

# SKELTON OF CYPRINOID FISHES IN RELATION TO PHYLOGENETIC STUDIES.

## IV. THE SKULL AND OTHER SKELETAL STRUCTURES OF GASTROMYZONID FISHES.

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### INTRODUCTION.

In a previous paper (Ramaswami, 1948), I described the structure of the skull of *Gastromyzon* Günther and compared it with that in a few genera of Homalopteridae that I had examined. Subsequently Dr. S. L. Hora, Director, Zoological Survey of India, Calcutta, made available to me a number of Homalopterid and Gastromyzonid genera for elucidating, from the view-point of skeletal anatomy, their origin and interrelationships.

According to Fang (1935), the Gastromyzonids are a polyphyletic assemblage of individuals, divisible into two groups, viz., the Crossostoma-association and the Gastromyzon-association. Of these two, the Crossostomid fishes derived from 'Nemachiloid ancestral stocks' evolved in three different lines. Fang also traced their interrelationships.

In describing the Homalopterid fishes, Hora (1932) noted that the Homalopteridae (= Homalopterinae, Hora, 1932) evolved from some Cyprinid ancestor while the Gastromyzonidae (= Gastromyzoninae, Hora, 1932) arose from some Cobitid stock and that the members of the Homalopterinae and Gastromyzoninae were probably polyphyletic, resembling one another only superficially due to similarity in life habits. Later Hora (1950), stressing the necessity for treating the two subfamilies independently, discussed in a thought-provoking paper (Hora, MS.) the polyphyletic origin of the Gastromyzonid fishes of the mainland of Asia and Borneo, a draft of which he very kindly made available to me. It is noticed that in the paper referred to above, Hora has taken examples all of which belong to the Gastromyzon-association of Fang (1935) and none to the Crossostoma-association.

Berg (1947), as recorded in my previous paper (Ramaswami, 1951c, in press), treated both the subfamilies Homalopterini and Gastromyzonini under the same family Homalopteridae.

Law (1950), after studying the scale structure in both the Crossostoma-association and Gastromyzon-association, came to the conclusion that specialisation had taken place independently among the genera. Further, according to him, the scales of *Gastromyzon* in general were of the Cobitid type and that the scales of *Beaufortia* differed from those of all the other Gastromyzonid fishes.

Having studied the skeletal structure of a number of Homalopterid genera (Ramaswami, 1951c, in press), I have been able to point out that a few skeletal structures supported the Cyprinid affiliations of the Homalopteridae. In this paper, I propose to examine the Gastromyzonid skeleton to see if it throws any light on the origin and relationship of the mainland (China) and of the Bornean genera.

## MATERIAL.

The following Gastromyzonid genera have been studied by me:

## A. Bornean forms—

*Glaniopsis hanitshi* Boulenger; *Protomyzon whiteheadi* (Vaillant); *Gastromyzon borneensis* Günther.

## B. Mainland or Chinese forms—

*Vanmanenia caldwelli* (Nichols); *Crossostoma davidi* Sauvage; *Pseudogastromyzon fasciatus* (Sauvage); *Beaufortia levertti* (Nichols and Pope).

This classification does not give us an idea of the *Crossostoma*- and *Gastromyzon*-associations created by Fang (1935). Under the latter, the first group includes *Annamia* Hora, *Parhomaloptera* Vaillant, *Linparhomaloptera* Fang, *Vanmanenia* Hora, *Praeformosania* Fang, *Formosania* Oshima and *Crossostoma* Sauvage. The second group comprises *Sewellia* Hora, *Paraprotomyzon* Pellegrin and Fang, *Pseudogastromyzon* Nichols, *Protomyzon* Hora, *Neogastromyzon* Popta, *Gastromyzon* Günther and *Beaufortia* Hora. This grouping is entirely based on the fact whether the gill opening extends to the ventral aspect in front of the pectoral fins (*Crossostomid* group) or is restricted above the bases of the pectoral fins (*Gastromyzonid* group). It must be noted that *Glaniopsis* is not included under either of these groupings; of the Bornean forms, it is also clear that I have examined examples belonging to both the groups. One peculiarity of the distribution of these forms is that the mainland forms are not represented on the island of Borneo and *vice versa*. For purposes of comparison, I have also studied the skeleton of the loaches *Nemachilus dayi* Hora and *Nemachilichthys ruppelli* (Sykes) [*Nemachilini*: *Cobitidae*].

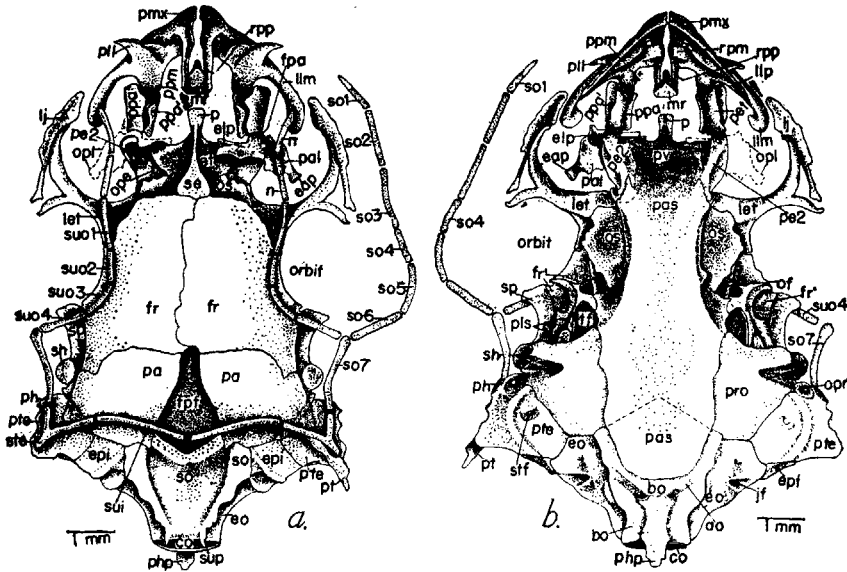
## OBSERVATIONS.

I shall not describe the Bornean and Chinese forms separately but shall take them collectively and give a comparative account of the osteological features.

*The ethmoid region.*—In the Gastromyzonid genera examined, *Glaniopsis* (fig. 1a), *Protomyzon* (fig. 2a) and *Vanmanenia* (fig. 3a) show the firmly articulated supraethmoid part (*se*) which, however, is not very broad; in *Glaniopsis* the supraethmoid resembles that in *Nemachilus* (*Cobitidae*). While the median prolongation of the supraethmoid (*p*) is short in *Protomyzon* (fig. 2a) and *Vanmanenia* (fig. 3a), it is long in *Glaniopsis* (figs. 1a, 1b) as in *Nemachilus*. In *Beaufortia* (figs. 4a, 4b), *Pseudogastromyzon* (figs. 5a, 5b), *Crossostoma* (figs. 6a, 6b) and *Gastromyzon*, the supraethmoid part (*se*) is broad (broader than in the foregoing genera) and the median anterior projection (*p*) is short. Laterally to the supraethmoid part in *Protomyzon* (fig. 2a) and *Vanmanenia* (fig. 3a), there is the ethmoid (*et*) extension noticed; in *Glaniopsis* (fig. 1a), however, this ethmoid extension (*et*) is large and winglike. In *Nemachilus*, the lateral ethmoid extension is not noticed on the dorsal side of the skull. Ventrally the ethmoid (*et*) is visible in *Protomyzon* (fig. 2b) and *Vanmanenia* (fig. 3b), on the lateral aspect of which the second preethmoid (*pe2*) articulates. In *Glaniopsis* (fig. 1b) a small portion of the ethmoid, with the large supraethmoid projection (*p*), is noticed since this region is covered by the asymmetrical prevomer (*pv*) and laterally to the ethmoid, the large second preethmoid (*pe2*) articulates. In *Nemachilus* the ethmoid is not visible ventrally since a large preethmoid covers it.

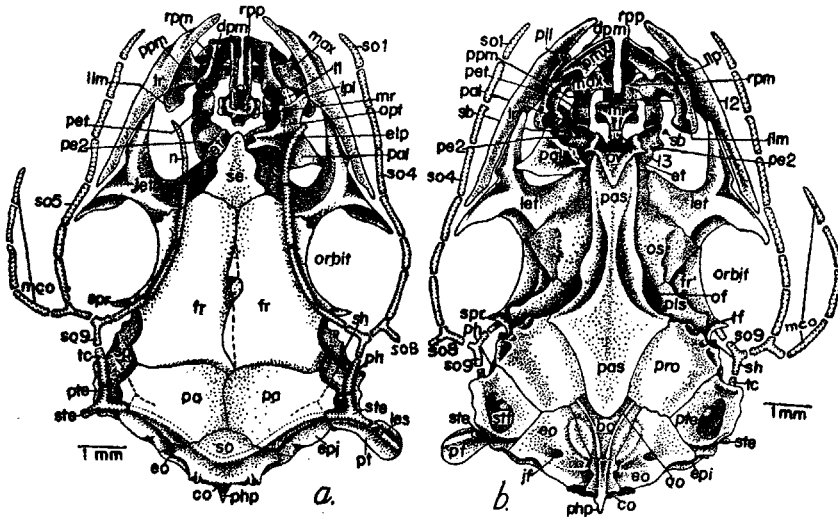
In *Beaufortia* (fig. 4a), *Pseudogastromyzon* (fig. 5a), *Crossostoma* (fig. 6a) and *Gastromyzon* (Ramaswami, 1948), in front of the supraethmoid and also laterally to it in *Beaufortia* (fig. 4a) and *Gastromyzon*, the ethmoid (*et*) part is visible dorsally;

ventrally also in the above genera, posteriorly to the large second preethmoid, a small portion of the ethmoid (fig. 4b et) is visible.



