SKELETON OF CYPRINOID FISHES IN RELATION TO PHYLOGENETIC STUDIES.

I. The Systematic position of the genus *Gyrinocheilus* Vaillant.

By L. S. Ramaswami, *Senior Research Fellow, N.I.S.I., Department of Zoology, Central College, Bangalore.*

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Introduction.

In his monograph on the family Homalopteridae, Hora (1932) after examining the external and a few skeletal characters recorded that the members comprising the family may have been polyphyletic in their origin and that the external or superficial resemblances were due to convergence on account of their life in torrential waters. Further, he divided the family tentatively into the Homalopterinae and Gastromyzoninae and derived the two subfamilies from cyprinid and cobitid ancestors respectively.

It occurred to me that a study of the cranial osteology of a few genera of the family might give us a better insight into the classification of these forms and accordingly, I studied and published (Ramaswami, 1948) an account of the skull structure of *Bhavania*, *Balitora* and *Gastromyzon*. At the time, I was not in a position either to confirm or disprove the polyphyletic origin of the Homalopteridae since I had not examined the cyprinid and cobitid genera which have been regarded as the possible ancestors.

However, the award of a senior research fellowship of the National Institute of Sciences of India has made it possible for me to devote uninterruptedly to an examination of the skeletal structures of the members of the Ostariophysi more thoroughly. The material for this study has been partly made available to me by the Director, Zoological Survey of India, to whom I am deeply thankful and has also been partly collected by me during my specimen collection tours. I also propose to examine a few foreign genera as and when material becomes available.

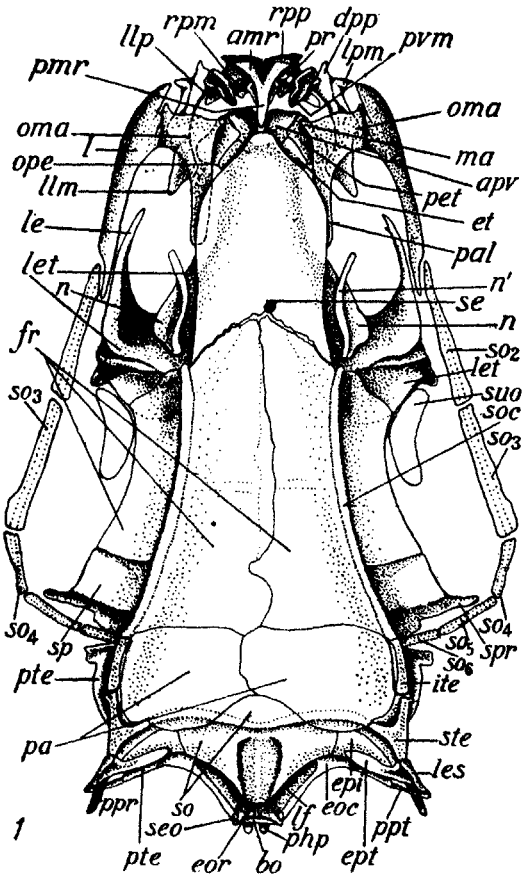
The results of my observations will be published in a series of papers and the skull of *Gyrinocheilus kaznakoi* Berg will form the theme of the first paper.

The systematic position of *Gyrinocheilus* was till recently unsettled; it was referred to the subfamily Homalopterinae by Vaillant and later Regan (1911) pointed out that to make it a type of a separate family or subfamily would be to obscure its cyprinid relationship and placed it next to *Crossocheilus* and *Garra* (*Discognathus*) in the Cyprinidae. Hora (1923), however, by a study of the external characters of the fish, while admitting the similarities between *Crossocheilus* and *Garra* on the one hand and *Gyrinocheilus* on the other, erected the family Gyrinocheilidae to accommodate it, a procedure also adopted by Berg (1940).

Popta (1906) described a fish *Paracrossocheilus bicornis* from Borneo showing greater similarities to *Gyrinocheilus* than to either *Garra* or *Crossocheilus*; however, I have not been able to study this fish on account of the paucity of material.

Observations.*

The ethmoid region: In the skull of *Gyrinocheilus*, the ethmoid is a prominent bone and the supraethmoid portion (figs. 1, 2, *se*) is particularly broad and articulates immovably with the frontals (fig. 1, *fr.*) as in the Cyprinidae and Catostomidae. In *Garra* (fig. 3, *se*) it is wider than long as seen in the dorsal aspect and the prevomer (figs. 3, 4, *apv*) extends considerably in front of it as a projection. In *Crossocheilus* (fig. 5, *se*) it is not so broad as in *Garra* leaving a small gap between the two prevomerine projections. In *Gyrinocheilus* the prevomerine extensions (figs. 1, 2, *apv*) are in the form of long anterior processes, one on either side of the posterior process of the median rostral (*pmr*). Articulating on either side of the ethmoid (figs. 1–6, *et*) and the prevomer (*pv*) in *Gyrinocheilus*, *Garra* and *Crossocheilus* there is a preethmoid (*pet*) with a rounded facet for articulation with the palatine (*pal*).



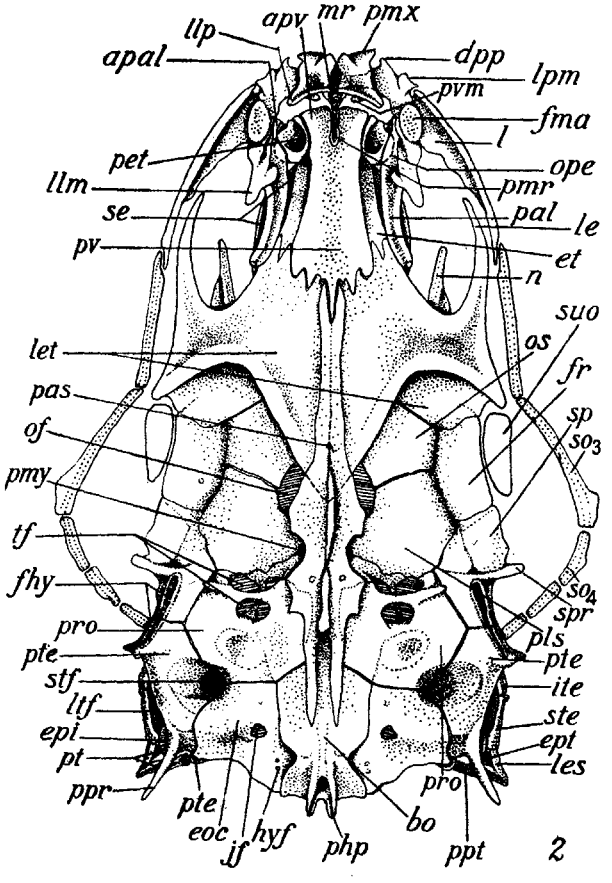


Fig. 1. Skull of *Gyrinocheilus kaznakoi* Berg. Dorsal aspect.
Fig. 2. Skull of *G. kaznakoi* Berg. Ventral aspect: the pterotic region is tilted to show the lateral temporal fossa.

