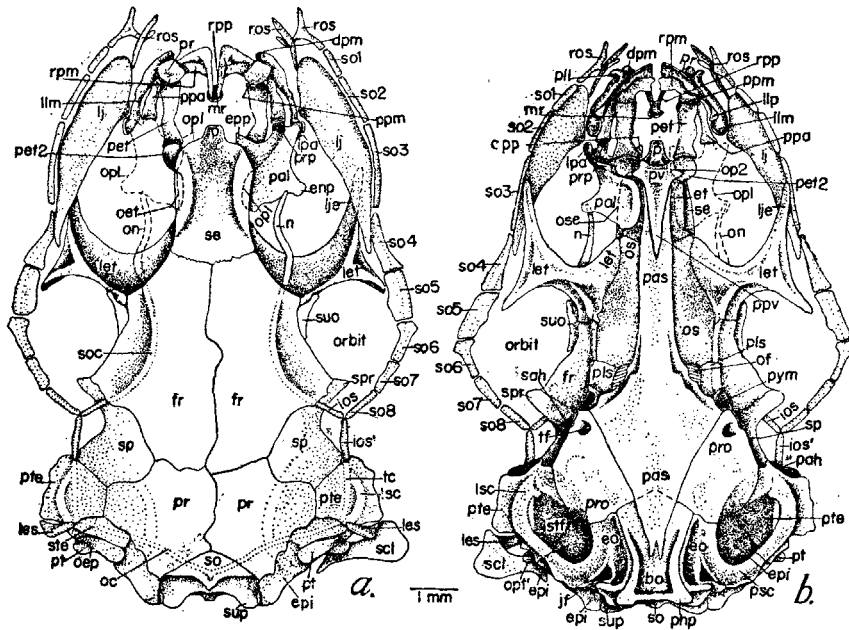
second preethmoid only which on account of its elongation has kept out the ethmoid as already remarked.

A pair of slender elongated nasal bones (figs. 1a-4a, 1b-4b, 3c n) is noticed laterally to the ethmoid in the Homalopteridae as in the Cyprinidae.

The median rostral.—In *Lepturichthys*, the dorsal aspect of the median rostral (fig. 4a mr) shows a deep depression and the rostral limbs (rpp) of the premaxilla

are noticed over this depression; there is also a short ventral projection from the median rostral (*mr*). While in the other examples of Homalopteridae studied, the rostral processes of the premaxillae rest on the dorsal aspect of the median rostral, in *H. rupicola*, they rest on the supraethmoid part. In *H. amphisquamata* (figs. 3a, 3b) there are two lateral processes for attachment of the ligament from the ventrolateral process of the maxilla. Obviously the median rostral shows variations in its structure within the family itself.

The orbitotemporal region.—On account of the general depression of the head, the frontals (figs. 1a-4a, 1b-4b, 3c *fr*) and parietals (*pa*) are large. In *Homaloptera*, however, the widening of the frontals is not so great as in the other examples, particularly in the region of the lateral ethmoid. The lateral extensions of the frontals become visible in the ventral aspect also; this is seen to the maximum extent in *Lepturichthys* (fig. 4b *fr*). In *H. rupicola* there is a large frontoparietal fontanel



TEXT FIG. 4a, 4b. Dorsal and ventral views respectively of the skull of *Lepturichthys nicholsi* Hora; the supraclithrum is shown on one side only.

(fig. 3c *fpf*) and this is the only instance among Homalopteridae where such a fontanel has been noticed by me. An extraordinary development of the frontals is also seen in unrelated forms like *Gyrinocheilus* (Ramaswami, 1952a) and *Parapsilorrhynchus* and *Psilorhynchus* (Ramaswami, 1952b), which are also hillstream or sand-burrowing forms. Flanking the frontals there are the supraorbitals (figs. 1a-4a, 1b-4b, 3c *suo*) very poorly developed in *H. amphisquamata* (figs. 3a, 3b *suo*). However, in *Gyrinocheilus* (Ramaswami, 1952a), the supraorbitals are completely wanting.

Ventrally the orbitosphenoids (figs. 1b-4b *os*) and the pleurosphenoids (*pls*) are prominent; the former bone is the larger of the two in all the examples studied except in *H. amphisquamata* (fig. 3b *pls*) where the pleurosphenoid is also well developed. In *H. ocellata* (Sagemehl, 1891) the pleurosphenoid (alisphenoid) is very small. In *Bhavanaia*, *Balitora*, *H. zollingeri*, *H. leonardi*, *H. rupicola* and

Lepturichthys the optic foramen is situated posteriorly accommodated between the orbitosphenoid (*os*), the pleurosphenoid (*pls*) and the parasphenoid (*pas*). In *H. amphisquamata* the optic foramen (fig. 3*b of*) is situated between the orbitosphenoid (*os*) and the pleurosphenoid (*pls*) and the parasphenoid (*pas*) does not contribute to bounding the foramen. The anterior extension of the parasphenoid (*pas*) in this species is very broad when compared with the other examples studied. In *H. ocellata* (Sagemehl, 1891) the parasphenoid bounds ventrally the optic foramen and is not broad.

In *H. zollingeri* the two orbitosphenoids (fig. 2*b os*) meet mesially and there is a slight projection from the parasphenoid meeting the united orbitosphenoids forming an interorbital septum. In no other Homalopterid do we notice an interorbital septum. Sagemehl (1891) also referred to the complete absence of an interorbital septum in *Homaloptera ocellata*.

In the Homalopteridae, the parasphenoid (figs. 1*b-4b pas*) is broad posteriorly and narrow anteriorly except in *H. amphisquamata* (fig. 3*b pas*) where it is also broad anteriorly.

In each bulbus oculi, there is a pair of large cup-shaped sclerotic bones.

The auditory region.—The auditory region of the Homalopteridae exhibits certain fundamental differences from the same in the Cyprinidae. The auditory capsule is formed by the sphenotic (figs. 1*b-4b sph*), the pterotic (*pte*), the epiotic (*epi*) and the prootic (*pro*); roofing this region there are the parietals (*pa*) and forming the floor of the same, the posterior part of the parasphenoid (*pas*) and the basioccipital (*bo*) are seen. There is no frontoparietal fontanel in the examined genera of Homalopteridae except, however, in *H. rupicola*, as noticed in Cobitidae, in *Catostomus* (Catostomidae), in *Cyprinus* and *Amblypharyngichthyes* (Cyprinidae) and *Homaloptera* (Sagemehl, 1891). Nor is there an ethmoid-frontal fontanel in the Homalopteridae as in *Psilorhynchus* (Ramaswami, 1952*b*). In *Bhavana*, *Balitora* (figs. 1*a, 1b so8*) and *Homaloptera* (figs. 2*a, 3a, 2b, 3b, 3c*) connecting the supraorbital sensory canal (*soc*) with the temporal (*tc*) there is a triradiate canal bone (*sog, to*). In *Homaloptera*, connecting the supraorbital (*soc*) and the triradiate sensory canal bones (*to*), there is a small independent canal ossicle (*ios*) sitting on the sphenotic (*sp*) anteriorly, or as in *Balitora* (fig. 1*a*), it may be disposed posteriorly on the sphenotic establishing connexion between the triradiate ossicle and the temporal canal. In *Lepturichthys* (figs. 4*a, 4b*) there are two independent ossicles (*ios, ios'*) establishing connexion between the supraorbital and temporal canals. In *H. rupicola* and *H. leonardi* the supraorbital limb of the triradiate ossicle (fig. 3*c so7*) reaches the above canal and therefore, there is no independent ossicle as in the other species of *Homaloptera*. It is important to note that the sensory canal does not pass through the sphenotic bone in these examples as it does in the pterotic region.