TEXT-FIGS. 1a & 1b. Dorsal and ventral views respectively of the skull of *Glaniopsis hamitshi* Boulenger.

Articulating anterolaterally with the ethmoid is the preethmoid bone (figs. 1a-6a, 1b-6b pe2). I label this as the second preethmoid as there is another one in front of this intercalated between it and the maxilla, which is the first preethmoid (pe1)



TEXT-FIGS. 2a & 2b. Dorsal and ventral views respectively of the skull of *Protomyzon whiteheadi* (Vaillant).

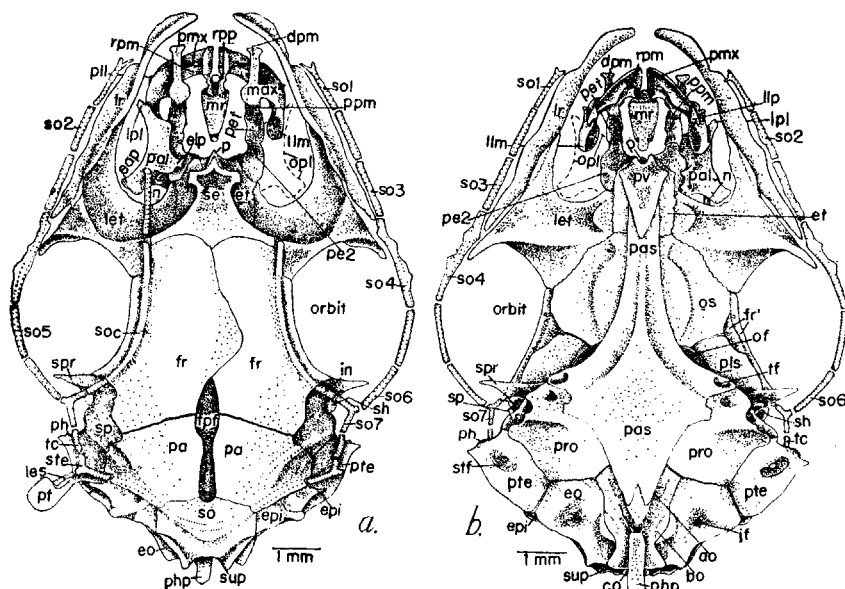
in all the genera examined by me. I have given reasons for considering these two as the first and second preethmoids in my previous paper (Ramaswami, 1951c). In *Glaniopsis* (figs. 1a, 1b) dorsally to the first preethmoid, which, however, is visible only in the ventral view (fig. 1b *pet*), there are two prepalatines (*ppa*, *ppa'*), the lateral of which (*ppa*) articulates posteriorly with the palatine (*pal*) and is free anteriorly while the mesial (*ppa'*) articulates with the prepalatine process of the maxilla (*ppm*) anteriorly and is free posteriorly. It is possible that a single ossification has split longitudinally to give rise to these two prepalatines. In *Nemachilus*, articulating with the maxilla and palatine and sitting laterally upon the first preethmoid, is a single prepalatine. In *Crossostoma*, however, there is a single prepalatine (figs. 6a, 6b *ppa*) on either side which while showing an articular facet towards the palatine does not reach the maxilla (*max*) anteriorly. In *Protomyzon*, *Vanmanenia*, *Beaufortia*, *Pseudogastromyzon* and *Gastromyzon*, the prepalatines are absent. It is interesting to note that of the examined genera only one member of the *Crossostoma*-association shows the prepalatine while *Vanmanenia* and the entire *Gastromyzon*-association are free from it.

The premaxillae show the elongated [*Glaniopsis* (fig. 1a), *Protomyzon* (fig. 2a), or comparatively short *Vanmanenia* (fig. 3a)] rostral processes (*rpp*) and the lateral limb (*llp*) may be short as in *Protomyzon* (fig. 2b), *Vanmanenia* (fig. 3b), *Beaufortia* (fig. 4b), *Pseudogastromyzon* (fig. 5b) or excessively long as in *Glaniopsis* (fig. 1b) and *Crossostoma* (fig. 6b). In *Gastromyzon* (Ramaswami, 1948) peculiarly the rostral process reaches the anterior edge of the cruciform median rostral while the lateral limb extends as far as the middle of the lateral ethmoid, a feature not noticed in any other *Gastromyzonid* examined.

The maxilla shows the characteristic Cyprinid processes in *Protomyzon* and *Vanmanenia*; the long and prominent dorsal premaxillary process (figs. 2a, 3a, 2b, 3b *dpm*) on which is the palatine ligament inserted (fig. 3 *ll*); the process (figs. 2b, 3a *pll*) for the insertion of the ligament of the adductor mandibulae muscle; the ventral rostral process (figs. 2a, 2b, 3a, 3b *rpm*) and posteromedially the rounded head (*ppm*) for the articulation of the first preethmoid (*pet*). In *Glaniopsis*, while the dorsal premaxillary process is absent as in *Nemachilus*, the process for the adductor muscle ligament (figs. 1a, 1b *pll*) is very prominent and the other processes are normally developed. In *Beaufortia* and *Pseudogastromyzon*, the dorsal premaxillary process (figs. 4a, 5a *dpm*) is well developed though not so prominently as in *Protomyzon* and *Vanmanenia*; the process for the adductor mandibulae muscle ligament (figs. 4a, 5a, 4b, 5b *pll*) is poorly developed. In *Crossostoma*, the dorsal premaxillary process (figs. 6a, 6b *dpm*) is short and broad while the process for the ligament (*pll*) is prominent and projects posteriorly. In *Gastromyzon* (Ramaswami, 1948, fig. 23), the ventral rostral process (*mp*) is very short resembling that in *Protomyzon* (fig. 2b, *rpm*); the dorsal premaxillary process in *Gastromyzon* (Ramaswami, 1948, fig. 23 *rp"*) is quite large and the lateral limb peculiarly possesses a conspicuous lateral process (*lp*) projecting from the middle of it not seen in any other *Gastromyzonid* form. This probably represents the process for the adductor mandibulae muscle ligament.

The prevomer is small in *Protomyzon* (fig. 2b *pv*) and *Vanmanenia* (fig. 3b *pv*) with a small posterior projection. In *Glaniopsis* (fig. 1b *pv*), the bone is asymmetrical and has no posterior limb. In *Nemachilus*, the posterior limb is very long. In *Gastromyzon* (Ramaswami, 1948), the prevomer is small and shows three short posterior projections of which the mesial is the longest and probably represents the posterior limb of other forms. In *Beaufortia* (fig. 4b) and *Pseudogastromyzon* (fig. 5b), the prevomer is Y- or V-shaped with a deep depression anteriorly and in the latter example, the posterior limb is almost absent; in *Beaufortia*, the posterior limb (fig. 4b *ppv*) is long and in *Crossostoma*, the prevomer (fig. 6b *ppv*) is large with a projection laterally towards the second preethmoid (*pe2*) and the posterior limb (*ppv*) is also broad.

In the *Gastromyzonidae*, the lacrimojugal is even larger than that in the *Homalopteridae*. In the examples of the latter family, I pointed out (Ramaswami,



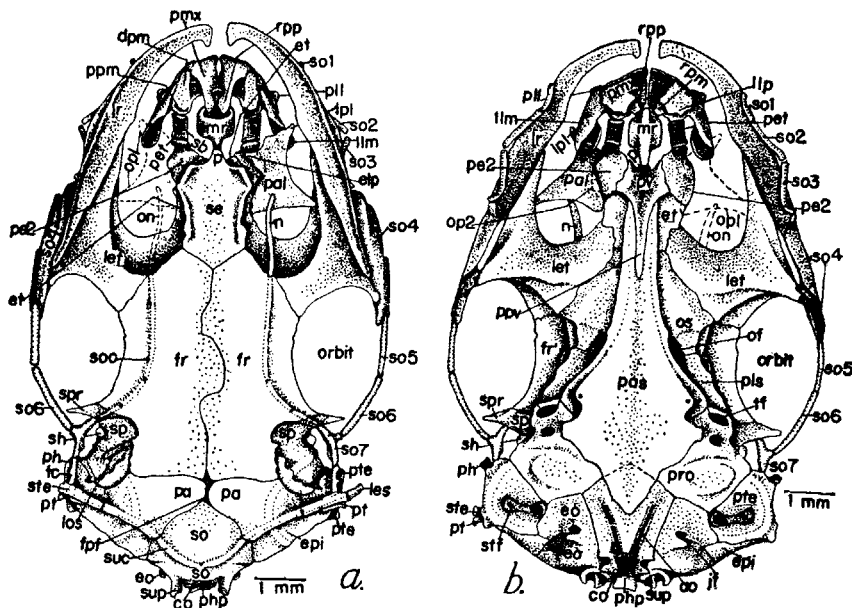
TEXT-FIGS. 3a & 3b. Dorsal and ventral views respectively of the skull of *Vanmanenia caldwelli* (Nichols).