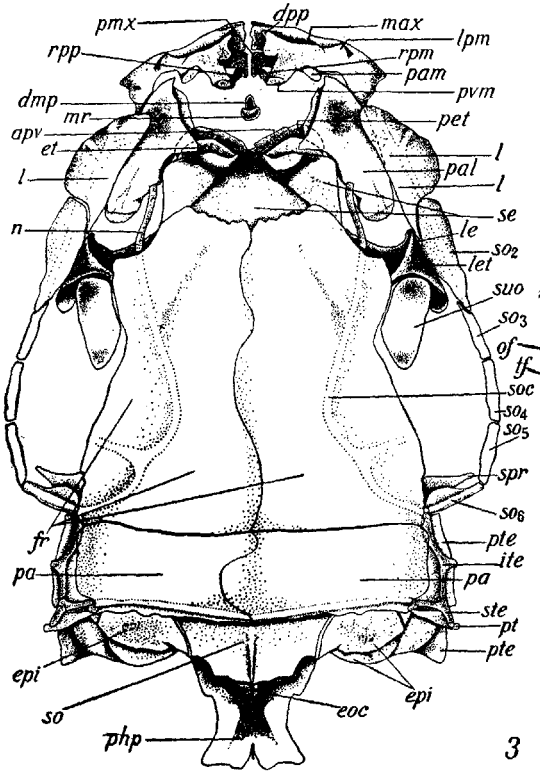
In front of the ethmoid is the median rostral (figs. 1–6, *mr*) and in *Gyrinocheilus* the rostral shows a long median process (figs. 1, 2, *pmr*) extending between the two

* All figures have been drawn at a magnification of × 17 (approx.), except figures 10–12*a*.

prevomerine extensions and anteriorly an expanded portion (fig. 1, *amr*) which comes in contact ventrally with the rostral process (*rpp*) of the premaxilla. The posterior portion of the median rostral also shows a winglike expansion on either side very near to where it expands. In *Garra* the two ends of the median rostral (figs. 3, 4, *mr*) are rounded and in the middle there is a dorsomedian projection (*dmp*); in *Crossocheilus* the middle portion shows two prominent lateral projections (fig. 5, *dlp*).

In *Gyrinocheilus*, as already said, the premaxilla shows a short but broad rostral process (fig. 1, *rpp*) and the lateral limb (*pp*) is exceedingly short. In *Garra* and *Crossocheilus* there is an elongated limb of the premaxilla towards the rostral (figs. 3–6, *rpp*) and the lateral limb (figs. 4, 6, *llp*) is short (*Crossocheilus*) or long (*Garra*).

The maxilla in *Gyrinocheilus* shows as in the Cyprinidae a premaxillary process (figs. 1, 2, *dpp*), a ventral rostral process (*rpm*), a posteriorly directed facet (*pvm*) towards the prevomer and a lateral process (*lpm*) for the attachment of the adductor mandibulae ligament. In *Garra* (figs. 3, 4) and in *Crossocheilus* (figs. 5, 6) while the above processes are noticed, however, from the posterior face of the maxilla, there are two articular facets: one (*pvm*) directed towards the prevomer and the other (*pam*) towards the palatine.



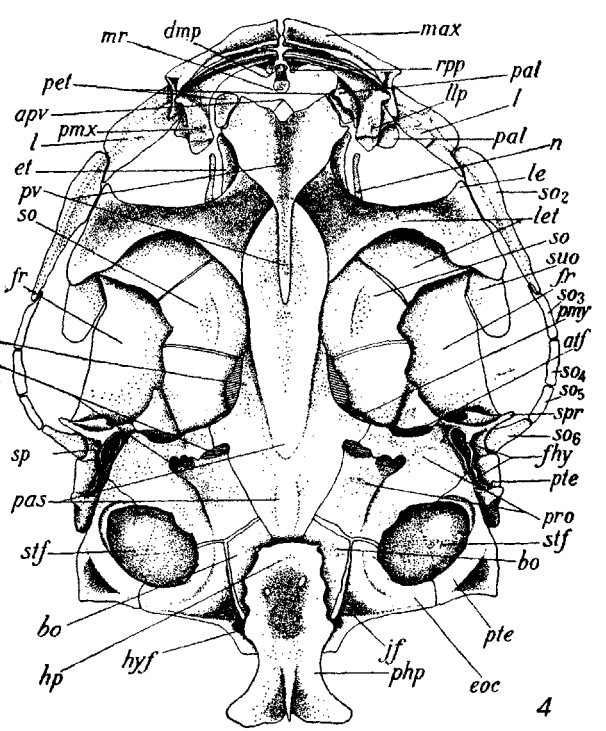


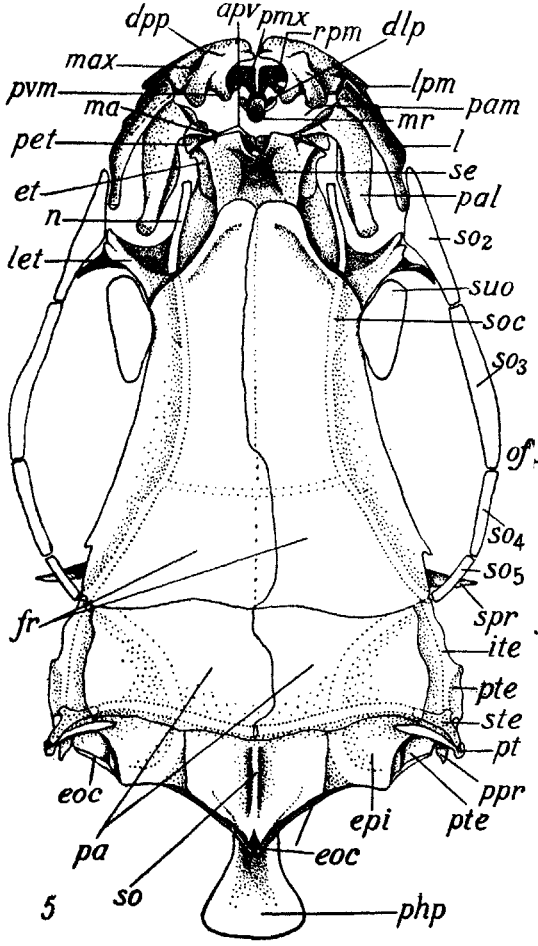
FIG. 3. Skull of *Garra mullya* Sykes. Dorsal aspect: the maxillae are pulled to show the processes.