Posteriorly there are two canal ossicles on the pterotico-epiotic region in all the Homalopterid examples studied except in *H. zollingeri*. One of these is larger (figs. 1*a, 3a, 3c, ste*) and mesial in position connecting the temporal canal with the occipital canal. In my previous paper (Ramaswami, 1948), I had labelled this bone the anterior extrascapular and after examining the Indian Cyprinidae, I find that it should be more correctly called the supratemporal. The lateral ossicle (figs. 1*a, 1b, 3a, 3c 4a, les*) establishes connexion between the temporal (*tc*) and lateral line canals and this is the extrascapular. Posterior to these two, there is a small bone (*pt*) which sits upon the epiotic (*epi*) and the supracleithrum (*scl*). I had labelled this as the posterior extrascapular and the supracleithrum as the post-temporal in my previous paper (*op. cit.*). They should be correctly called the post-temporal and the supracleithrum respectively. A part of the occipital canal, it is noticed in the Homalopteridae, runs in the parietal bone also.

In *H. zollingeri* the supratemporal appears to be absent and the lateral extrascapular and the post-temporal seem to have fused to form a U-shaped bone (figs.

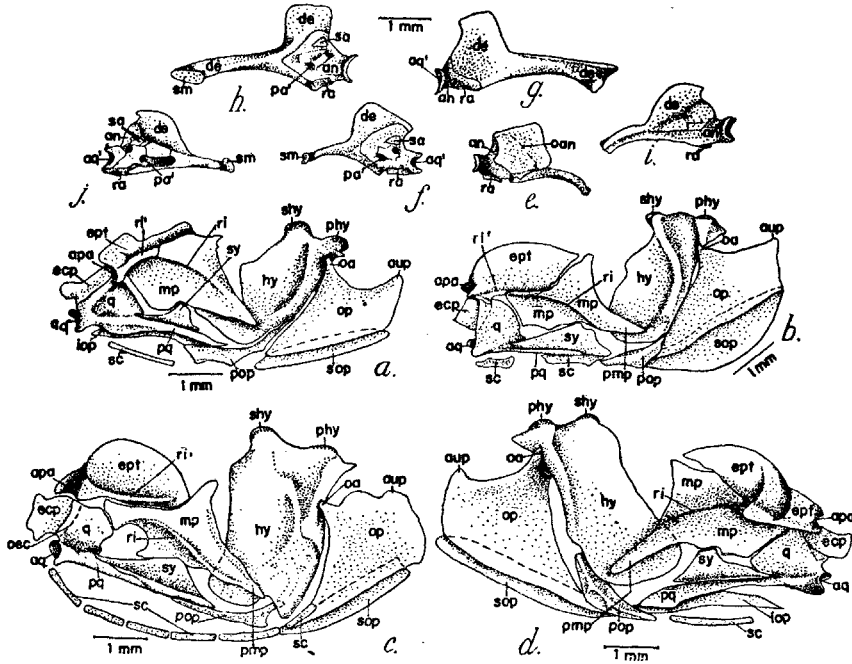
2a, 2b *lpt*). This is a peculiar modification of the lateral extrascapular and the post-temporal. Ventrally the subtemporal fossa (figs. 1b-4b *stf*) is conspicuously noticed. It may be bounded by the prootic, the pterotic, the epiotic and the exoccipital (*H. zollingeri*, *Lepturichthys*, *Balitora* and *Bhavana*) or it may be seen largely as a depression in the pterotic (*H. rupicola*, *H. amphisqueamata*). In all these cases the roof of the subtemporal fossa is formed by the pterotic and epiotic bones. In *H. leonardi* the roofing pterotic wall is thin laterally to the epiotic and moreover, where the temporal canal passes into the supraoccipital one, there is no ossification surrounding the canal so that through these orifices or gaps, one could easily pass a bristle into the subtemporal fossa from the dorsal aspect. From the ventral aspect, these gaps and the temporal and occipital canals can be easily made out through the deep subtemporal fossa. It may not be out of place to mention here that in the Cyprinid examples studied by me, the post-temporal does not convey the sensory canal nor does it show only one articulation with the auditory region in the majority of forms.

The occipital region shows certain interesting features. The supraoccipital (figs. 1a-4a *so*) excludes the exoccipital from forming the roof of the foramen magnum. The supraoccipital may project posteriorly in the form of two prominent processes as in *Balitora* (figs. 1a, 1b *sup*), *H. leonardi*, *H. amphisqueamata* (figs. 3a, 3b *sup*) and *Bhavana* or as blunt projections as in *Lepturichthys* (figs. 4a, 4b *sup*) or they may be absent as in *H. zollingeri* and *H. rupicola*. The exoccipitals are not visible dorsally except in *H. zollingeri* (fig. 2a *eo*). The lateral fenestra so commonly seen in the exoccipitals of catostomids, cyprinids and cobitids is absent in the Homalopteridae, a fact also recorded by Sagemehl (1891). The basioccipital (figs. 1b-4b *bo*) shows a prominent condyle (*con*) which may be projecting as in *H. zollingeri* (fig. 2b *con*) and the pharyngeal processes so commonly met with in the Cyprinidae are absent. However, in *Lepturichthys* (fig. 4b), the basioccipital shows a pair of lateral projections (*php*) and the aorta does not run dorsally to these projections. Sagemehl (1891) also noted the absence of the pharyngeal processes in the Homalopteridae.

In a median sectional view of the auditory region of the Homalopteridae, an interesting feature is noticed. While in the cyprinid *Labeo*, a portion of the pterotic is visible in the mesial view, showing the anterior opening of the lateral semicircular canal, in *Bhavana* which I have sagittally bisected and studied, it is kept out. In *Bhavana*, the openings of the anterior semicircular canal are noticed in the sphenotic, those of the lateral and posterior semicircular canals in the sphenotic and epiotic.

The upper jaw.—The upper jaw shows certain features in which it stands apart from the cyprinid one. The operculum (figs. 5a-5d *op*) is generally elongated anteroposteriorly and the upper edge of it may show two prominent processes. In describing the catostomid opercular series, Nelson (1949) delineated in the upper border of the operculum a posterodorsal auricular process and an anterodorsal opercular arm and a small articular process just above the articulation with the hyomandibula. In all the Homalopteridae the opercular arm is prominent and while the auricular process is rounded in *H. amphisqueamata*, it is more pointed in *H. zollingeri*, *H. rupicola*, *H. leonardi*, *Balitora* and *Lepturichthys*. A lower articular process is not developed in the Homalopteridae. The metapterygoid (*mp*) has a prominent posterior process (*pmp*) which lies laterally to the hyomandibula (*hy*). It shows also a prominent ridge (*ri*). The ectopterygoid (*ecp*) projects in front of the quadrate (*q*) ventrally to the entopterygoid (*ept*). The entopterygoid (*ept*) shows a prominent articular facet for the palatine (*apa*) and in *H. amphisqueamata* a prominent ridge (fig. 5c *ri*) is also seen. In *H. rupicola* and *H. leonardi* the entopterygoid is bent at right angle laterally from the ridge. The symplectic (figs. 5a-5d *sy*) is large and I labelled this bone the 'posterior ectopterygoid' in my previous paper (Ramaswami, 1948). At the time I argued that in *Bhavana* the

bone which I labelled symplectic showed no sensory canal in it and therefore, it could not be a preopercular and I accordingly called it the symplectic. Having studied a large number of forms, I hasten to correct the nomenclature previously employed and the bones labelled symplectic and posterior ectopterygoid in *Bhavania Balitora* and *Gastromyzon* (Ramaswami, 1948) must now be read as preopercular and symplectic respectively. There is a set of two independent sensory canal ossicles (fig. 5*b* *sc*) in front of the preopercular (*pop*) in *H. zollingeri*, *H. rupicola* and *H. leonardi* or a set of six sensory canal ossicles (fig. 5*c* *sc*) ventrally to the preopercular (*pop*), the first one being disposed on the lower portion of the hyomandibula as in *H. amphisquamata*. While in *H. zollingeri* and *H. rupicola* the