1951c, in press) that the lacrimojugal was devoid of a sensory canal in it and the bone was definitely larger in size than that in the *Cyprinidae*. In *Protomyzon* (figs. 2a, 2b), *Vanmanenia* (figs. 3a, 3b) and *Crossostoma* (figs. 6a, 6b), the lacrimojugal-rostral is of one size and it assumes even larger proportions in *Gastromyzon* (Ramaswami, 1948), *Beaufortia* (figs. 4a, 4b) and *Pseudogastromyzon* (figs. 5a, 5b) where each lacrimojugal-rostral takes a bend mesially; there is also a small spinelike process laterally in *Gastromyzon*. It is likely that this large bone is a composite one formed at least by the union of a large lacrimojugal and a rostral; in the *Homalopterid* examples there is a large lacrimojugal in front of which there is a rostral and it was assumed that the former was formed by the union of a lacrimal and a jugal. In the *Gastromyzonidae*, I have labelled this large bone as lacrimojugal-rostral. In *Glaniopsis* (figs. 1a, 1b), the lacrimojugal is not very big resembling that in the *Homalopteridae* and does not extend as far as the premaxilla and a rostral is also absent in front of it. It looks, therefore, more like the *Homalopterid* lacrimojugal in size with the sensory canal ossicle independently situated. In *Nemachilus*, the anterior rostral is small with a long lacrimojugal behind and the sensory canal ossicles are situated laterally to the lacrimojugal. Chranilov (1927) showed only a 'preorbital' in *Nemachilus barbatus* and did not refer to the sensory canal ossicles and the same figure has been reproduced by Berg (1947, p. 267). In *Beaufortia* (figs. 4a, 4b so1-so4) and *Gastromyzon* (Ramaswami, 1948), the lacrimojugal is very closely associated with the sensory canal bones of the infraorbital series.

The lateral ethmoid (*let*) is well developed in *Protomyzon* (figs. 2a, 2b), *Vanmanenia* (figs. 3a, 3b), *Beaufortia* (figs. 4a, 4b), *Pseudogastromyzon* (figs. 5a, 5b) and *Crossostoma* (figs. 6a, 6b); the lacrimojugal-rostral process of the lateral ethmoid is more well developed in all than the posterior process; in *Nemachilus*, the lateral ethmoid is also small with both the processes short. In *Gastromyzonidae* (except

*Glaniopsis*), one is struck with the width of the lateral ethmoid as opposed to that in the Homalopteridae and in *Nemachilus*.

As in the Homalopteridae, the palatine (*pal*) shows a process (figs. 1a, 1b, 2a, 3a, 4a, 5a, 6a *elp*) towards the ethmoid and this process is very small in *Vanmanenia* (fig. 3a) and *Beaufortia* (fig. 4a). There is one towards the entopterygoid (figs. 1a, 3a, 6a, 1b, 5b, 6b *eap*) and the bone articulates ventromesially with the second preethmoid (*pe2*). In *Protomyzon* (fig. 2a), *Vanmanenia* (figs. 3a, 3b), *Beaufortia* (figs. 4a, 4b), *Pseudogastromyzon* (figs. 5a, 5b) and *Gastromyzon* (Ramaswami, 1948), it also shows anterolaterally a process (*lpl*) towards the lacrimojugal-rostral. However, in *Crossostoma* (figs. 6a, 6b), such a process is absent. In *Glaniopsis*, the diminutive palatine shows the processes described above except the lacrimojugal process. In this and in *Crossostoma*, since a prepalatine (or prepalatines) is noticed, the palatine also shows a rounded articulating facet (figs. 1a, 6a *fpa*) anteriorly for articulation with the prepalatine.



TEXT-FIGS. 4a & 4b. Dorsal and ventral views respectively of the skull of *Beaufortia levertii* (Nichols and Pope).

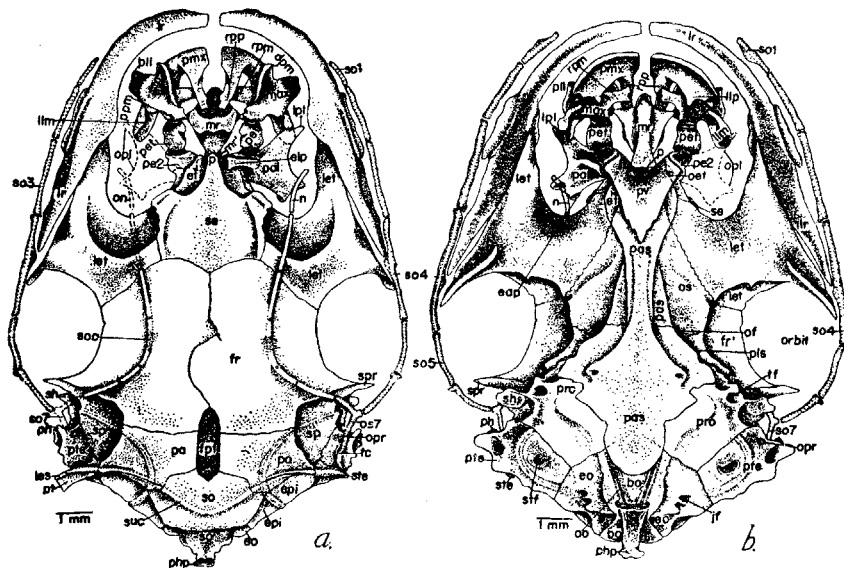
The nasal (*n*) is represented in all these forms by one (figs. 2a–6a, 4b–6b *n*) or two small canal bones as in *Glaniopsis* (fig. 1a *n*).

In *Protomyzon* (figs. 2a, 2b *mr*) and *Gastromyzon* (Ramaswami, 1948), the median rostral is cruciform; in *Vanmanenia* (figs. 3a, 3b), it is elongated and broad where the limbs of the premaxillae rest. In *Beaufortia* (figs. 4a, 4b), it is also large and may be described as cruciform with the posterior portion situated ventrally to the median projection (*p*) of the supraethmoid (*se*); similarly in *Pseudogastromyzon* (figs. 5a, 5b), the median rostral is large and the posterior projection (*mr'*) lies below the supraethmoid extension (*p*). In *Crossostoma* (figs. 6a, 6b) and *Glaniopsis* (figs. 1a, 1b), it is small and roughly triangular.

*The orbitotemporal region.*—The general flattening of the skull has resulted in the widening of the frontals and parietals; the frontals (figs. 1a–6a, 1b–6b *fr*) extend laterally in the orbital region so much that on the ventral aspect also a large part of the bone (*fr'*) is visible.

In *Glaniopsis* (fig. 1a), *Vanmanenia* (fig. 3a), *Pseudogastromyzon* (fig. 5a) and *Crossostoma* (fig. 6a), a large fontanel (*fpf*) is included between the frontals anteriorly, the parietals laterally and the supraoccipital posteriorly. In *Glaniopsis* (fig. 1a), the fontanel is broad posteriorly and the two independent supraoccipital sensory canal ossicles lie over the fontanel; in *Beaufortia* (fig. 4a), the fontanel (*fpf*) is a chinklike space. In *Nemachilus* also a frontoparietal fontanel is present.

Generally flanking the frontals on either side in the Cyprinidae, Psilorhynchidae and Homalopteridae, there is the supraorbital. In Gyriinocheilidae, the Gastromyzonidae (except *Gastromyzon*) and in *Nemachilus*, a supraorbital is absent. In *Gastromyzon* (Ramaswami, 1948), however, the supraorbital is a very small sickle-shaped bone.



TEXT-Figs. 5a & 5b. Dorsal and ventral views respectively of the skull of *Pseudogastromyzon fasciatus* (Sauvage).

Ventrally the orbitosphenoids (figs. 1b–6b *os*) and the pleurosphenoids (*pls*) are prominent. The optic foramen (*of*) is included between the orbitosphenoid, the pleurosphenoid and the parasphenoid (*pas*). In all these forms, an interorbital septum is absent on account of the general flattening of the skull. Peculiarly in one species of Homalopteridae, *Homaloptera amphisquamata* (Ramaswami, 1951c, in press), an interorbital septum is noticed. In *Nemachilus* also an interorbital septum is absent; the orbitosphenoids are united and is a single ossification as in other Cobitidae.