FIG. 4. Skull of *G. mullya* Sykes. Ventral aspect: the bony process for the horny pad is incomplete.

The lateral ethmoid (figs. 1–6, *let*) is a fairly large bone on either side of the ethmoid-frontal; in *Gyrinocheilus* the bone shows a long lacrimal process (figs. 1, 2, *le*) and opposite this, there is a short projection from the lateral ethmoid.

Mesially, the two lateral ethmoids extend posteriorly far into the optic foramen (fig. 2, *of*) dorsally to the parasphenoid (*pas*), a feature not noticed in any other cyprinid fish studied by me. While in *Garra* (figs. 3, 4, *le*) the lateral processes referred to above are diminutive, they are feebly developed in *Crossocheilus*.

Flanking the lateral ethmoid in *Gyrinocheilus*, *Garra* and *Crossocheilus* there are five or six suborbital bones (figs. 1–6, *so1–so6*), the anteriormost of which is usually called the lacrimal (*l*). In *Gyrinocheilus*, the lacrimal may represent a united lacrimorostral or a lacrimojugal.



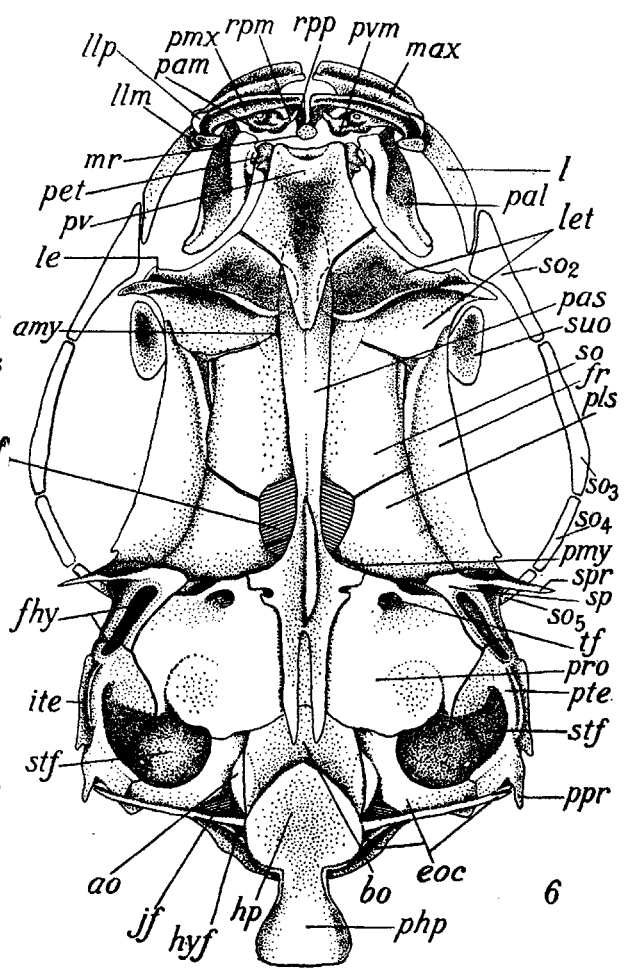


FIG. 5. Skull of *Crossocheilus latius* (Ham.). Dorsal aspect.
FIG. 6. Skull of *C. latius* (Ham.). Ventral aspect.

Ventrally, the shape of the prevomer differs in the three genera; in *Gyrinocheilus* the prevomer (fig. 2, *pv*) extends anteriorly in the form of two processes (*apv*) with an indentation in between in which, as already said, the posterior limb of the median rostral (*pmr*) is seen. The posterior portion of the prevomer is broad and a very tiny projection of it lies ventrally to the parasphenoid (*pas*). In *Garra* the anterior portion of the prevomer (fig. 4, *pv*) spreads out (*apv*) and there is a long postero-

median portion; in *Crossocheilus* while the anterior portion of the prevomer (fig. 6, *pv*) is not so broad as in *Garra*, there is a blunt posterior portion.

The orbitotemporal region: The supraorbitals (figs. 1–6, *suo*), the frontals (*fr*) with the supraorbital sensory canal (*soc*) in them, the four (*Crossocheilus*) or five (*Gyrinocheilus* and *Garra*) suborbital bones excluding the lacrimal, the large orbitosphenoids (figs. 2, 4, 6, *os, so*) and the pleurosphenoids (*pls*) and the anterior extension of the parasphenoid dorsally to the prevomer are all common to the three genera studied. Generally in the Cyprinidae, not much variation is noticed in the bones of this region.

The interorbital septum in some cyprinids (e.g. *Labeo*) is formed by a ventromedian portion of the two orbitosphenoids coming in contact with a dorsomedian portion of the parasphenoid in front of the optic foramen. In *Garra* and *Gyrinocheilus* the two orbitosphenoids are wide apart and thus there is no interorbital septum; in *Crossocheilus* however, the orbitosphenoids and the parasphenoid form a typical septum.

In each eyeball, there are two cup-shaped sclerotic bones.

The auditory region: The sensory canal does not pass through independent ossicles in this region as in the orbital. On the dorsal aspect of the pterotic region of *Garra* and *Crossocheilus*, the sensory canal in the intertemporal ossicular region (figs. 3, 5, *ite*) passes in the pterotic bone like the supraorbital canal in the frontal. Posteriorly, there is also a triradiate canal connecting the temporal and the occipital canals and leading to the lateral line; the lateral limb of this is very small. This is the supratemporal ossicular region. Similarly in *Gyrinocheilus* leading from the supraorbital canal, the temporal canal passes in the pterotic probably representing the intertemporal of other forms while posteriorly, in the same bone, it passes through the Y-shaped supratemporal (*ste*) region. The supratemporal establishes contact with the occipital sensory canal mesially and anteriorly with the temporal canal and posteriorly with the lateral line ossicle (*les*) on the post-temporal. In these features *Gyrinocheilus* resembles the cyprinids closely.