TEXT FIG. 5*a*. Lateral aspect of the upper jaw of *Balitora brucei* var. *mysorensis* Hora.
 " 5*b*. Lateral aspect of the upper jaw of *H. zollingeri* Bleeker.
 " 5*c*. Lateral aspect of the upper jaw of *H. amphisquamata* W. & de B.
 " 5*d*. Lateral aspect of the upper jaw of *Lepturichthys nicholsi* Hora.
 " 5*e*, 5*f*. Lateral and mesial aspects respectively of the lower jaw of *H. zollingeri* Bleeker.
 " 5*g*, 5*h*. Lateral and mesial aspects respectively of the lower jaw of *H. amphisquamata* W. & de B.
 " 5*i*, 5*j*. Lateral and mesial aspects respectively of the lower jaw of *Lepturichthys nicholsi* Hora.

preopercular carries the sensory canal in it, in *H. amphisquamata* the preopercular is free of it and the chain of six ossicles referred to above carries it into the lower jaw. In *Balitora* and *Lepturichthys* the preopercular (figs. 5*a*, 5*d* *pop*) has a large sensory canal ossicle (*sc*) in front of it. The posterior process of the quadrate (*pq*) is very large in these two genera while in *Homaloptera* (figs. 5*b*, 5*c* *pq*), it is comparatively smaller.

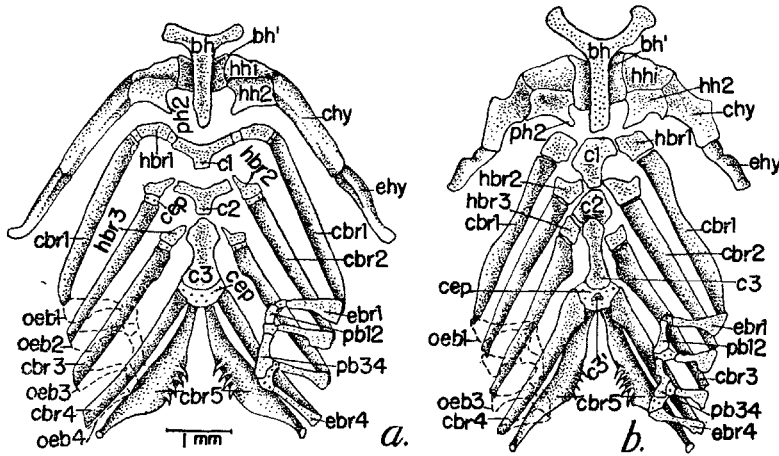
The palatine has already been described.

The lower jaw.—Each ramus of the lower jaw shows the four bones, viz., the angular (figs. 5*e*–5*j* *an*), the retroarticular (*ra*), the dentary (*de*) and the mesial one

(figs. 5f, 5h) or two (fig. 5j) sesamoid angulars (*sa*). Peculiarly, there is a passage (figs. 5f, 5h, 5j *pa'*) in the angular (*an*) covering Meckel's cartilage. I have already described this passage as a sensory canal in *Bhavana* and *Balitora* (Ramaswami, 1948).

The hyobranchial apparatus.—Certain interesting features are noticed in the hyobranchial apparatus of the Homalopteridae. In the hyoid cornu there is a median bony piece (figs. 6a, 6b *bh'*) connecting the two cornua and dorsally to this, there is a Y-shaped basihyal (*bh*). Probably the ventral piece is also a part of the basihyal. There are two pairs of hypohyals (*hh1*, *hh2*) and the posterior one in each shows a spinous projection posteriorly. There are three pairs of hypobranchs (*hbr1*, *hbr2*, *hbr3*) as in the Cyprinidae and three copulae (*c1*, *c2*, *c3*); the first two copulae are cruciform in *Homaloptera* and *Balitora* while in *Bhavana* and *Lepturichthys* (fig. 6b *c1*, *c2*) they are irregular in outline. The original cartilaginous reminiscences (*cep*) have been drawn in the figures wherever they were seen clearly.

There are two pairs of pharyngobranchs (figs. 6a, 6b *ph12*, *ph34*) connected together by cartilaginous epiphyses. These pharyngobranchs probably represent



TEXT FIG. 6a. The hyobranchial apparatus of *H. amphisquamata* W. & de B.
 ,, 6b. The hyobranchial apparatus of *Lepturichthys nicholsi* Hora.

the united first and second, and the third and fourth pharyngobranchs respectively. The fifth ceratobranch (*cbr5*) carries teeth which are regularly arranged.

The parathyoid is winglike and is attached anteriorly to the hypohyals by a pair of strong ligaments and the bone is thin and long posteriorly.

The Weberian Ossicles.—The gasbladder in the Homalopteridae is completely divided into two, and the two parts are, however, connected by a commissure posteriorly. The divided gasbladder and the posterior commissure are all encased in bone. In the structure and disposition of the gasbladder and the associated Weberian ossicles, the Homalopteridae resemble the Nemachilini (Cobitidae).

Projecting posteriorly from the commissural portion in *H. leonardi*,* there is a long posterior portion of the gasbladder reminiscent of the condition seen in the Cyprinidae or that in the cobitid *Nemachilus* (Chranilov, 1927). In *H. zollingeri* also there is a posterior bag which, however, is small (fig. 7f *pgb*) and oval in outline. In other species of *Homaloptera* as also in the other genera of the family examined by me, this posterior portion of the gasbladder is absent. Sagemehl (1891) did

* I have examined only one specimen and I do not know if this is an individual variation.

not refer to a posterior sac in *H. ocellata* and obviously it must have been absent in it.

In the Nemachilini (Cobitidae) according to Chranilov (1927) the first four vertebrae take part in the formation of the capsule and the Weberian ossicles. The ribs and transverse processes of the second vertebra form the anterior wall of the capsule; the remaining covering of the capsule is derived from the ossa and the transverse processes of the fourth vertebra. Laterally there is a big gap in the wall of the capsule where the gasbladder can be seen projecting. In the Cyprinidae there is generally an os suspensorium developed from the mesial aspect of the pleural ribs of the fourth vertebra. In the Nemachilini, on the other hand, the medial and lower wall of the capsule and also the wall of the transverse canal are formed by the ossa suspensoria (Chranilov, 1927). Dorsally the intercalarium and the V-shaped tripus are enclosed in the paravertebral space by the extension of the pedicel of the united second and third vertebrae. On the ventral aspect, there is a mesial depression in which the centrum of the united second and third vertebrae, that of the fourth vertebra, the transverse canal and a pair of anterior orifices through which the articulation of the mesial limb of the tripus with the united centrum of the second and third vertebrae is seen, are visible.