The parasphenoid (figs. 1b–6b *pas*) is broad posteriorly and narrow anteriorly [*Vanmanenia* (fig. 3b), *Beaufortia* (fig. 4b)] or broad posteriorly and the anterior portion is also broader than in the previous examples [*Glaniopsis* (fig. 1b), *Protomyzon* (fig. 2b)] or broad both anteriorly and posteriorly with a waist [*Pseudogastromyzon* (fig. 5b), *Crossostoma* (fig. 6b), *Gastromyzon* (Ramaswami, 1948)]. Thus the shape of the parasphenoid is not uniform in the family.

The eye muscle canals are noticed in all these examples; the position of the two canals, viz., the anterior myodome and the posterior myodome, is indicated only in the ventral view of *Crossostoma* (fig. 6b *amy*, *pmy*). In *Nemachilus* also the two poorly developed myodomies are seen.





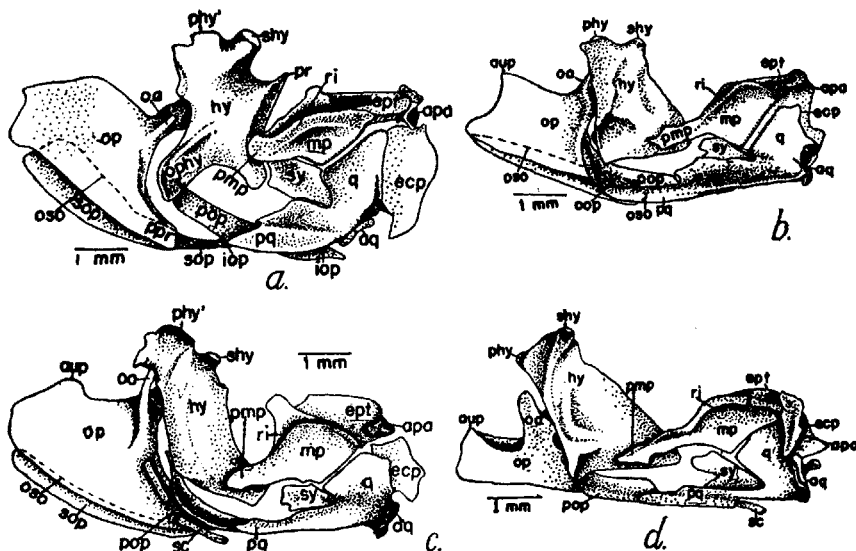
In *Vanmanenia* (fig. 3a), *Crossostoma* (fig. 6a) and *Gastromyzon* (Ramaswami, 1948), the supraorbital canal (*soc*) is incorporated in the frontal and this extends into a small ossicle on the sphenotic (*in*) as in the Homalopteridae, connecting a triradiate one (*so7*) which in turn is connected with a triradiate supratemporal (*ste*) through a small ossicle (fig. 3a *tc*; fig. 6a *so8*) disposed on or in front of the pterotic. In *Pseudogastromyzon* (fig. 5a) the supraorbital canal which is noticed in the frontal leads into a triradiate ossicle (*so7*) which in turn leads into an ossicle (*tc*) on the pterotic which is connected with the supratemporal (*ste*) which, however, is not triradiate. In *Beaufortia* (fig. 4a), the supratemporal is also not triradiate and the sensory canal passes in front of this in the pterotic (*tc*) and is connected with the triradiate ossicle (*so7*). The supraorbital canal (*soc*) is noticed in the frontal. Peculiarly towards the posterolateral edge of the frontal in *Beaufortia*, there are two sensory canal ossicles sitting on the sphenotic (*ios*) with apparently no connection either with the supraorbital canal or with the triradiate ossicle (*so7*). What exactly is the nature of these ossicles, I am at present unable to say. In no other *Gastromyzonid* have I noticed such a feature. In *Nemachilus*, the supraorbital sensory canal leads into the suborbital by an independent ossicle sitting on the sphenotic region; the supratemporal is triradiate and leads into the supraoccipital canal mesially and the temporal canal anteriorly in the pterotic.

The pterotic shows a feeble depression ventrally in *Gastromyzon* (Ramaswami, 1948), *Glaniopsis* (fig. 1b), *Vanmanenia* (fig. 3b), *Beaufortia* (fig. 4b) and *Crossostoma* (fig. 6b) representing the subtemporal fossa (*stf*), but in *Protomyzon* (fig. 2b) the subtemporal fossa (*stf*) seems to be better developed. This fossa is for the insertion of the hyobranchial muscles. While in all these examples the hyobranchial apparatus is well developed, the feeble development of the subtemporal fossa in the majority of the *Gastromyzonidae* becomes difficult to explain.

As in the Homalopteridae, the exoccipital (figs. 1a-6a, 1b-6b *eo*) is excluded from forming the roof of the foramen magnum in *Gastromyzonidae*. The supraoccipital (*so*) may project posteriorly as two processes (*sup*). The exoccipitals do not disclose the fontanel so commonly seen in the catostomids, the cyprinids and the cobitids. The basioccipital (*bo*) shows a prominent pharyngeal process (*php*) and the dorsal aorta running dorsally to this divides anteriorly into two branches (*ao*). In *Glaniopsis* also such an arrangement is noticed resembling *Nemachilus*.

*The upper jaw.*—The palatine bone has already been described. The upper jaw of *Glaniopsis* shows certain features in which it stands apart from the other *Gastromyzonid* genera and resembles more *Nemachilus*. The operculum (fig. 7a *op*) projects by an anterior process (*ppr*) and articulates with the hyomandibula by a prominent socket near which there is a spinelike articular process (*oa*). A process from the posterodorsal edge of the operculum called the auricular process is absent. The hyomandibula (*hy*) shows a large boss by which it fits into a socket in the sphenotic (*shy*) and a flat facet (*phy'*) for articulation with the pterotic region. There is also a prominent process (*pr*) in front of the sphenotic articulation. From the ventral border of the hyomandibula, there arises a prominent backwardly directed process (*ophy*) with which the preoperculum (*pop*) comes in contact. Such a process is not seen in the other *Gastromyzonid* examples. However, in *Nemachilus*, such an opercular process of the hyomandibula is noticed. The quadrate (*q*) has a short and broad posterior limb (*pq*). The metapterygoid (*mp*) has a very short limb (*pmp*) towards the hyomandibula (*hy*). In *Pseudogastromyzon* (fig. 8a), the operculum shows prominent auricular (*aup*) and articular (*oa*) processes; the hyomandibula (*hy*) and the preopercular (*pop*) are large, the posterior process of the quadrate (*pq*) is long and the symplectic (*sy*) is small and is wedged in between the metapterygoid (*mp*) and the quadrate (*q*). The hyomandibula (*hy*) is broad and the boss for articulation with the pterotic region is mesially situated and, therefore, is not shown in the figure. In *Beaufortia* (fig. 7d), the articular process (*oa*) is prominent and an auricular process (*aup*) is just indicated. In *Protomyzon*

(fig. 7b), *Vanmanenia* (fig. 7c), *Crossostoma* (fig. 8b), there is a short articular process (*oa*) and the auricular process is just indicated as in *Beaufortia*. The metapterygoid



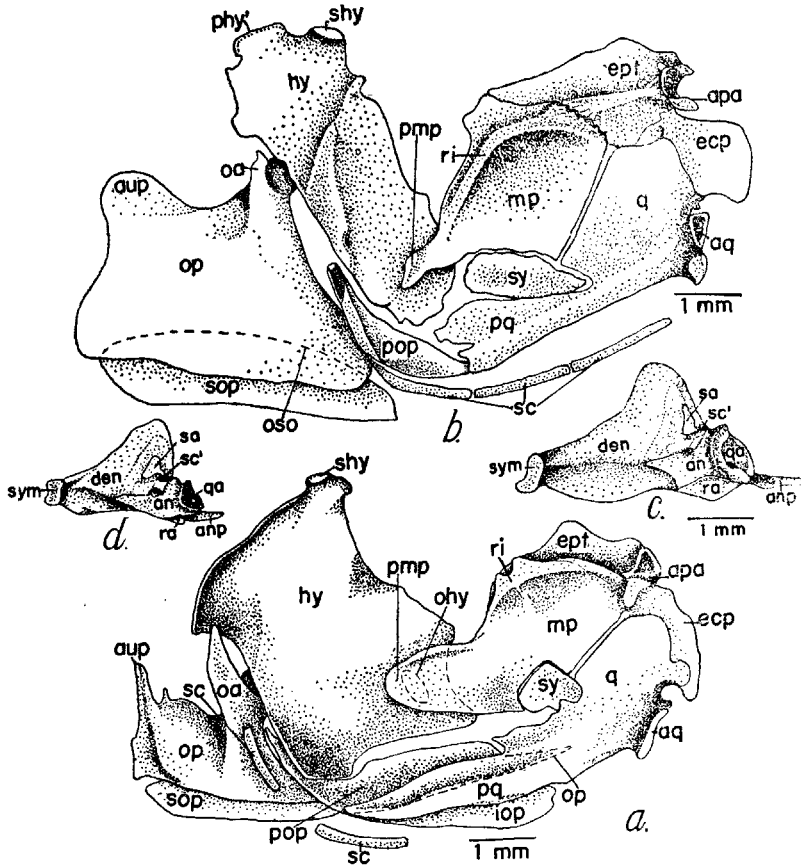
TEXT-FIG. 7a. Lateral view of the right upper jaw of *Glaniopsis hanitshi* Boulenger.  
 ,, 7b. Lateral view of the right upper jaw of *Protomyzon whiteheadi* (Vaillant).  
 ,, 7c. Lateral view of the right upper jaw of *Vanmanenia caldwelli* (Nichols).  
 ,, 7d. Lateral view of the right upper jaw of *Beaufortia leverti* (Nichols and Pope).