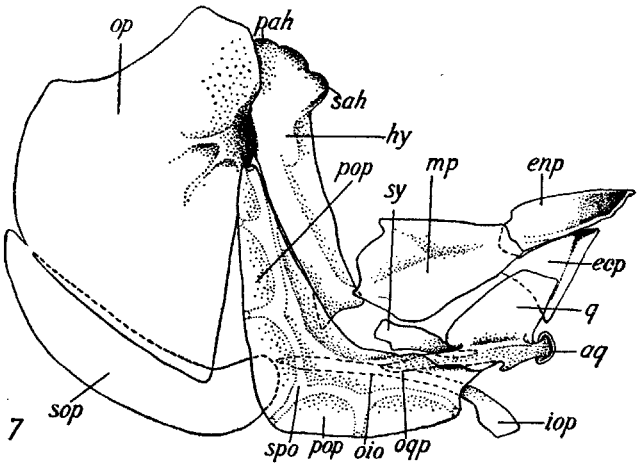


FIG. 7. Lateral aspect of the right upper jaw and opercular bones without the palatine of *Gyrinocheilus kaznakoi* Berg.

On the ventral aspect, the sphenotic (figs. 2, 4, 6, *sp*) and the pterotic (*pte*) show articular facets for the hyomandibula (*fhy*) in all the three genera examined and peculiarly in *Gyrinocheilus* (figs. 1, 2) and *Crossocheilus* (figs. 5, 6) the pterotic shows a spinelike process (*ppr*) posteriorly.

The prootic shows in *Gyrinocheilus*, *Garra* and *Crossocheilus* the orifices (figs. 2, 4, 6, *tf*) for the exit of the branches of the fifth and seventh cranial nerves. Similarly in all the three examples, the external opening of the posterior myodome (*pmy*) is noticed between the lateral limb of the parasphenoid and the dorsally lying pleurosphenoid; in addition an anterior myodome (fig. 6, *amy*) is also noticed in *Crossocheilus*.

In *Gyrinocheilus*, there is a large lateral temporal fossa (fig. 2, *ltf*) bounded mesially by the epiotic (*epi*) and the pterotic (*pte*), posteriorly by the epiotic and anteriorly by the pterotic. Dorsally there is the parietal (*pa*) and forming the edge of the latter, the pterotic with the intertemporal (*ite*) and supratemporal (*ste*) are present. The subtemporal fossa (*stf*) projects into the fossa above. A lateral temporal fossa is absent not only in *Garra* and *Crossocheilus* but also in the other cyprinids studied by me.

The shallow subtemporal fossa referred to above is formed by the three bones, viz., the prootic, the pterotic and the exoccipital in *Gyrinocheilus* (fig. 2, *stf*); in *Garra* (fig. 4) and *Crossocheilus* (fig. 6, *stf*) it is large and is bounded by the prootic, the epiotic, the pterotic and the exoccipital.

The exoccipitals (fig. 1, *eoc*) in *Gyrinocheilus* do not extend dorsally and form the roof for the foramen magnum posterior to the supraoccipital as in the case of *Garra* (fig. 3, *eoc*) and *Crossocheilus* (fig. 5, *eoc*). They also do not show a fontanel as in the cyprinid examples. However, between the supraoccipital (fig. 1, *so*) and the exoccipital (*eoc*) on either side of the foramen magnum, there is a large gap (*lf*) very suggestive of a reminiscent fontanel in *Gyrinocheilus*.

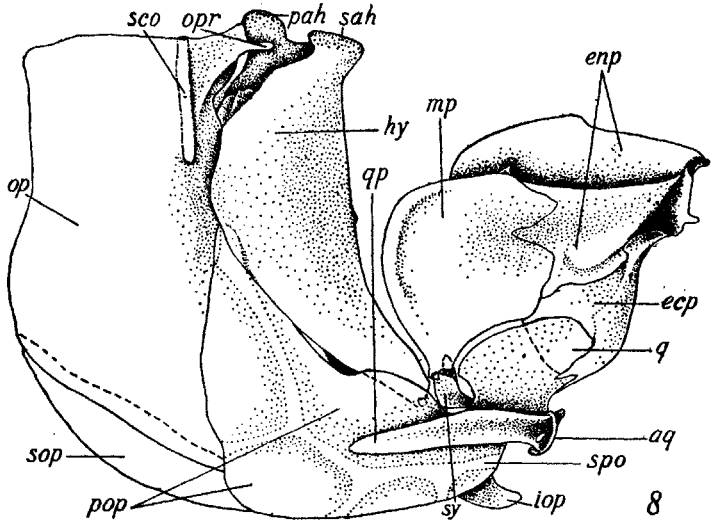


FIG. 8. Lateral aspect of the right upper jaw and opercular bones, without the palatine of *Garra mullya* Sykes.

Further, as in the Cyprinidae and the Cobitidae each exoccipital in *Gyrinocheilus* gives rise to a projection mesially (fig. 1, *eor*) and between the projections of the exoccipital and the dorsal aspect of the basioccipital (*bo*) is the recess for the sinus impar which opens posteriorly by an orifice (*seo*) in each exoccipital.

The basioccipital in *Gyrinocheilus* (fig. 2, *bo*) shows only two posterior projections (figs. 1, 2, *php*) which do not unite below the dorsal aorta; in *Garra* and *Crossocheilus* (figs. 4, 6, *php*) there is a well developed pharyngeal process extending below the aorta and also an anteriorly expanded plate (*hp*) for the attachment of a horny

pad. The absence of such an anterior projection for the attachment of a horny pad in *Gyrinocheilus* has already been noted by Regan (1911).

The supraoccipital (fig. 1, *so*) roofs the foramen magnum in *Gyrinocheilus* and between it and each exoccipital, as already noted, there is a large gap (*lf*).