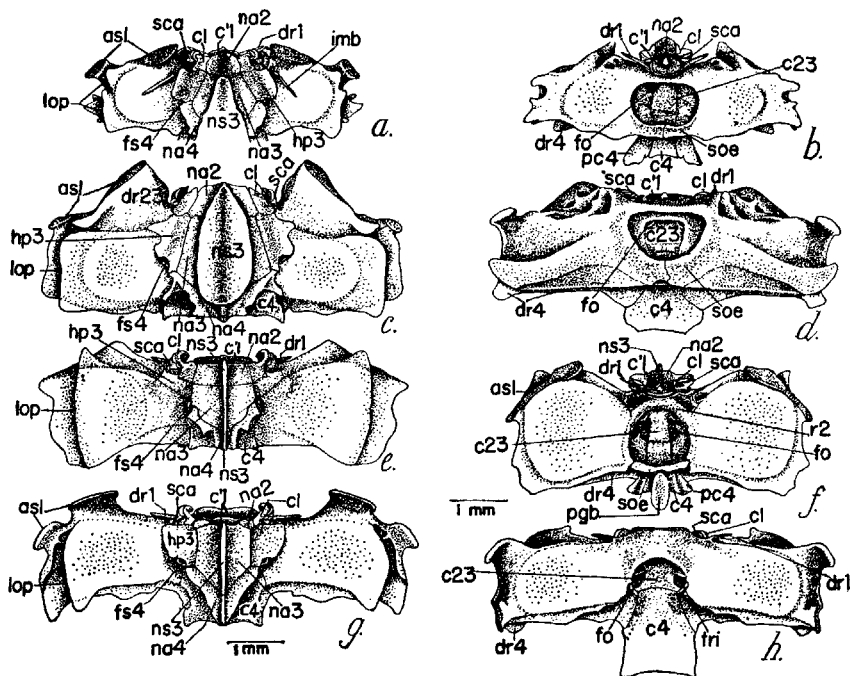
Watson (1939) who studied the development of the Weberian ossicles in the goldfish differed from the observations of the previous workers and I have also followed the nomenclature employed by Watson in my previous papers. He, however, did not study the development of a nemachiline or a homalopterid gasbladder where the latter possesses a capsule derived from vertebral parts. Nor have I been able to study the development of the capsule or ossicles but I am following the description of Chranilov (1927) with regard to the capsule and that of Watson with regard to the origin of the ossicles.

If Chranilov's (1927) description of the gasbladder and the Weberian ossicles is also applicable to the Homalopteridae, then in this family as in the Nemachilini, the first four vertebrae take part in the formation of the bony capsule and also the Weberian ossicles. The anterior part of the capsule is partly formed by the dorsal ribs* (the transverse processes of Chranilov) of the second vertebra and in front of this, the small centrum (figs. 7a, 7b, 7d-7g c'1) of the first vertebra with a pair of dorsal ribs (*dr1*) is seen. It is difficult to demarcate the contribution of the second pleural ribs towards capsule formation in the adult. In a form like *Psilorhynchus* (Ramaswami, 1952b) where the gasbladder is encased only anteriorly, I have pointed out that the capsule is probably derived from the dorsal ribs of the second vertebra. It is very likely that the large articulating processes in *Lepturichthys* (fig. 7c *asl*) forming the anterior wall of the gasbladder is also formed by the dorsal ribs of the second vertebra, probably with a contribution from the third (*dr23*). In the Homalopteridae, the second vertebral neural arch arising probably independently of the basidorsals, shows on either side the claustrum (figs. 7a, 7c, 7e, 7g *cl*); this arch does not show a neural spine in the genera examined by me and in *Lepturichthys* and *H. zollingeri*, the neural spine of the third vertebra projects anteriorly over this. The third pedicel shows a dorsolateral extension (*hp3*)† which covers the paravertebral space and also a prominent neural arch (*na3*), which like the second has arisen

* Watson (1939) described that the so-called 'transverse processes' were really in the nature of dorsal ribs of the piscine vertebra. The referee kindly pointed out to me that the 'transverse processes', in the Cyprinids at any rate, are the pleural ribs. Not having examined embryonic stages of the fish studied by me, I am unable to comment on this.

† On a comparison of the third vertebral elements of the Cyprinidae and Homalopteridae, it is noticed that the structure which I have called a dorsolateral extension of the third pedicel in the Homalopteridae has been labelled the neural arch in Cyprinidae by Chranilov (1927, fig. 4) and Berg (1940, fig. 154); the one I have labelled neural arch is considered by them as neural spine. Peculiarly the so-called third neural arch is not in line with those of second and fourth vertebrae. However, a study of the development of the anterior vertebrae would throw a lot of light on this.

probably independently. The third neural spine may be high and elevated as in *Homaloptera* or become broadened out as in *Balitora* and *Lepturichthys*. Posterior to the lateral extension of the third pedicel, there is an orifice for the fourth spinal nerve (*fs4*). The united centrum of the second and the third vertebrae (figs. 7*b*, 7*d*, 7*f*, 7*h* *c23*) is visible on the ventral aspect. In *H. zollingeri* on the ventral aspect, between the capsules and the united centrum, a ridge (fig. 7*f* *r2*) is noticed probably contributed by the dorsal ribs of the second vertebra, dorsally to which there is a passage; this is not noticed in the other examples studied by me. Further, the posterior transverse bony canal in which the commissural portion of the gasbladder lies, may be small (figs. 7*b*, 7*f* *soe*) or broad (fig. 7*d* *soe*) representing probably the united *ossa suspensoria* and the esophageal processes. It is important to note



TEXT FIG. 7*a*, 7*b*. Dorsal and ventral views respectively of the gasbladder capsule and the Weberian ossicles of *Balitora brucei* var. *mysorensis* Hora.
 ,, 7*c*, 7*d*. Dorsal and ventral views respectively of the gasbladder capsule and the Weberian ossicles of *Lepturichthys nicholsi* Hora.
 ,, 7*e*, 7*f*. Dorsal and ventral views respectively of the gasbladder capsule and the Weberian ossicles of *H. zollingeri* Bleeker.
 ,, 7*g*, 7*h*. Dorsal and ventral views respectively of the gasbladder capsule and the Weberian ossicles of *H. amphisquamata* W. & de B.

that the neural arches of the second and third vertebrae are separate as in *Labeo* (Sarbah, 1932), *Catostomidae* (Nelson, 1948) and *Gyrinocheilus* (Ramaswami, 1952*a*). The fourth pedicel in the Homalopteridae also shows a neural arch (figs. 7*a*, 7*c*, 7*e*, 7*g* *na4*) which may project as a neural spine (*Lepturichthys*, *H. amphisquamata*) or as in *Balitora*, may be covered over by the flattened spine of the third vertebra. The centrum of the fourth vertebra (figs. 7*b*–7*h* *c4*) is large and usually shows lateral winglike extensions (*pc4*). The remaining posterior part of the bony capsule of the gasbladder is formed by the dorsal ribs (*dr4*) and *ossa suspensoria* of the fourth vertebra.

The Weberian ossicles are also based on the nemachiline plan. The claustrum (figs. 7a, 7c, 7e, 7g cl) probably arising independently in the region of the first vertebra, articulates laterally with the reduced neural arch of the second vertebra. It shows a flat piece (corpus claustri) with which it comes in contact with the second neural arch and a cuplike (scutulum claustri) ventral portion which closes a similar cup of the scaphium enclosing the atrium sinus imparis.

The second of the series of the Weberian ossicles is the scaphium (figs. 7a, 7c, 7e, 7g sca). This is a modification of the basidorsal of the first vertebra according to Watson (1939) in the goldfish, and in the Homalopteridae, the scaphium is in the form of a funnel whose spout is short and solid. The funnel,—the concha stapedis, forms with the scutulum claustri a case for the atrium sinus imparis. Like that of *Nemachilus* (Chranilov, 1927), the scaphium shows only the processus articularis stapedis and also a region where the interosseous ligament (ligamentum incudo stapedium) is inserted. An orifice for the first spinal nerve seen in some cyprinids and the processus ascendens stapedis are not present in the homalopterid scaphium.

The intercalarium is a small ossification (sesamoid) in the ligament connecting the scaphium and the tripus. Following Watson (1939), it also probably arises in the Homalopteridae in the interosseous ligament. In the goldfish, according to Watson, the basidorsal of the second vertebra contributes that part of the ossicle which articulates with the second centrum. This latter part is absent in the Homalopteridae unlike the Psilorhynchidae (Ramaswami, 1952b) and the Cyprinidae.