process (*pmp*) is short and broad in *Pseudogastromyzon* (fig. 8a), while in *Glaniopsis* (fig. 7a), *Vanmanenia* (fig. 7c), *Beaufortia* (fig. 7d), *Crossostoma* (fig. 8b) and *Gastromyzon* (Ramaswami, 1948), it is narrow. Further, the metapterygoid in all these forms shows a prominent ridge (*ri*); sometimes this ridge may be in continuation of the ridge (*ri'*) on the entopterygoid also as in *Pseudogastromyzon* (fig. 8a), *Glaniopsis* (fig. 7a), *Beaufortia* (fig. 7d) and *Crossostoma* (fig. 8b). The hyomandibula may show two articular bosses [*Protomyzon* (fig. 7b), *Beaufortia* (fig. 7d), *Pseudogastromyzon* (fig. 8a) and *Gastromyzon* (Ramaswami, 1948)] or one boss (*shy*) and one facet (*phy'*) as in *Glaniopsis* (fig. 7a), *Vanmanenia* (fig. 7c) and *Crossostoma* (fig. 8b). Laterally there may be two independent ossicles (*sc*) as in *Pseudogastromyzon* (fig. 8a) and *Vanmanenia* (fig. 7c) or three as in *Crossostoma* (fig. 8b) or there may be a single one leading from the preopercular in front of the quadrate process as in *Beaufortia* (fig. 7d). In *Glaniopsis* (fig. 7a) and *Protomyzon* (fig. 7b), independent sensory canal ossicles are not noticed. In *Nemachilus*, the opercular is elongated in the anteroposterior direction and shows a prominent articular process; the preopercular is long and shows in front a sensory canal ossicle and the metapterygoid carries a prominent ridge.

*The lower jaw.*—There is an uniformity in the disposition of the structures of the lower jaw but for the shape of the bones.<sup>1</sup> A large edentulous dentary (figs. 8c, 8d *den*), an angular (*an*) with which the quadrate articulates (*qa*), a small retroarticular (*ra*) and a mesially situated sesamoid angular (*sa*) are uniformly noticed in all the genera examined by me. In *Pseudogastromyzon* (fig. 8c) and

<sup>1</sup> Berg (1947) while pointing out that the current nomenclature of the bones of the lower jaw of teleosts is incorrect, still prefers to use the same 'to avoid misunderstanding'; however, I have followed in all my papers on fish skull, the correct nomenclature (Haines, 1937).

*Beaufortia* (fig. 8d) only, the angular projects posteriorly in the forms of a process (*anp*). Mesially there is also a canal (*sc'*) in all these forms through which a bristle



TEXT-FIG. 8a. Lateral view of the right upper jaw of *Pseudogastromyzon fasciatus* (Sauvage)  
 ,, 8b. Lateral view of the right upper jaw of *Crossostoma davidi* Sauvage.  
 ,, 8c. Mesial view of the right lower jaw of *Pseudogastromyzon fasciatus* (Sauvage).  
 ,, 8d. Mesial view of the right lower jaw of *Beaufortia leverthi* (Nichols and Pope).

could be easily passed. This is, probably, the mandibular sensory canal; in the Homalopteridae and the Nemachilinae also there is a mesial sensory canal. In the majority of fishes, however, the mandibular sensory canal is *laterally* disposed.

In the hyobranchial apparatus the arrangement of parts is very much like that in the Homalopteridae (Ramaswami, 1951c, in press). Connecting the two pairs of hypohyals, there is a median ossification probably also a part of the basihyal and dorsally to this, a three-pronged basihyal is noticed. There are three copulae usually, three pairs of hypobranchs and two pairs of pharyngobranchs; in *Beaufortia* the median copulae are four in number and in *Glaniopsis*, a small third pharyngobranch ossification is also seen. Dorsal gillrakers extending on the hypobranch and the median copulae are noticed in all the examples. The occurrence of the gillrakers is conspicuously noticed in the Gastromyzonidae and not a single species of Homalopteridae examined by me exhibited this character.

*The Weberian apparatus.*—As far as I am aware, the Weberian apparatus in no Gastromyzonid example has so far been described. It does not, however, differ from that in the Homalopteridae.

I have already described the arrangement of parts with regard to the gasbladder capsule and the associated Weberian ossicles in the Homalopteridae.

It is noticed that in the nemachiline Cobitidae, Homalopteridae and Gastromyzonidae the gasbladder is completely divided into two and is enclosed in an osseous capsule. Chranilov (1927), having studied the structure of the gasbladder in a number of Cobitid genera, divided them into two structural types. While in the first the capsule is single (*Misgurnus*, etc.), in the second the capsule is divided into two, the two being connected by a posterior commissure as in *Nemachilus*. In the Gastromyzonidae, it is also noticed that projecting from this commissure posteriorly there is a small posterior portion of the gasbladder as in *Beaufortia*, *Protomyzon* (fig. 9b mgb) and *Crossostoma*; in *Glanioptis* and *Pseudogastromyzon*, this posterior portion of the gasbladder is absent. It may also be remarked here that in the Homalopterid, *Homaloptera leonardi*, there is a long posterior portion of the gasbladder and in *H. zollingeri* there is a small oval posterior portion. In *Nemachilus*, Chranilov (1927) showed a large posterior portion.

It has also been remarked by me (Ramaswami, 1952c, in press), that the gasbladder capsule of the Homalopteridae and the Gastromyzonidae resembles that in Nemachilini (Cobitidae). In *Nemachilus*, the capsule is formed by the dorsal ribs (transverse processes of previous authors) of the second and fourth vertebrae, the pleural ribs of the second and the ossa suspensoria of the fourth vertebra according to Chranilov (1927). The ossa suspensoria contribute the mesial wall, a part of the lower osseous wall and the wall of the transverse canal; while the dorsal ribs of the second vertebra form the antero-dorsal and the pleural, the antero-ventral walls of the capsule, the dorsal ribs of the fourth vertebra form the postero-dorsal and postero-ventral walls. In *Nemachilus dayi* which I have examined, each half of the gasbladder capsule is composed of the ribs (dorsal and pleural) of the second and fourth vertebrae; the large posterior portion is formed by the dorsal ribs of the fourth vertebra and the smaller anterior portion is formed by those of the second vertebra, the sutural line between the two being clearly visible only anterodorsally. I have also noted such a sutural line in another nemachilid *Nemachilichthys* which I have examined. However, in *Nemachilus*, the disposition of the prominent parapophyses<sup>1</sup> of the second vertebra indicates their extension ventrally and laterally to these, the wall is formed by the pleural ribs. I am unable to make out the contribution of the ossa suspensoria towards the formation of the capsule and the transverse canal. Laterally each capsule shows two openings: an anterior smaller and a posterior larger one (apertura magna externa) through which the gasbladder of the animal can come in contact with the skin.

The neural arch of the second vertebra of *Nemachilus*, whose exact derivation I am unable to say, is noticed middorsally as a keystone arch in front of the third neural arch; the latter is in continuity on either side with the gasbladder capsule. Laterally to the second arch referred to above, the claustrum and scaphium are noticed. The first vertebral centrum carries an independent pair of dorsal ribs. The fourth neural arch, shows a prominent spine and the centrum is also large

<sup>1</sup> Berg (1947) labelled in *Nemachilus strauchi* the 'transverse processes' as parapophyses. The referee has kindly pointed out that 'The term parapophysis indicates the structure which represents the rib-bearing process of the haemal arch. Actually the basiventrals of the anterior region of a fish vertebra are misquoted as parapophyses'. We read in Goodrich (1930, p. 73) that the pleural ribs may articulate with rib-bearing processes of basiventrals as in *Cyprinus* and that these processes arise independently. Whether in *Nemachilus* the so-called parapophyses arise independently and later fuse with the basiventrals or they merely represent the basiventrals, when according to the referee, they should not be called parapophyses, I am unable to say at present as I have not examined developmental stages.

and no indication of the fusion of the third centrum with it is noticeable. The horizontal process described in the Homalopteridae (Ramaswami, 1952c, in press), as extending over the paravertebral space in front of the orifice for the fourth spinal nerve and probably arising from the third neural arch, is not seen in *Nemachilus* or *Nemachilichthys*.