The upper jaw: The upper jaw shows the characteristic bones, viz., the hyomandibula (figs. 7, 8, 9, *hy*), the metapterygoid (*mp*), the entopterygoid (*enp*), the ectopterygoid (*ecp*), the quadrate (*q*) with its posterior process (*qp*), the symplectic (*sy*), the preopercular (*pop*) and the other opercular bones (*op*, *iop*, *sop*) associated with it in all the three genera *Gyrinocheilus*, *Garra* and *Crossocheilus*. The preopercular (figs. 7, 8, 9, *pop*) is large showing the passage of the sensory canal (*spo*) in it. While in these features there is close similarity of the upper jaw bones in the three genera, there are however, some important differences. The opercular of *Garra* (fig. 8, *op*) and of *Crossocheilus* (fig. 9, *op*) shows a large sensory canal (*sco*) which connects the temporal and the preopercular canals. There is also a prominent process (*opr*) given off from the opercular towards the hyomandibula near the latter's pterotic articular facet; the opercular of *Gyrinocheilus* (fig. 7, *op*) does not show these two features. The posterior limb of the quadrate in *Gyrinocheilus* (*oqp*) is mesially lodged in a groove of the preopercular while in *Garra* (fig. 8, *qp*) and *Crossocheilus* (fig. 9, *qp*) the posterior process of the quadrate is lateral to the preopercular (*pop*).

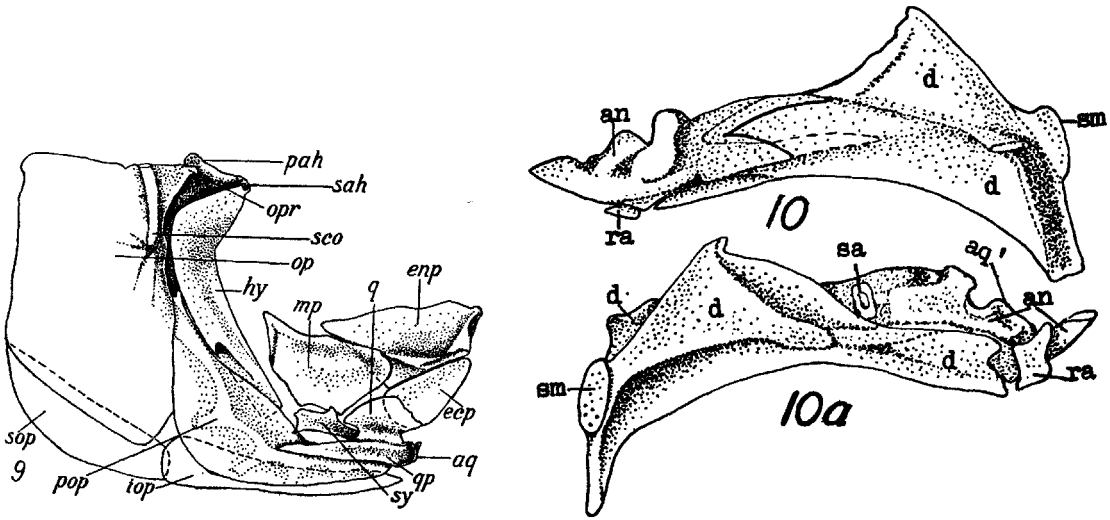


FIG. 9. Lateral aspect of the right upper jaw and opercular bones, without the palatine of *Crossocheilus latius* (Ham.).
FIG. 10. Lateral aspect of the right ramus of the lower jaw of *Gyrinocheilus kaznakoi* Berg.
FIG. 10*a*. Mesial aspect of the same.

The lower jaw: As in *Garra* (fig. 11) and *Crossocheilus* (fig. 12), the lower jaw of *Gyrinocheilus* (fig. 10) shows the four bones, viz., the dentary (*d*), the angular (*an*), the sesamoid angular mesially (*sa*), and the retroarticular (*ra*), the last being a cartilage bone. In *Garra* (fig. 11) and *Crossocheilus* (fig. 12) the dentary and the angular show the passage of sensory canals (*scd*, *asc*) in them; in *Gyrinocheilus* (fig. 10) the passage of the canal was not clear. There is not much difference between the lower jaw of *Gyrinocheilus* and that of the Cyprinidae except however, in the shape of the bones.

The hyobranchial apparatus: The hyobranchial apparatus of *Gyrinocheilus* shows many interesting features. There is a median basihyal (fig. 13, *bh*) lying dorsally to the two pairs of hypohyals (hh_1, hh_2); there are four median bony copulae

(cop_1–cop_4) representing the united basibranchials. As pointed out by Vaillant (1902) there are two pairs of gillrakers on the dorsal aspect of each branchial arch and these rakers extend in double rows on the dorsal aspect of the median copulae also. There are only *two* pairs of hypobranchs (hb_1, hb_2) in connexion with the first two branchial arches. In the cyprinid examples studied by me and in the Cyprinidae in general, there are uniformly the first three pairs of hypobranchs, the last two pairs of branchial arches being devoid of them. There are three pairs of pharyngobranchs (pb_1, pb_2, pb_3) in *Gyrinocheilus* representing the first, the second and probably the fused third and fourth pharyngobranchs. The fifth pair of ceratobranchs (cb_5) is thin and slender and is devoid of teeth unlike what is noticed in the cyprinid examples studied. The parahyoid is attached to the basihyal by means of two processes while posteriorly it shows a winglike expansion resembling the cyprinid one. Thus in the possession of two hypobranchs, four copulae, three pharyngobranchs and the edentulous fifth pair of ceratobranchs, the hyobranchial apparatus of *Gyrinocheilus* differs from that of the Cyprinidae.

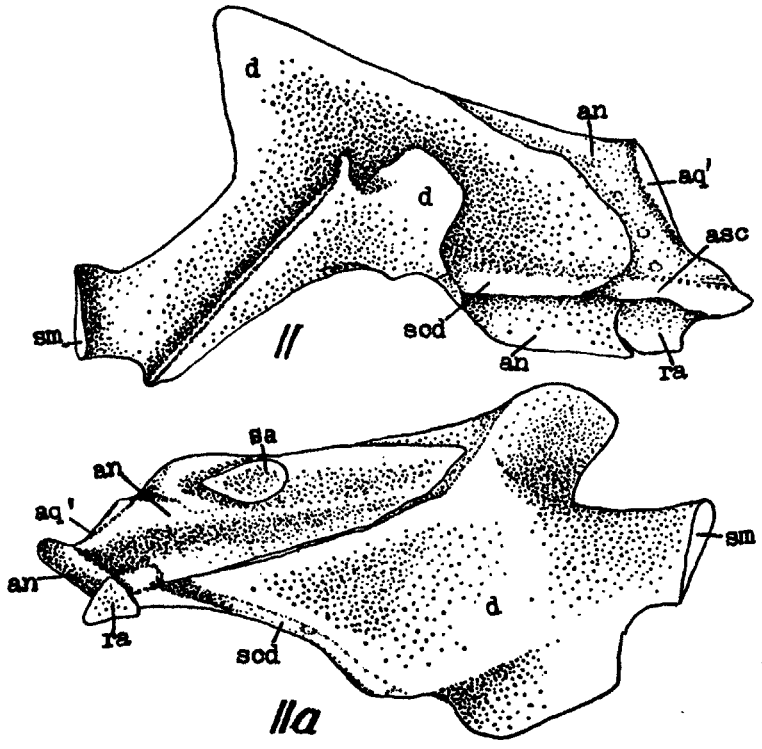


FIG. 11. Lateral aspect of the right ramus of the lower jaw of *Garra mullya* Sykes.
FIG. 11a. Mesial aspect of the same.