The tripus is the last of the series and is derived from the basiventral of the third vertebra with the addition of a mesenchymatous mass according to Watson (1939). Whether the tripus arises similarly in the Homalopteridae, I am at present unable to say. The large tripus with the characteristic three processes seen in the Cyprinidae is reduced in the Homalopteridae as in Nemachilini. In the Homalopteridae, the posterior process is short and laterally disposed coming in contact with the gasbladder. The anterior and the articular processes of the tripus are cylindrical and the latter process comes in contact with the centrum of the third vertebra.

Having studied the Weberian apparatus in the Gyriinocheilidae and Psilorhynchidae, I am able to compare the apparatus in these three families. In *Gyriinocheilus* the triangular tripus is partially covered over by the horizontal extension of the third pedicel, the neural arches of the second and third vertebrae are independent and the pleural ribs of the second and fourth vertebrae are united, thus resembling the condition in the Catostomidae (Nelson, 1948); in the disposition of the other structures of the apparatus, *Gyriinocheilus* resembles the Cyprinidae. In *Psilorhynchus* (Ramaswami, 1952b), the gasbladder is incompletely divided and each part is covered partially anteriorly by a capsule formed by the dorsal ribs (transverse processes of most previous authors) of the second vertebra and this condition may be considered as the first step towards the modification of the bladder and its capsule noticed in the Homalopteridae. The tripus in *Psilorhynchus* (Ramaswami, 1952b), is still triangular and has not become triradiate as in the Nemachilini and Homalopteridae but is partially covered by the capsule.

The basiptyerygium.—Fang (1930) utilised the nature of the basiptyerygium in separating the 'Homalopterini' from 'Gastromyzonini'; according to him, the basiptyerygium of the Homalopteridae possesses a lateral foramen and dorsally at the region of the foramen, a modified rib gains attachment by means of a ligament. In *Balitora*, *Lepturichthys* and *Homaloptera* the basiptyerygium shows the lateral orifice but in *H. zollingeri* instead of a large orifice, there are two small foramina; in *Lepturichthys* and *H. amphisquamata* there is in addition a large anterior foramen also. The usefulness of this character can only be judged after examining a few more genera of Homalopteridae.

In the arrangement of the caudal fin skeleton of the Homalopteridae, the number of hypurals attached to the last vertebra varies. Ventrally to the urostyle

there may be six (*Balitora*, *H. amphisquamata*), seven (*H. zollingeri*, *H. rupicola*) or eight (*H. leonardi*) hypurals. I was not able to study the caudal fin of *Lepturichthys* as it was damaged.

DISCUSSION.

It was pointed out by Hora (1932) that among the Homalopteridae, the genus *Homaloptera* was very generalised and it formed the starting point for the evolution of the other genera of Homalopteridae.

In the structural organization of the skull, the four species of *Homaloptera* examined by me, viz., *rupicola*, *leonardi*, *zollingeri* and the much flattened *amphisquamata* show so much of difference that to start with a genus like *Homaloptera* to study the evolution of other homalopterid forms, it becomes extremely difficult. After studying the scale structure of homalopterid fishes, Law (1950) stated that 'the genus *Homaloptera* as constituted at present is probably a heterogeneous assemblage of forms'.

H. amphisquamata stands apart from the other Homalopteridae and also from its relatives like *zollingeri*, *rupicola* and *leonardi*. At least nine important features could be recounted in which *amphisquamata* differs from the other species. They are:

- (1) the prevomer is short and broad,
- (2) the lacrimojugal is not associated closely with the sensory canal bones,
- (3) the lateral ethmoid processes are short and blunt,
- (4) the median articulation of the palatine is only with the elongated second preethmoid,
- (5) the median rostral has two lateral projections for the maxillary ligaments,
- (6) the anterior part of the parasphenoid is very broad,
- (7) the optic foramen is between the orbitosphenoid and pleurosphenoid,
- (8) the subtemporal fossa is a depression in the pterotic only, a feature which it shares with *rupicola*,
- (9) the prepalatine articular facet of the palatine is long,
- (10) the palatine does not show a lacrimojugal facet, a feature also shared by *rupicola*.

In the ethmoid region, the broad supraethmoid portion of the ethmoid is firmly articulated with the frontals, a feature also noticed in the Cyprinidae. In *H. zollingeri* there is a peculiar depression in the anterior end of the supraethmoid whose significance, it is difficult to understand. In *H. rupicola*, a frontoparietal fontanel is noticed. In *Psilorhynchus** (Ramaswami, 1952b), a similar fontanel is noticed in between the supraethmoid and the frontals; in the Cobitidae and a few genera of Gastromyzonidae (*Vanmanenia*, *Crossostoma*, *Ghaniopsis*) there is a frontoparietal fontanel. Though Sagemehl (1891) considered the occurrence of the frontoparietal fontanel as without any significance, the hillstream and the sand-burrowing forms and other loaches may be having them for serving some physiological purpose.

The median process of the supraethmoid is excessively long in *H. amphisquamata*; in *Psilorhynchus* (Ramaswami, 1952b) a similar elongated process is noticed.

The maxilla of the Homalopteridae shows a very prominent dorsal premaxillary process; the rostral process of the maxilla almost stretches at right angle to the dorsal process and therefore, the fork in which the premaxilla is held is very wide.

* In the *Psilorhynchus* specimens sent to me from Lucknow by Dr. B. S. Kaushiva, I notice two fontanels; one between the supraethmoid and the frontals and the other between the frontals, parietals and supraoccipital which latter, I have called the frontoparietal fontanel.

The rostral process of the premaxilla is very long in *H. amphisquamata*, *Balitora* and *Lepturichthys* while in *H. zollingeri*, it is very short. In all the genera the tips of the rostral processes come in contact with the median rostral or extend slightly beyond but in *H. rupicola*, the tips rest on the supraethmoid.

The prepalatine and the first preethmoid are prominent bones; in *H. zollingeri* and *Balitora* the prepalatine is short. The prepalatine may articulate directly with a facet on the posterior face of the maxilla laterally to the articulation with the first preethmoid as in *Homaloptera* and *Lepturichthys* while in *Balitora* there is a small sesamoid bone intercalated in between. It was pointed out that in order to promote greater movability of the ethmoid region, these hillstream forms developed a second preethmoid with which anteriorly the first preethmoid articulated and laterally, the palatine; in *H. amphisquamata* the second preethmoid is so large that the palatine does not articulate with the ethmoid at all. In *H. rupicola* the lacrimojugal process of the palatine comes in contact with the lacrimojugal and at this region the prepalatine articulates; there is no separate articular facet for it.

In the Homalopteridae there is a large lacrimojugal with the sensory canal excluded from it; Hora (1932) called it a preorbital bone. It is difficult to say if this composite bone is really formed by the fusion of a lacrimal and a jugal since in those fossil forms where a lacrimojugal is described (Moy-Thomas, 1937), it always leads the suborbital sensory canal. While in the cyprinid examples and in several other genera also, the short lacrimal is the anteriormost of the suborbital series of bones, always canalculated and leading the suborbital sensory canal, in the Homalopteridae the sensory canal ossicles are independent and they may be closely associated with the lacrimojugal as in *Balitora brucei* and *H. zollingeri* or may lie separately. Moreover, the size of the lacrimojugal in the Homalopteridae is larger than that in the other subfamilies and therefore, I propose to call it a lacrimojugal as I have already done in my previous paper (Ramaswami, 1948) for describing the bone following Moy-Thomas (1937). At any rate, associated with this enlarged lacrimojugal, as already said, there are sensory canal ossicles. In *H. zollingeri*, *H. rupicola* and *H. leonardi* three ossicles are noticeable ventrally to the lacrimojugal while in *amphisquamata*, there are a few by the side of the lacrimojugal and an enlarged one extending in front of it. In *Balitora* there is one in front of the lacrimojugal associated with a triradiate ossicle. Probably the bony ossicle in front of the lacrimojugal or just below anteriorly to it represents a rostral (Moy-Thomas, 1937). Sometimes when the lacrimal itself accommodates the sensory canal in it as in *Psilorhynchus* (Ramaswami, 1952b), it may be possible to call the large one posterior to it a jugal, but in the Homalopteridae, where the sensory canal ossicles are independent of the 'lacrimal', nomenclature of the former becomes difficult. I have therefore, cautiously labelled the suborbital ossicles by the ordinals 1, 2, 3 etc.