In the Bornean Gastromyzonidae like *Glaniopsis* and *Protomyzon*, the sutural demarcation described above between the second and fourth dorsal ribs anterodorsally of the capsule wall is not seen. In the Homalopteridae while *Lepturichthys* and *Homaloptera leonardi* show such a sutural line, *Balitora* and *H. rupicola* do not. However, in *Glaniopsis* and *Protomyzon* the third (plus 2nd?) neural arch is clearly seen and between it and that of the fourth, the spinal nerve orifice discloses the ventrally lying tripus. The 'keystone arch', described in *Nemachilus* as lying in front of the third neural arch, is wanting in the examined genera of Bornean Gastromyzonids<sup>1</sup>. The short centrum of the first vertebra, which is opisthocelous, carries a pair of independent dorsal ribs. The gasbladder capsule shows laterally paired orifices as in *Nemachilus* and the Homalopteridae. Ventrally the parapophyses of the second vertebra are prominent and no indication of a separate third centrum is noticeable.

The mainland forms show certain peculiarities. In *Vanmanenia* and *Crossostoma*, the dorsal demarcation between the second and fourth rib extensions on the gasbladder is absent; however, the neural arches of those vertebrae could be clearly made out. While in *Crossostoma*, the dorsal ribs of the first centrum are united terminally with the anterior face of the gasbladder capsule, in *Vanmanenia*, the ribs are free. *Pseudogastromyzon* and *Beaufortia* resemble each other closely. The ribs of the first centrum (fig. 9c dr1) are fused with the gasbladder capsule and as in the Bornean forms, no sutural demarcation is noticed on the dorsal aspect of the capsule. The neural arches of the second and fourth vertebrae are peculiarly broadened out to form horizontal processes (ex24). The transverse canal (*trc*) shows only partial encasement by bone. The claustrum (*cl*) articulates with the anterior face or edge of the second neural arch, the 'keystone arch' being not formed in the above two forms.

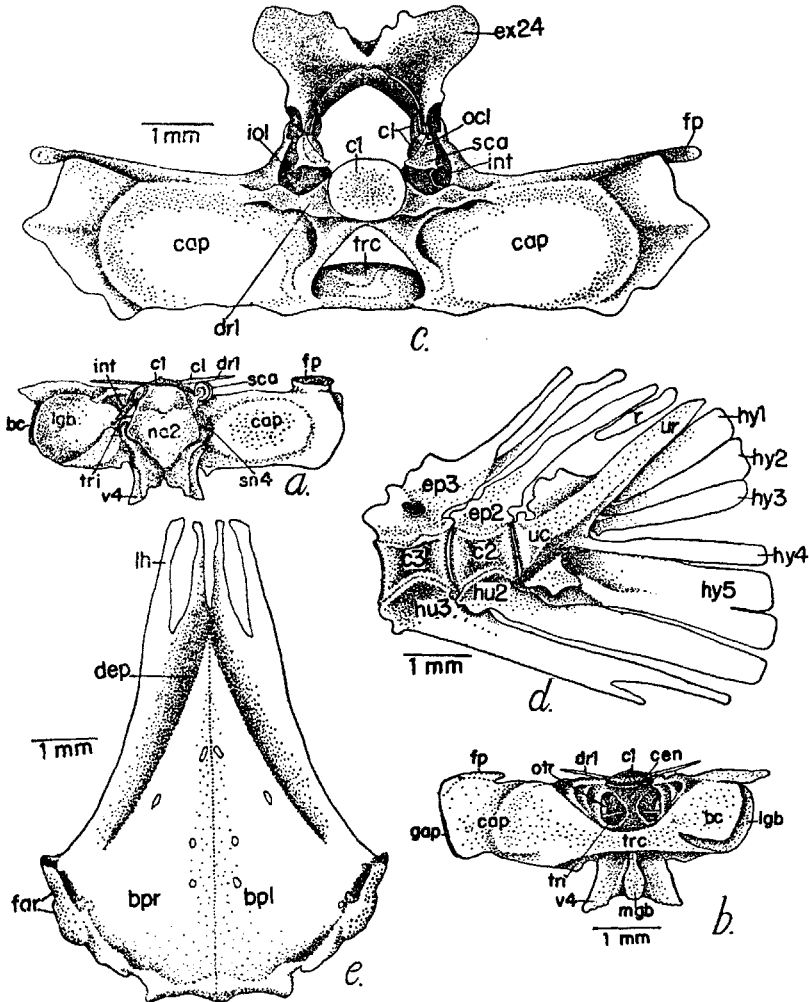
The Gastromyzonid gasbladder capsule differs from that of the Homalopteridae in not possessing a horizontal process extending on the paravertebral space of either capsule from the third neural arch and resembles thereby the Nemachilini.

As in the Cobitidae and Homalopteridae, associated with the second neural arch is the claustrum (figs. 9a, 9c cl) and between it and the funnel-shaped scaphium (*sca*) the posterior portion of the sinus impar of the united endolymphatic canal is enclosed. The scaphium is in contact with the triradiate tripus (fig. 9a tri) through the rodlike intercalarium (figs. 9a, 9c int) in the interosseous ligament (*iol*). One limb of the triradiate tripus (fig. 9a tri) is in contact with the gasbladder without its transmitting process, while the other limb (fig. 9b tri) is in contact with the centrum (*cen*) of the fused vertebrae. Probably the derivation of these ossicles is not very different from what has been described by Watson (1939) in the goldfish.

*The caudal fin skeleton.*—The last three vertebrae support the rays of the caudal fin. The last vertebra, whose anterior face shows a typical concavity characteristic of the piscine vertebra, projects posterodorsally as the urostyle (fig. 9d ur). The hypochordal lobe of the caudal fin is therefore larger than the epichordal and the fin is apparently symmetrical. The urostyle has a free radial (*r*) anteriorly usually, but in *Beaufortia* there are two; posteriorly to the urostyle, there are five (fig. 9d) or six hypurals (*Glaniopsis*, *Protomyzon*, *Beaufortia*, *Vanmanenia* and *Crossostoma*). The attachment of the hypurals is rather interesting; there are three hypurals (*hy1-hy3*) immediately posteriorly to the urostyle articulating with it, the fourth

<sup>1</sup> It is likely that the second neural arch is fused with the third as there is no clear demarcation between the two in the adult.

hypural (*hy4*) is fused with the last vertebral centrum and ventrally to this, there are two hypurals in all *Gastromyzonidae* (except *Pseudogastromyzon*) of which the



- TEXT-FIG. 9a. Dorsal aspect of the gasbladder capsule and Weberian ossicles of *Protomyzon whiteheadi* (Vaillant).  
 ,, 9b. Ventral aspect of the gasbladder capsule and Weberian ossicles of *Protomyzon whiteheadi* (Vaillant).  
 ,, 9c. Front view of the gasbladder capsule and Weberian ossicles of *Pseudogastromyzon fasciatus* (Sauvage).  
 ,, 9d. The caudal fin skeleton of *Pseudogastromyzon fasciatus* (Sauvage); fin rays are not shown.  
 ,, 9e. Ventral view of the basipterygia of *Glaniopsis hanitshi* Boulenger.

first (or fifth in the series) articulates and the next (or sixth) is fused with the base of the last centrum. In these forms therefore, there are two fused and four articulating hypurals. In *Pseudogastromyzon* (fig. 9d), however, the last two (fifth and sixth) have united together into a single hypural (*hy5*) which, of course, is fused with the base of the centrum of the last vertebra. While the hypurals and

epurals of the penultimate vertebra are normal, in the vertebra preceding this, the elements are forked in *Pseudogastromyzon*, a feature also shared by *Vanmanenia*.

In *Nemachilus* (Cobitidae), the number of hypurals on the posterior aspect of the urostyle is seven with a single radial anteriorly to it; in the Homalopteridae (Ramaswami, 1952c, in press), the hypurals on the posterior aspect of the urostyle varies from 6 to 8.