The Weberian apparatus: The Weberian apparatus is closely associated with the first four vertebrae and that in the Ostariophysi has been exhaustively described by previous workers (Sagemehl, 1885; Hora, 1922; Evans, 1925; Chranilov, 1927; Watson, 1939; Krumholz, 1943; Nelson, 1948). For purposes of comparison, I have drawn a figure of the Weberian apparatus and the first five vertebrae of *Garra* (fig. 14). In *Garra* the short first centrum (c_1) with its elongated dorsal rib is devoid of its dorsal part. This dorsal part has, however, been noticed in *Labeo* (Sarbahi, 1932) where it is described as the keystone part. What exactly

is the origin of this Λ-shaped piece, it is difficult to say now. It is very likely that just as 'a large mass of cartilage which, in the adult stage, when the centra of the second and third vertebrae have fused, becomes ossified to form the neural spine and arches of the "compound" vertebra' (Watson, 1939), this also represents an ossification in the region of the second vertebra and not first, and we are therefore justified in calling it the second neural arch and spine (fig. 14, na_1) as has been done by me. However, Matveiev (1929) and Watson (1939) referred to a peculiar ring of cartilage surrounding the spinal cord in the region of the first vertebra and the latter author opined that it might be the extension of the exoccipitals and in the adult it formed a bony covering for the cavum sinus imparis. The centra of the second and third vertebrae are fused in *Garra* as in *Labeo* (Sarbahi, 1932); however, in the Cyprinidae Regan (1911) recorded that the first two vertebrae were free. Anteriorly from the centrum of the second vertebra there arises a large dorsal rib in *Garra* (fig. 14, pr_2). As described by Watson (1939) in the goldfish, the neural arch in the region of the third vertebra in *Garra* may also be an ossification in a large mass of cartilage in this region. The fourth vertebra is typical and shows an elongated dorsal rib (fig. 14, pr_4) and a large neural spine (ns_4).

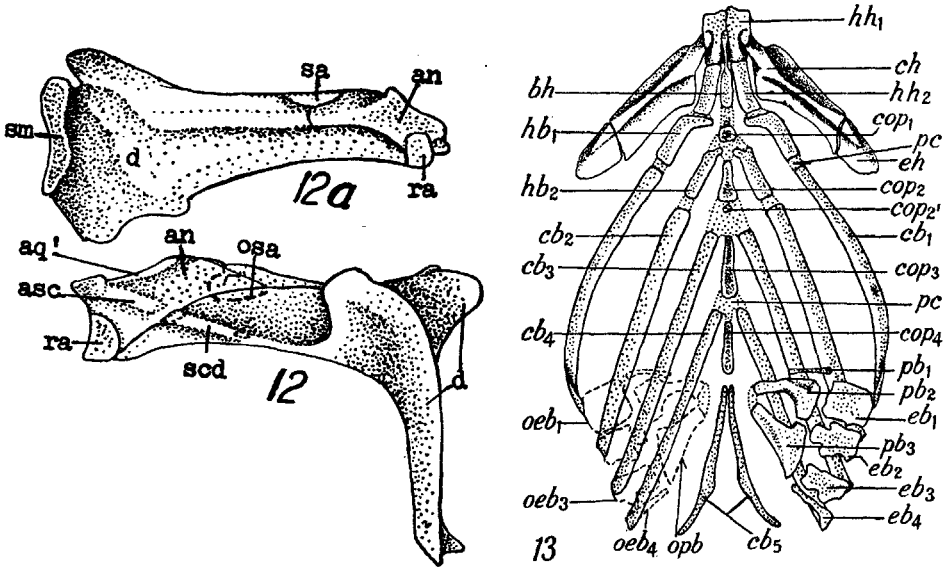
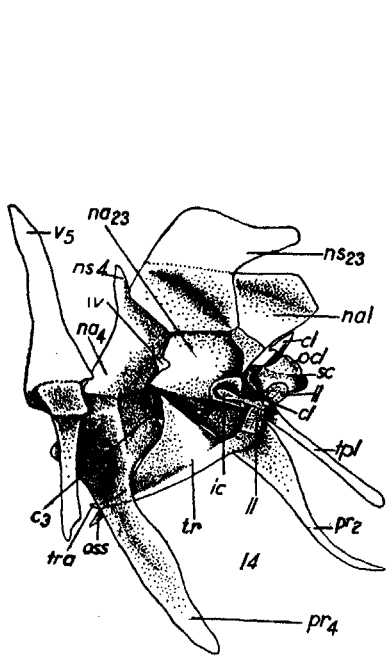


FIG. 12. Lateral aspect of the right ramus of the lower jaw of *Crossocheilus latius* (Ham.).
FIG. 12*a*. Mesial aspect of the same.
FIG. 13. Hyobranchial apparatus of *Gyrinocheilus kaznakoi* Berg.

Associated with the second neural arch described above, there is the claustrum (fig. 14, *cl*) in *Garra* and it fits into the cupshaped second bone,—the scaphium (*sc*) of the apparatus. From the scaphium there arises the thick interosseous ligament (*li*) in which the outer end of the intercalarium (*ic*) is noticed with its inner end (the basidorsal portion) coming in contact with the neurocentral suture of the second vertebra resembling exactly the figure of the cyprinid type of the Weberian apparatus drawn by Chranilov (1927). From the outer end of the ligament in *Garra*, there is the large triradiate tripus (*tr*); a mesial limb of this comes in contact with the posterior part of the united centrum of the second and third vertebrae. The bent spinelike posterior end of the tripus is attached to the anterior wall of the gasbladder.