The prevomer may be narrow with a fairly long posterior process as in *H. zollingeri*, *H. rupicola*, *H. leonardi*, *B. brucei*, *B. brucei* var. *mysorensis*, and *Lepturichthys* while in *H. amphisquamata* the prevomer is broad with a short posterior process. In *Balitora* only, on the dorsal aspect, an anterior extension of the prevomer is noticed while in all other genera the prevomer does not extend anteriorly. In *Gyrinocheilus* (Ramaswami, 1952a), the prevomer anteriorly gives rise to two prominent processes with an indentation in between while the posterior short blunt process is like that in *H. amphisquamata*. In *Psilorhynchus* (Ramaswami, 1952b), the bone extends in front and posteriorly shows a long slender process; in *Parapsilorhynchus* (Ramaswami, 1952b) the bone is broad as in *H. amphisquamata* and shows only a short process. A similar short posterior process has been observed by me in a large number of cyprinids studied by me.

The lateral ethmoid shows a longish lacrimojugal process in *Balitora*, *Bhavana* and *Lepturichthys* and a similar shorter process posteriorly. The anterior process

obviously supports the lacrimojugal. In *Homaloptera* peculiarly the lateral processes are short resembling those in *Psilorhynchus* and *Parapsilorhynchus* (Ramaswami, 1952b) and the other cyprinids studied by me. In *Gyrinocheilus* (Ramaswami, 1952a) the processes are fairly well developed.

In the orbitotemporal region the frontals are generally broad and on either side may show the supraorbital as in *Balitora*, *Lepturichthys*, *H. zollingeri*, *H. rupicola* while in *H. amphisqueamata* the supraorbitals are poorly developed. In *Psilorhynchus* (Ramaswami, 1952b) the supraorbitals are absent.

Ventrally there is an exceedingly interesting peculiarity in the orbitotemporal region. In *Balitora*, *Lepturichthys* and *H. zollingeri* the orbitosphenoid is fairly large and between it and the small posterior pleurosphenoid and the parasphenoid, the optic foramen is noticed; in *H. amphisqueamata* the orbito- and pleuro-sphenoids are small and they include in between them the optic foramen, the parasphenoid being kept out. In *Gyrinocheilus* (Ramaswami, 1952a) it was noticed that the lateral ethmoid also extended posteriorly to bound the optic foramen; in *Psilorhynchus* and *Parapsilorhynchus* (Ramaswami, 1952b) the orbitosphenoid, pleurosphenoid and parasphenoid bound the optic foramen.

In the auditory region, the homalopterid skull shows certain peculiarities. In *Balitora* and *Lepturichthys* the dorsal aspect of the skull discloses a large part of the sphenotic and a triradiate sensory canal bone connects the supraorbital and posteriorly the temporal canal as in *Balitora*, or as in *Lepturichthys* there are two independent ossicles connecting the canals; there is also an independent sensory canal ossicle sitting on the sphenotic posteriorly in *Balitora*. In *H. amphisqueamata* and *H. zollingeri* the triradiate ossicle establishes connexion with the supraorbital by means of an independent ossicle sitting on the sphenotic; in *H. rupicola* an independent ossicle is absent.

In *Balitora*, *Lepturichthys* and *H. amphisqueamata* connecting the temporal canal with the supraoccipital there are two sensory canal ossicles, and connecting the former with the lateral line canal, there is an ossicle. In my previous paper (Ramaswami, 1948) I described these three ossicles as anterior, posterior and lateral extrascapulars. The large mesial one corresponds with the supratemporal of the cyprinids which nomenclature I am now using; the posterior one is the posttemporal which connects the supracleithrum with the skull and the lateral one is the lateral extrascapular leading the temporal canal to the lateral line. In the Cyprinidae, the posttemporal is generally connected to the epiotic and the pterotic regions of the skull by two processes of the posttemporal.

In *H. zollingeri* the supratemporal is absent and the lateral extrascapular and the posttemporal appear to be united into a single U-shaped canal ossicle whose lateral limb connects the lateral line canal while the mesial limb sits on the epiotic.

There is a well formed subtemporal fossa on the ventral aspect seen accommodated between the exoccipital, the prootic and the pterotic in *Balitora*, *Lepturichthys* and *H. zollingeri*; the epiotic also forms the roof of it. However, in *H. amphisqueamata* the subtemporal fossa is seen as a depression in the pterotic, bone only. In *Gyrinocheilus* (Ramaswami, 1952a) there is a shallow subtemporal fossa; laterally there is also a lateral temporal fossa so far noticed only in this example and the Cobitidae by me. In *Psilorhynchus* (Ramaswami, 1952b) also there is a shallow subtemporal fossa.

In the Cyprinidae and the Psilorhynchidae the basioccipital shows a prominent pharyngeal process ventrally to the condyle through which the dorsal aorta passes and the process is covered by a large horny pad; in Gyrinocheilidae, from the posterior portion of the basioccipital, two processes are present which however, do not completely enclose the aorta. In the Homalopteridae blunt projections are noticed from the posterior portion of the basioccipital in *Balitora* and *Lepturichthys*; in *Homaloptera* even these blunt processes are wanting; the absence of the horny pad has already been recorded by Regan (1911).

In the upper jaw the opercular shows prominently the opercular arm and the auricular processes; the sensory canal noticed in the opercular of some Cyprinidae is absent in the Homalopteridae. In the hyobranchial apparatus the basihyal consists of two parts: a dorsal Y-shaped portion resting on a rectangular one. There are uniformly three copulae, three hypobranchs and two pharyngobranchs as in the Cyprinidae. The lower jaw shows peculiarly one or two sesamoid angulars on the mesial aspect which are also seen in the nemachiline genera examined by me. In *Gyrinocheilus* (Ramaswami, 1952a) there are three pharyngobranchs and in *Psilorhynchus* (Ramaswami, 1952b) there are only two.

The palatine normally articulates ventrally with the second preethmoid and dorsally the ethmopalatine projection is connected with the median process of the ethmoid by a ligament. Anterolaterally *Balitora*, *Lepturichthys* and *H. zollingeri* show a prominent process towards the lacrimojugal. Posteriorly the entopterygoid articulates with the palatine.

The Weberian apparatus of the Homalopteridae resembles that seen in the Nemachilini and to a limited extent the Psilorhynchidae. The tripus in the Homalopteridae is modified into a Y-shaped structure with one of the shorter limbs of the Y in contact with the ligament and the other articulating with the fused third vertebral centrum. The dorsal ribs of the second and fourth vertebrae are so modified as to form a capsule for the divided gasbladder, the two parts of the latter being connected by a commissure. Possibly the pleural ribs (ossa suspensoria) of the fourth vertebra also take part in the formation of the capsule wall ventrally as in the Nemachilini (Chraniiov, 1927). With regard to the large supraclithral articular facet of the gasbladder capsule in *Lepturichthys*, I have hazarded that it may have been formed by the dorsal ribs of the second and third vertebrae, though the third vertebra is usually described as having no parapophyses or ribs. In the Cyprinidae the Weberian ossicles are not enclosed by the extensions of the neural arches.