*The basipterygia*.—The nature of the basipterygium is of great systematic importance (Fang, 1930; Hora, 1932). While the basipterygia of a large number of Gastromyzonids have been described, those of *Glaniopsis* are unknown. *Glaniopsis* also shows the two basipterygia (fig. 9e *bpr*, *bpl*) united mesially as in the Gastromyzonidae and the Homalopteridae. Each basipterygium, however, shows anteriorly a lateral horn (*lh*) characteristic of the Gastromyzonidae; but the forking to produce the horn is narrow as in the Cyprinidae, though, however, in the latter the two basipterygia do not approximate mesially. In the Homalopteridae generally, the horns are absent but a lateral foramen is noticed at the region the modified rib comes in contact with it (Hora, 1932). In *Glaniopsis*, there is a deep depression (fig. 9e *dep*) noticed starting from the anteromesial edge and progressing laterally posteriorly. There are also a number of symmetrically placed foramina in the two basipterygia. Thus in the basipterygia possessing lateral horns, *Glaniopsis* resembles the other Gastromyzonid genera studied.

#### DISCUSSION.

In describing the Homalopteridae (including the Gastromyzonidae) Hora (1932) noted that the two genera *Octonema* and *Glaniopsis* were Cobitids and they belonged to the genus *Nemachilus*. Particularly with regard to *Glaniopsis*, he recorded that 'Their almost terminal mouth, the plain and fleshy lips, the long barbels and the beaked condition of the jaws especially the upper one, indicate close relationship between *Glaniopsis* and *Nemachilus*. . . In my opinion *Glaniopsis* should be placed in the Cobitidae among *Nemachilus*-group (without suborbital spine). . . . I have examined the skeletal characters of *Glaniopsis*, and *Octonema* was not available to me. Undoubtedly the Bornean *Glaniopsis* shows a large number of *Nemachiline* features but it also exhibits a few characteristic Gastromyzonid features which cannot, however, be overlooked. The *Nemachiline* features exhibited by *Glaniopsis* are as follows:

- The possession of 1. a narrow supraethmoid,  
 2. a pair of prepalatines,  
 3. poorly developed lateral ethmoids,  
 4. small lacrimojugal,  
 5. very small subtemporal fossa,  
 6. a projecting preopercular process,  
 7. a posteriorly directed opercular process of the hyomandibula,  
 8. a prominent ridge on the metapterygoid,  
 9. a divided gasbladder enclosed in a bony capsule with the Weberian ossicles associated with each.

The features in which *Glaniopsis* differs from *Nemachilus* may now be recounted.

- In *Glaniopsis* 1. the pharyngeal process is large,  
 2. the exoccipital fenestrae are absent and the exoccipitals do not roof the foramen magnum,  
 3. the posterior process of the quadrate is short and broad,

4. the hyomandibula shows a flat facet for articulation with the pterotic,
5. the orbitosphenoids are double,
6. an independent sensory canal bone is absent in front of the preopercular,
7. the posterior commissure connecting the two parts of the gasbladder does not show a posterior gasbladder,
8. the basipterygia are mesially united and show lateral horns.

It is clear that in a number of internal (as enumerated above by me) and external characters [as stated by Hora (1932)], *Glaniopsis* resembles *Nemachilus*. But in possessing independent sensory canal ossicles in the supraorbital, suborbital, temporal and supraoccipital regions and in not having the exoccipital fenestrae *Glaniopsis* stands apart from the Cobitids. In the latter feature, however, it resembles the Homalopteridae and the Gastromyzonidae. Of these two families, it is more Gastromyzonid because of the possession of a shallow subtemporal fossa, of a hyomandibula showing a flat pterotic articular facet, of a large pharyngeal process, of dorsal gillrakers on the branchial arches and of the mesially united basipterygia showing no lateral foramen. It is evident in view of the above observations that *Glaniopsis*, though showing a number of internal and external Nemachiline features, has progressed towards the Gastromyzonidae. It could, therefore, be treated as a member of the Gastromyzonidae<sup>1</sup>; it may not be incorrect to treat *Glaniopsis* as the type of a group (or association of Fang) under the Gastromyzonidae in addition to the *Gastromyzon*- and *Crossostoma*-groups created by Fang (1935). It is very likely that a loachlike ancestral Glaniopsid adapted itself to a life in torrential waters and developed Gastromyzonid features; and such an ancestor was the progenitor of the modern Gastromyzonids in Borneo.

Since *Glaniopsis* is restricted to Borneo and is not found on the mainland, it stands to reason to assume that a separate ancestral type gave rise to the Chinese forms and Hora (1951) has come to the conclusion that the mainland and the Bornean forms had no geographical continuity during their evolutionary history. Thus the Chinese and Bornean forms have evolved independently and curiously many parallel features are seen among them. The Bornean *Protomyzon* and the Chinese *Vanmanenia* resemble each other: the moderately large lacrimojugal-rostral, the large dorsal premaxillary process of the maxilla, the narrow supraethmoid portion, the absence of the prepalatine, the large lateral ethmoid and the occurrence of two preethmoids are all common features. Only in *Protomyzon* the supraorbital and temporal canals are independent of the skull bones resembling thereby *Glaniopsis*. Hora (*in litt.*) informs me that there are resemblances between *Glaniopsis* and *Protomyzon* and the two could be connected by an intermediate form like *Parhomaloptera* which, unfortunately, I have not been able to secure for examination. Except for the points mentioned above, the skull of *Glaniopsis* differs widely from that of *Protomyzon*. However, in showing a large lacrimojugal-rostral, a premaxilla with a very large lateral limb and in the disposition of its dorsal process in front of the rostral and in the possession of a small supraorbital, the Bornean *Gastromyzon* (Ramaswami, 1948) is unique and must have evolved

<sup>1</sup> In a recent article in the *Records of the Indian Museum* (Vol. 48, pt. 2, pp. 85-88, 1950, Hora and Jayaram have re-described *Glaniopsis* and have discussed from a purely taxonomic point of view. They have concluded that:

'In its general form and structure, *Glaniopsis* differs little from *Nemachilus* and allied Cobitid genera, but in its greatly depressed head and anterior part of the body, and the division of the pectoral fin into an adhesive outer portion and a vibrating inner portion, it shows an advance over the Cobitidae and approaches the Gastromyzonidae. *Glaniopsis* could thus be considered as a less specialised genus in the Gastromyzonid group of fishes.'



independently of the other Bornean genera. Judging by the characters exhibited by *Gastromyzon*, it would be incorrect to imagine that a form like that could have descended from a *Glanioptid*-like ancestor.

On the mainland also, while *Beaufortia* and *Pseudogastromyzon* show similarities in the nature of lacrimojugal-rostral (comparable with the big one in *Gastromyzon*), in the large supraethmoid, in the possession of a frontoparietal fossa, of a supra-temporal which is not triradiate and of a rostral which is in contact with the supraethmoid process, *Crossostoma* shows a comparatively small lacrimojugal-rostral (more like that in *Vanmanenia* and the Bornean *Protomyzon*), a small rostral and a pair of prepalatines and a very broad prevomer. It is difficult to derive *Crossostoma* from any mainland or Bornean form examined since in none of these a prepalatine is developed; it is only in the present-day *Glanioptis* that the prepalatines are noticed and, therefore, it is likely that on the mainland also a *Crossostoma*-like ancestor gave rise to the existing forms. Hora (*in. litt.*) writes that *Crossostoma* shows certain resemblances to *Vanmanenia* and an evolutionary series like *Vanmanenia*—*Preformosania*—*Formosania*—*Crossostoma* could be established. However, *Vanmanenia* and *Crossostoma* resemble each other as already said, only in the relatively small lacrimojugal-rostral. According to me, as our knowledge of the *Gastromyzonid* skeleton stands today, three trends of evolution seem to have taken place on the mainland from an ancestral *Crossostomid*: one resulted in the present-day *Crossostoma* with the prepalatines; the other two lines branched off before the appearance of the prepalatines in the ancestral *Crossostomid* and gave rise to *Vanmanenia* on the one hand and on the other to *Beaufortia* and *Pseudogastromyzon*.

Thus there appears to be two independent lines of evolution of the *Gastromyzonid* forms; one on the mainland and the other in Borneo, the evolution therefore being diphyletic and as already remarked, most of these forms show parallel features in their organization.

It may not be out of place here to mention that there are four important features in which the skeleton of the examined genera of the *Gastromyzonidae* differs from that of the *Homalopteridae*. The *Homalopterid* subtemporal fossa is very large while in the *Gastromyzonidae*, it is very shallow and the pharyngeal process is also very well developed in the latter family. While in some *Gastromyzonidae*, the hyomandibula shows a flat articular facet for articulation with the pterotic region, in no *Homalopterid* is such a feature noticed. The basipterygium of the *Gastromyzonidae* shows the lateral horn and lacks the characteristic *homalopterid* lateral foramen. The hyobranchial apparatus of the *Gastromyzonidae* exhibit the dorsal gillrakers, completely wanting in the *Homalopteridae*.