Watson (1939) derived the Weberian ossicles in the goldfish somewhat differently from the previous authors. According to him, the claustrum arose as a membrane

bone in the mesenchymatous mass in the inner wall of the atrium sinus imparis. The scaphium was of dual origin; the basidorsal of the first vertebra united with a few mesenchymatous cells to give rise to this second ossicle. The intercalarium also arose in part (the articular process) from the basidorsal of the second vertebra and partly as a sesamoid bone (manubrium incudis). The anterior and articulating processes of the tripus were basiventral derivatives of the third vertebra; the main body of it was derived from a mesenchymatous mass and the rib rudiment gave rise to the transformator processes which latter came in contact with the gasbladder.



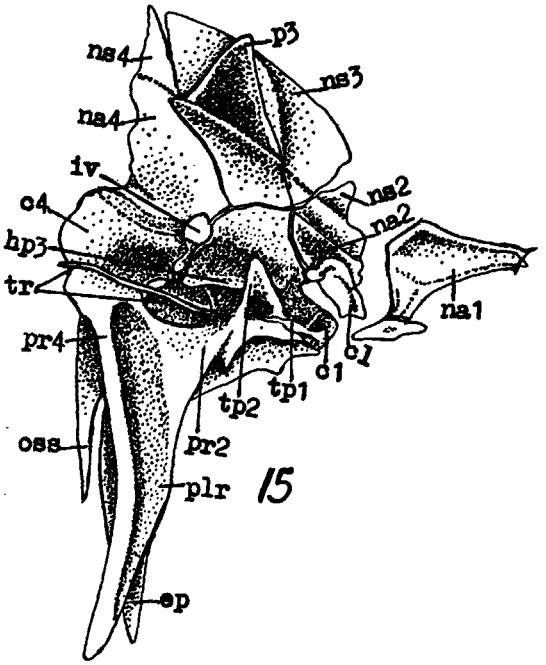


FIG. 14. Right lateral view of the first five vertebrae and Weberian ossicles of *Garra mullya* Sykes.

FIG. 15. Right lateral view of the first four vertebrae of *Gyrinocheilus kaznakoi* Berg.

With this as the background if we examine the Weberian apparatus of *Gyrinocheilus*, certain important differences are noticed. The first thing that one notices is the semicircular arch (fig. 15, na_1) in front of the first vertebra. As already said, this may represent an ossification of an independent piece of cartilage in front of the first pair of basidorsals. Just as Watson (1939) has labelled similar ossification in the second-third vertebral region as neural arch and spine, I have also called this the first neural arch in *Gyrinocheilus* (fig. 15, na_1). The first vertebra is represented by the centrum (c_1), a pair of dorsal ribs (tp_1) or transverse processes according to older nomenclature, and the scaphium (not shown in the figure) which, following Watson (1939), is probably derived from the basidorsal of this segment. The centra of the second and third vertebrae are fused and anteriorly, the centrum of the second vertebra shows a laterally directed short dorsal rib (tp_2) and a pleural rib (pr_2) which has united with a similar pleural rib (pr_4) of the fourth vertebra simulating the condition met with in the Catostomidae (Nelson, 1948). The third vertebra is devoid of dorsal or pleural ribs; the neural arches and spines of the second and third vertebrae (fig. 15, na_2, ns_2, ns_3) are *not* fused but are independent as in the Catostomidae. The neural arch and spine of the third vertebra in *Gyrinocheilus* is also expanded as in the Catostomidae (Nelson, 1948) and is probably

formed by the addition of the interspinous elements and represents, like the catostomid one, a neural complex. Further, the neural complex also bears on either side a prominent process (p_3) in *Gyrinocheilus*, which however, is not seen in Catostomidae. In the Cyprinidae, the neural arches of the second and third vertebrae arising independently of their basidorsals unite to form a composite structure (Sarbahi, 1932; Watson, 1939). There is a lateral shelflike projection (hp_3) from the pedicel of the third vertebra in *Gyrinocheilus* mesially to the dorsal rib (tp_2) of the second vertebra extending anteriorly over the united second and third centra. A similar shelf is also described in the Catostomidae by Chranilov (1926) and Nelson (1948). The pleural rib* (pr_2) arising from the centrum of the second vertebra in *Gyrinocheilus* and uniting with that of the fourth vertebra (pr_4) leaves a large paravertebral gap below the shelf referred to above between the third and fourth vertebrae. The neural arch (na_4) and neural spine (ns_4) of the fourth vertebra are slightly enlarged and there is a large intervertebral foramen (iv) between the third and fourth neural arches. The pleural ribs of the fourth vertebra are not united mesially to form a 'transverse plate' as in the Catostomidae (Chranilov, 1926; Nelson, 1948) but each shows from its incomplete transverse projection an elongated posterior process,—the os suspensorium (*oss*) representing the haemapophyses of the segment and also an esophageal process (*ep*) supporting the esophagus as in the Catostomidae. This arrangement of parts in the first four vertebrae of *Gyrinocheilus* suggests a possible evolution towards the catostomid type.

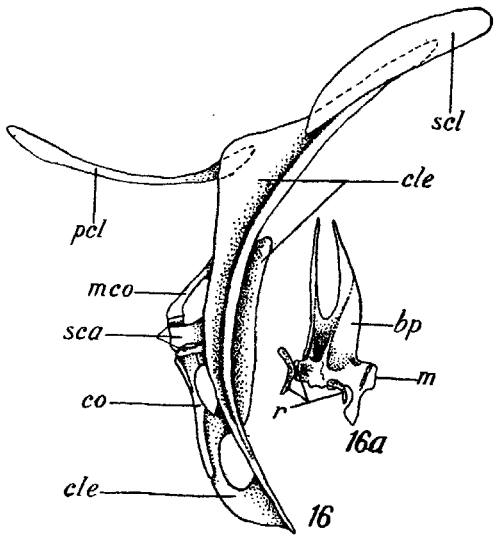


FIG. 16. Pectoral girdle of the right side of *Gyrinocheilus kaznakoi* Berg.
FIG. 16*a*. Pelvic girdle of the right side of *G. kaznakoi* Berg.