The Homalopteridae are characterised as fishes possessing no posterior portion of the gasbladder. However, I have noticed the occurrence of a short posterior one in *H. zollingeri* and a long one in *H. leonardi*. In a few Gastromyzonid examples like *Beaufortia*, *Protomyzon* and *Crossostoma*, I have also noticed the occurrence of a small posterior portion of the gasbladder.

A comparative study of the skull structure of the Homalopterid genera discloses certain interesting points about their relationships. The Homalopteridae show a number of Cyprinid features which are as follows:

- (1) the firmly articulated supraethmoid and frontals,
- (2) the maxillae and the premaxillae show the characteristic cyprinid features, viz., the dorsal premaxillary process of maxilla, the ventral rostral process, and the rostral process of the premaxilla,
- (3) the palatine articulates with the ethmoid and the preethmoid,
- (4) the orbitosphenoid, the pleurosphenoid and the parasphenoid enclose the optic foramen generally,
- (5) the occurrence of only four otic bones, viz., the prootic, the pterotic, the sphenotic, and the epiotic and the absence of the opisthotic,
- (6) the prootic, the pterotic and the exoccipital accommodate the subtemporal fossa generally,
- (7) the occurrence of three copulae, three hypobranchs and two pharyngobranchs.

The Homalopteridae (*sen. stric.*) having taken their origin from an ancestral cyprinid stock evolved in a different environment altogether; the genera adapted themselves to fast running brooks and as a result, exhibit certain characteristic features:

- (1) Like the head of loaches living in crevices, etc., the ethmoid region of the Homalopteridae also developed the preethmoids and the prepalatines to obtain greater freedom of movement of the snout but the ethmoid remained unaffected,
- (2) The lacrimal, bereft of the sensory canal, increased in size probably uniting with a posterior jugal (also without a sensory canal in it) to support the snout as a lacrimojugal and with a rostral in front,
- (3) The lateral ethmoid developed laterally anterior and posterior processes, the former supporting the lacrimojugal,
- (4) The firm articulation of the supracleithrum with the side of the gasbladder capsule has already been noted by previous workers (Hora, 1932).

Associated with the characters enumerated above, there are others which distinguish the Homalopteridae from the Cyprinidae: they are,

- (1) In the upper jaw, the opercular is elongated in the linear axis of the animal, the preopercular is reduced in size and the posterior process of the quadrate is large. In addition, generally a set of sensory canal ossicles is noticed leading to the mandible.
- (2) In the lower jaw, the sensory canal (?) is peculiarly noticed on the mesial side in the angular and not on the lateral side as in the Cyprinidae.
- (3) The divided gasbladder is enclosed in a capsule which is formed by the dorsal ribs of the second and fourth vertebrae; probably the pleural ribs also take part in it. The tripus is completely modified in its shape; it is Y-shaped with one of its anterior limbs short which is connected with the interosseous ligament. The other limb articulates with the centrum of the fused third vertebra and the short posterior portion of the Y-shaped tripus comes in contact with the gasbladder.
- (4) The basipterygium differs in its shape from that in the Cyprinidae. The occurrence of a lateral foramen in the basipterygium which is considered as a diagnostic feature of the Homalopteridae by Fang is also noticed by me; in *H. zollingeri*, however, there are two small foramina instead of a large one.

Sagemehl (1891) who studied the cyprinid skull in great detail pointed out that in the possession of the subtemporal fossa and the 'labyrinthische', *Homaloptera*, the only genus which he studied, resembled Barbidae and at the same time pointed out also its cobitid affinities in possessing six barbels, in the bones of the upper jaw, of the preopercular, and of the gasbladder. Berg (1947) as already pointed out, included the Homalopteridae comprising the Homalopterini and Gastromyzonini under the suborder Cyprinoidei (Eventognathi).

I have studied a number of genera of Cobitidae and I do agree with Sagemehl that the Homalopteridae resemble the Cobitidae, if by Cobitidae he meant the nemachiline subdivision. This affinity according to me is purely due to convergence and is of little phylogenetic significance. For, if we assume that nemachiline ancestors gave rise to the homalopterid forms, it becomes difficult to explain how the slender supraethmoid part of the ethmoid of the former could have become so broad in the Homalopteridae where the said bone is uniformly broad as in the Cyprinidae; how the very shallow subtemporal fossa of the Nemachilini could have given rise to the deep subtemporal fossa of the Homalopteridae like that of the Cyprinidae; how the supraorbital which is absent in the Cobitidae could have reappeared in the Homalopteridae as noticed in the cyprinids. While there are four copulae in the Nemachilini, there are only three in the Homalopteridae and Cyprinidae. Therefore, I propose to derive the Homalopteridae from a remote

cyprinid ancestor, and the cobitids which also took their origin from a similar cobitid ancestor moved on parallelly with the Homalopteridae.

It has not been possible for me to find out any cyprinid genus which may have given rise to the Homalopteridae. But a study of the cyprinid, cobitid and homalopterid skull leaves no doubt that the Homalopteridae evolved from a remote cyprinid-like ancestor and moved parallelly with the cobitids. It may not be out of place to point out here that the Psilorhynchidae also appear to be evolving to show homalopterid affinities. That the Gastromyzonidae show a number of features in which they resemble the Homalopteridae is undoubted but the former seem to have taken their origin separately altogether and therefore, there is ample justification for raising the two subfamilies Homalopterini and Gastromyzonini to the rank of families.

SUMMARY.

1. The four species of *Homaloptera* examined show great structural variations that it is not possible to trace the evolution of the Homalopteridae starting from a genus like *Homaloptera*.

2. Laterally to the ethmoid and prevomer, a second preethmoid is developed in the Homalopteridae and the elongated first preethmoid articulates with this. The development of this bone is probably to give greater mobility to the jaws.

3. The Homalopteridae show a prominent lacrimojugal and this enlargement is obviously an adaptation to torrential life.

4. The subtemporal fossa is large and is accommodated by the exoccipital, prootic and pterotic; the epiotic also roofs it. In *H. amphisquamata* the fossa is noticed only in the pterotic.

5. The typical pharyngeal processes through which the dorsal aorta passes are not noticed in the Homalopteridae.

6. The Weberian apparatus and the gasbladder resemble the Nemachiline ones. The dorsal ribs of the second and fourth vertebrae mostly form the gasbladder capsule and the two halves are connected by a posterior commissure; it is difficult to make out the contribution of the pleural ribs towards capsule formation. Peculiarly a posterior portion of the gasbladder is also seen in *H. leonardi* and *H. zollingeri*.

7. The Homalopteridae resemble the Cyprinidae in many features but differ from them in possessing an elongated opercular bone, mesial sensory canal in the lower jaw, the laterally divided gasbladder enclosed in bone and in the structure of the basipterygoids.

8. It is argued that the Homalopteridae took their origin from a cyprinid-like ancestral stock and evolved parallelly with the Cyprinidae; the Cobitidae which arose from a Cobitid stock also show many similarities.

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LETTERING.