#### SUMMARY.

1. The Bornean *Glanioptis* exhibits a number of *Nemachiline* features, *viz.*, narrow supraethmoid, prepalatines, poorly developed ethmoid, small subtemporal fossae and divided gasbladder enclosed in bony case. But it differs from it in not having united orbitosphenoids, in the absence of exoccipital fenestrae and in possessing the mesially united basipterygoids. Therefore, it cannot be considered a *Nemachiline Cobitid*. It is more *Gastromyzonid* in showing shallow subtemporal fossae, dorsal gillrakers on the branchial arches and the mesially united basipterygoids with no lateral foramina. It is argued that a *Glanioptid*-like ancestor may have given rise to the Bornean *Gastromyzonid* genera.

2. Since *Glanioptis* is restricted to Borneo, it is likely that some other form must have given rise to the *Gastromyzonidae* on the mainland of China. The mainland forms vary among themselves very much and they are a polyphyletic assemblage. It is argued, therefore, that an ancestral *Crossostomid* may have given rise to at least three branches; the first is represented by *Crossostoma*, the second by *Vanmanenia* and the third branch by *Beaufortia* and *Pseudogastromyzon*.

3. Two independent lines of evolution of the *Gastromyzonidae* have therefore taken place; one on the island of Borneo and the other on the mainland of China. It is known that there was no geographical continuity at any time between the two areas.

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## KEY TO ABBREVIATIONS.

<i>amy</i>	.. anterior myodome.	<i>fra</i>	.. facet of palatine for lateral prepalatine articulation.
<i>an</i>	.. angular.	<i>fpf</i>	.. frontoparietal fontanel.
<i>ao</i>	.. passage for aortic branch.	<i>fr</i>	.. frontal.
<i>apa</i>	.. articular facet of entopterygoid for palatine.	<i>fr'</i>	.. ventral aspect of frontal.
<i>aq</i>	.. articular facet of the quadrate for lower jaw.	<i>gap</i>	.. lateral opening in the gasbladder capsule.
<i>aup</i>	.. auricular process.	<i>hu2</i>	.. hypural of penultimate vertebra.
<i>bc</i>	.. broken gasbladder capsule.	<i>hu3</i>	.. hypural of vertebra in front of the penultimate.
<i>bo</i>	.. basioccipital.	<i>hy</i>	.. hyomandibula.
<i>bpl</i>	.. left basipterygium.	<i>hy1</i>	.. } hypurals associated with uro-
<i>bpr</i>	.. right basipterygium.	<i>hy5</i>	.. } style and last centrum.
<i>cap</i>	.. gasbladder capsule.	<i>in</i>	.. independent sensory canal ossicle.
<i>cen</i>	.. fused centra.	<i>int</i>	.. intercalarium.
<i>cl</i>	.. claustrum.	<i>iop</i>	.. interopercular.
<i>co</i>	.. occipital condyle.	<i>ios</i>	.. independent sensory canal ossicles on sphenotic.
<i>c1</i>	.. first centrum.	<i>iol</i>	.. interosseous ligament.
<i>c2</i>	.. } penultimate centrum and	<i>if</i>	.. jugular foramen.
<i>c3</i>	.. } one behind it.	<i>les</i>	.. lateral extrascapular.
<i>den</i>	.. dentary.	<i>let</i>	.. lateral ethmoid.
<i>dep</i>	.. depression in the basipterygia.	<i>lgb</i>	.. lateral wall of gasbladder.
<i>dpm</i>	.. dorsal premaxillary process.	<i>lh</i>	.. lateral horn.
<i>dr1</i>	.. first pair of dorsal ribs.	<i>lj</i>	.. lacrimojugal.
<i>eap</i>	.. entopterygoid articulation facet of palatine.	<i>llm</i>	.. lateral limb of maxilla.
<i>ecp</i>	.. ectopterygoid.	<i>lpl</i>	.. lacrimojugal-rostral process of palatine.
<i>elp</i>	.. ethmoid limb of palatine.	<i>lr</i>	.. lacrimojugal-rostral.
<i>eo</i>	.. exoccipital.	<i>l1</i>	.. ligament between dorsal process of maxilla and palatine.
<i>epi</i>	.. epiotic.	<i>l2</i>	.. ligament between rostral process of maxilla and median rostral.
<i>ept</i>	.. entopterygoid.	<i>l3</i>	.. ligament between median rostral and anterior process of ethmoid.
<i>ep2</i>	.. epural of the penultimate vertebra.	<i>mco</i>	.. mandibular sensory canal ossicles.
<i>ep3</i>	.. bifid epural.		
<i>et</i>	.. ethmoid.		
<i>ex24</i>	.. expanded neural arches of second and fourth vertebrae.		
<i>far</i>	.. articular facet for the radials.		
<i>fp</i>	.. facet for the articulation of supracleithrum.		

<i>mgb</i>	.. median portion of gas-bladder.	<i>ppa'</i>	.. median prepalatine.
<i>mp</i>	.. metapterygoid.	<i>ppm</i>	.. articular facet of maxilla with prepalatine.
<i>mr</i>	.. median rostral.	<i>ppr</i>	.. process of operculum.
<i>mr'</i>	.. posterior portion of median rostral.	<i>pq</i>	.. posterior process of quadrate.
<i>n</i>	.. nasal.	<i>pr</i>	.. process of the hyomandibula
<i>na2</i>	.. fused second and third neural arches.	<i>pt</i>	.. posttemporal.
<i>oa</i>	.. articular process of operculum.	<i>pte</i>	.. pterotic.
<i>ocl</i>	.. outline of claustrum.	<i>pv</i>	.. prevomer.
<i>of</i>	.. optic foramen.	<i>q</i>	.. quadrate.
<i>ohy</i>	.. outline of orifice in hyomandibula.	<i>qa</i>	.. articular facet in the angular for quadrate.
<i>on</i>	.. outline of nasal.	<i>r</i>	.. radial.
<i>oop</i>	.. outline of opercular.	<i>ra</i>	.. retroarticular.
<i>op</i>	.. opercular.	<i>ri</i>	.. ridge on the metapterygoid.
<i>ope</i>	.. orifice in the second pre-ethmoid.	<i>ri'</i>	.. ridge on the entopterygoid.
<i>ophy</i>	.. opercular process of hyomandibula.	<i>rpm</i>	.. rostral process of maxilla.
<i>opl</i>	.. outline of palatine.	<i>rpp</i>	.. rostral process of premaxilla.
<i>opop</i>	.. outline of preopercular.	<i>sa</i>	.. supraangular.
<i>opr</i>	.. orifice in prootic.	<i>sb</i>	.. sesamoid bone.
<i>op2</i>	.. outline of second pre-ethmoid.	<i>sc</i>	.. sensory canal ossicle.
<i>os</i>	.. orbitosphenoid.	<i>sc'</i>	.. mesial sensory canal.
<i>oso</i>	.. outline of subopercular.	<i>sca</i>	.. scaphium.
<i>os7</i>	.. outline of so7.	<i>se</i>	.. supraethmoid.
<i>otr</i>	.. orifice for the tripus.	<i>sh</i>	.. sphenotic facet for hyomandibular articulation.
<i>p</i>	.. anterior process of ethmoid.	<i>shy</i>	.. facet of hyomandibula for articulation with sphenotic.
<i>pa</i>	.. parietal.	<i>sn4</i>	.. orifice for fourth spinal nerve.
<i>pal</i>	.. palatine.	<i>so</i>	.. supraoccipital.
<i>pas</i>	.. parasphenoid.	<i>sop</i>	.. subopercular.
<i>pet</i>	.. first preethmoid.	<i>sol-so9</i>	.. sensory canal ossicles 1-9.
<i>pe2</i>	.. second preethmoid.	<i>sp</i>	.. sphenotic.
<i>ph</i>	.. facet for hyomandibular articulation.	<i>spr</i>	.. sphenotic process.
<i>php</i>	.. pharyngeal process.	<i>ste</i>	.. supratemporal.
<i>phy</i>	.. facet of hyomandibula for articulation with pterotic.	<i>stf</i>	.. subtemporal fossa.
<i>phy'</i>	.. flat facet of hyomandibula.	<i>sui</i>	.. supraoccipital sensory canal.
<i>pl</i>	.. process of maxilla for adductor mandibular muscle ligament.	<i>suol-suo4</i>	.. supraorbital sensory canal ossicles 1-4.
<i>pls</i>	.. pleurosphenoid.	<i>sup</i>	.. supraoccipital process.
<i>pmx</i>	.. posterior process of metapterygoid.	<i>sy</i>	.. symplectic.
<i>pmy</i>	.. posterior myodome.	<i>sym</i>	.. symphysis meckelii.
<i>pmx</i>	.. premaxilla.	<i>tc</i>	.. temporal canal.
<i>pop</i>	.. preopercular.	<i>tf</i>	.. trigeminofacialis opening.
<i>ppa</i>	.. lateral prepalatine.	<i>trc</i>	.. transverse canal.
		<i>tri</i>	.. tripus.
		<i>uc</i>	.. ultimate centrum.
		<i>ur</i>	.. urostyle.
		<i>v4</i>	.. postzygapophysial part of fourth vertebra.