<i>an</i>	..	angular;	<i>cbr1</i>	..	} ceratobranchials 1-5;
<i>apa</i>	..	facet of the entopterygoid for articulation with palatine;	<i>cbr2</i>	..	
<i>apv</i>	..	anterior projection of prevomer;	<i>cbr3</i>	..	
<i>aq</i>	..	articular facet of quadrate with lower jaw;	<i>cbr4</i>	..	
<i>aq'</i>	..	articular facet of the lower jaw with quadrate;	<i>cbr5</i>	..	
<i>asl</i>	..	articular facet of the capsule with the supracleithrum;	<i>cep</i>	..	cartilaginous epiphysis;
<i>aup</i>	..	auricular process;	<i>chy</i>	..	ceratohyal;
<i>bh</i>	..	basihyal;	<i>cl</i>	..	claustrum;
<i>bh'</i>	..	ventral piece of basihyal;	<i>con</i>	..	condyle;
<i>bo</i>	..	basioccipital;	<i>de</i>	..	dentary;
<i>cl-<i>c3</i></i>	..	copulae 1, 2, 3;	<i>dpm</i>	..	dorsal premaxillary process of maxilla;
<i>c3</i>	..	ossification posterior to copula 3;	<i>dr1</i>	..	} dorsal rib of vertebrae 1 and 4;
<i>c' 1</i>	..	} centrum of vertebra 1 and 4;	<i>dr4</i>	..	
<i>c' 4</i>	..		<i>dr23</i>	..	
<i>c23</i>	..	united centrum of vertebrae 2 and 3;	<i>ebr1</i>	..	} epibranchial 1 and 4;
			<i>ebr4</i>	..	
			<i>ecp</i>	..	
			<i>ehy</i>	..	epihyal;

<i>eo</i>	..	exoccipital;	<i>op2</i>	..	outline of second preethmoid;
<i>enp</i>	..	articular facet of palatine with entopterygoid;	<i>os</i>	..	orbitosphenoid;
<i>epi</i>	..	epiotic;	<i>ose</i>	..	outline of supraethmoid;
<i>epp</i>	..	ethmoid process of palatine;	<i>ost</i>	..	outline of supratemporal;
<i>ept</i>	..	entopterygoid;	<i>p</i>	..	anteromedian process of supraethmoid;
<i>et</i>	..	ethmoid;	<i>pa</i>	..	parietal;
<i>fac</i>	..	an articular facet on the ventral aspect of maxilla;	<i>pa'</i>	..	sensory canal passage in the angular;
<i>fo</i>	..	foramen in gasbladder capsule;	<i>pal</i>	..	palatine;
<i>fo4</i>	..	foramen for the 4th spinal nerve;	<i>pah</i>	..	articular facet for the hyomandibula in the pterotic;
<i>fpf</i>	..	frontoparietal fontanel;	<i>pas</i>	..	parasphenoid;
<i>fr</i>	..	frontal;	<i>pb12</i>	..	united pharyngobranchs 1 and 2;
<i>g</i>	..	gap in the supraethmoid;	<i>pb34</i>	..	united pharyngobranchs 3 and 4;
<i>hh1</i>	..	hypohyal 1;	<i>pc4</i>	..	winglike projection from the fourth centrum;
<i>hh2</i>	..	hypohyal 2;	<i>pet</i>	..	first preethmoid;
<i>hbr1</i>	..	} hypobranchs 1, 2, 3;	<i>pet2</i>	..	second preethmoid
<i>hbr2</i>	..		<i>pgb</i>	..	posterior gasbladder;
<i>hbr3</i>	..		<i>ph2</i>	..	process from the posterior hypohyal;
<i>hp3</i>	..	horizontal process (neural arch ?) from the third vertebral pedicel;	<i>php</i>	..	lateral projection from the basioccipital;
<i>hy</i>	..	hyomandibula;	<i>phy</i>	..	articular head of hyomandibula with the pterotic facet;
<i>imb</i>	..	intermuscular bone;	<i>pill</i>	..	maxillary process for the ligament of the adductor mandibulae muscle;
<i>iop</i>	..	interopercular;	<i>pls</i>	..	pleurosphenoid;
<i>ios</i>	..	anterior independent sensory canal ossicle;	<i>pmp</i>	..	posterior process of metapterygoid;
<i>ios'</i>	..	posterior independent sensory canal ossicle;	<i>pmx</i>	..	premaxilla;
<i>jj</i>	..	jugular foramen;	<i>pmy</i>	..	posterior myodome;
<i>les</i>	..	lateral extrascapular;	<i>pop</i>	..	preopercular;
<i>let</i>	..	lateral ethmoid;	<i>ppa</i>	..	prepalatine;
<i>lj</i>	..	lacrimojugal;	<i>ppm</i>	..	process of maxilla for articulation of the prepalatine;
<i>lje</i>	..	lacrimojugal process of lateral ethmoid;	<i>ppv</i>	..	posterior process of prevomer;
<i>llm</i>	..	lateral limb of maxilla;	<i>pq</i>	..	posterior process of quadrate;
<i>lp</i>	..	lateral limb of premaxilla;	<i>pr</i>	..	process of the maxilla;
<i>lop</i>	..	lateral opening of gasbladder capsule;	<i>pro</i>	..	prootic;
<i>lpa</i>	..	lacrimojugal process of palatine;	<i>prp</i>	..	palatine facet for articulation of prepalatine;
<i>lpt</i>	..	united lateral extrascapular and posttemporal;	<i>pse</i>	..	posterior semicircular canal;
<i>lsc</i>	..	lateral semicircular canal;	<i>pt</i>	..	posttemporal;
<i>max</i>	..	maxilla;	<i>pte</i>	..	pterotic;
<i>mp</i>	..	metapterygoid;	<i>q</i>	..	quadrate;
<i>mr</i>	..	median rostral;	<i>r2</i>	..	ridge formed on the ventral aspect of the second vertebra (its dorsal rib ?);
<i>n</i>	..	nasal;	<i>ra</i>	..	retroarticular;
<i>na2</i>	..	} neural arch 2, 3 and 4;	<i>ri</i>	..	ridge in the metapterygoid;
<i>na3</i>	..		<i>ri'</i>	..	ridge in the entopterygoid;
<i>na4</i>	..		<i>ros</i>	..	rostral;
<i>ns3</i>	..	neural spine 3	<i>rpm</i>	..	rostral process of maxilla;
<i>oa</i>	..	opercular arm;	<i>rpp</i>	..	rostral process of premaxilla;
<i>oan</i>	..	outline of angular;	<i>sa</i>	..	sesamoid angular;
<i>oc</i>	..	occipital sensory canal;	<i>sah</i>	..	articular facet in the sphenotic;
<i>oeb1</i>	..	} outline of the epibranchs, 1, 2, 3 and 4;	<i>sb</i>	..	sesamoid bone;
<i>oeb2</i>	..		<i>sc</i>	..	sensory canal ossicle;
<i>oeb3</i>	..		<i>sca</i>	..	scaphium;
<i>oeb4</i>	..		<i>scl</i>	..	supraclithrum;
<i>oec</i>	..	outline of ectopterygoid;	<i>se</i>	..	supraethmoid;
<i>oep</i>	..	outline of epiotic;	<i>shy</i>	..	hyomandibular facet for articulation with the sphenotic;
<i>oet</i>	..	outline of ethmoid;			
<i>of</i>	..	optic foramen;			
<i>olm</i>	..	outline of lateral limb of maxilla;			
<i>on</i>	..	outline of nasal;			
<i>op</i>	..	operculum;			
<i>opa</i>	..	outline of prepalatine;			
<i>opet</i>	..	outline of first preethmoid;			
<i>opl</i>	..	outline of palatine;			
<i>opt</i>	..	outline of pterotic;			
<i>opt'</i>	..	outline of posttemporal;			

<i>sm</i>	..	symphysis meckelii;	<i>sp</i>	..	sphenotic;
<i>so</i>	..	supraoccipital;	<i>spr</i>	..	sphenotic process;
<i>sol</i>	..	} suborbital sensory canal ossicles	<i>ste</i>	..	supratemporal;
<i>so8</i>	..		1-8;	<i>stf</i>	..
<i>soc</i>	..	suparorbital sensory canal;	<i>suo</i>	..	supraorbital;
<i>soe</i>	..	united suspensorial and esophageal processes of fourth vertebra;	<i>sup</i>	..	supraoccipital process;
<i>soo</i>	..	suborbital sensory canal ossicles;	<i>sy</i>	..	symplectic;
<i>sop</i>	..	subopercular;	<i>tc</i>	..	temporal canal;
			<i>tf</i>	..	trigemino-facialis foramen;
			<i>tri</i>	..	tripus.