Fitting into the inner face of the claustrum in *Gyrinocheilus* (fig. 15, *cl*) is the scaphium (not drawn in the figure) from the ventral face of which is a ligament in which a nodulelike intercalarium is seen. The ligament passes below the shelflike extension of the third neural arch and meets the tripus (*tr*). The tripus which is lodged in the paravertebral gap between the third and fourth vertebrae, articulates with the third centrum by a facet and posteriorly has a process which comes in contact with the gasbladder.

* Following the nomenclature of Nelson (1948).

The arrangement of the first four vertebrae and the disposition of the ossicles in *Gyrinocheilus* resembles more the condition met with in the Catostomidae and, therefore, differs from the Cyprinid type.

The girdles: The pectoral girdle of *Gyrinocheilus* (fig. 16) differs from that of the Cyprinid only in shape while all the bones of the girdle, viz., the supracleithrum (*scl*), the cleithrum (*cle*), the coracoid (*co*), the mesocoracoid (*mco*), the postcleithrum (*pcl*) and the scapula (*sca*) are noticed. The pelvic girdle (fig. 16*a*) possessing a large pair of pelvic bones (*bp*) resembles that of the cyprinid in shape also.

Discussion.

There are a few features in which the skull of *Gyrinocheilus* resembles that of *Garra* and *Crossocheilus* or the Cyprinidae in general but there are a number of important features in which it differs.

The possession of a broad supraethmoid part of the ethmoid bone which firmly articulates with the frontals and the anterolaterally situated nodule of bone,—the pre-ethmoid articulating with the anterior extension of the prevomer and the ethmoid are characteristic of Cyprinidae. In *Gyrinocheilus* also, the firmly united supra-ethmoid portion of the ethmoid and the pre-ethmoid are noticed.

The premaxillae and maxillae of *Gyrinocheilus* though showing the characteristic processes noticed in the Cyprinidae, differ in size and disposition. The rostral process of the premaxilla, however, is very short and does not lie dorsally to the rostral and the lateral process of the premaxilla is also very short; it does not run in companionship with that of the maxilla as in the cyprinids. From the posterior face of the maxilla there is a large prominent prevomerine process in *Gyrinocheilus* while in the Cyprinidae, there are two; one for the articulation with the palatine and the other with the prevomer.

The median rostral itself differs in shape from what is seen in the Cyprinidae. The bone is almost anchorshaped and as recorded above, it is not overlain by the premaxillary process. The posteromedian limb is noticed between the anterior projections of the prevomer.

The prevomer of *Gyrinocheilus* in its anterior extensions and in its articulation with the pre-ethmoid resembles the Cyprinidae; but the shape of the entire bone is very different from what is seen in the Cyprinidae. The long or short posteromesial process so commonly met with among the Cyprinidae is not so prominently noticed in *Gyrinocheilus*; the anterior processes of the prevomer are long and invariably in the Cyprinidae, the ethmoid extends as a median projection dorsally to the prevomer and this projection is absent in *Gyrinocheilus*, where however, the posterior process of the rostral is accommodated in between the two projections of the prevomer.

The lateral ethmoid of *Gyrinocheilus* differs from that seen in the Cyprinidae in two important respects; while the lacrimal process (or lacrimojugal process) of the lateral ethmoid in *Gyrinocheilus* is long unlike in *Garra* and *Crossocheilus*, the posterior process is considerably reduced. Further, on the ventral aspect, the lateral ethmoids extend far posteriorly so as to underlie the optic foramen, a feature not met with in any cyprinid studied.

In a number of cyprinids the ventral portions of the orbitosphenoids come together and project to meet a dorsal process coming up from the parasphenoid to form an interorbital septum; in others this septum may be absent. In *Gyrinocheilus* an interorbital septum is wanting.

The sensory canal bones conform to the cyprinid type. The lacrimal in *Gyrinocheilus* is a fairly long bone coming in contact with the lateral aspect of the palatine. It is not possible to say if this bone represents an united lacrimojugal or lacrimorostral. There are six canal bones in the suborbital series including the lacrimal.

In the pterotic region the canal bones are not independent but are incorporated in the roof of the pterotic; there is one corresponding to the intertemporal or temporal

and a posterior triradiate one corresponding to the supratemporal, the latter establishing connexion with the occipital canal mesially and the lateral line posteriorly. In the cyprinids also, the intertemporal or temporal and the supratemporal are not seen as independent bones but the canal passes through the dorsal aspect of the pterotic.

There is a very peculiar feature in the pterotic region of *Gyrinocheilus*. There is a lateral temporal fossa which is bounded mesially by the epiotic and the pterotic and posteriorly and anteriorly by the epiotic and pterotic respectively. Dorsally the parietal roofs it. In his description of the Cyprinidae, Regan (1911) did not refer to this interesting feature in *Gyrinocheilus*, a species of which he examined. The fossa in *Gyrinocheilus* does not correspond with the one described by Regan either in the Catostomidae or Cyprinidae. In the former family, he stated that paired fossae were present in the temporal region 'open above and closed behind but no posterior temporal fossae'. Similarly in the Cyprinidae he recorded that there were no temporal depressions, 'but supratemporal fossae more or less distinct, open behind, roofed by the posttemporal and sometimes by the pterotic and parietal' were present. Obviously, *Gyrinocheilus* in possessing a lateral temporal fossa which in being closed above differs from the Catostomidae and in being closed behind differs from the Cyprinidae.

The auditory region of *Gyrinocheilus* also shows a subtemporal fossa accommodated in the pterotic, prootic and exoccipital bones like the cyprinids and catostomids and this fossa gently projects into the lateral temporal fossa.

In the Cyprinidae the two exoccipitals bound the foramen magnum dorsally. They also extend mesially over the basioccipital to form a chamber for the accommodation of the sinus impar of the endolymphatic sacs; a lateral fenestra is also seen in each exoccipital. In *Gyrinocheilus*, the exoccipitals do not bound the foramen magnum nor do they disclose fontanels. However, there is a large notch between the supraoccipital and each exoccipital suggestive of a reminiscent fontanel.

The basioccipital in *Gyrinocheilus* shows two projections posteriorly which however, do not unite below the aorta and therefore, the condition resembles that in the Homalopteridae (Regan, 1911). It has already been recorded by Regan that a horny pad covering the bony extension of the basioccipital, a distinguishing feature of the Cyprinidae is absent in *Gyrinocheilus*.

In possessing the typical bones of the upper and lower jaws, *Gyrinocheilus* resembles closely the Cyprinidae; but there are at least three important differences noticed in the upper jaw of that species. In *Garra* and *Crossocheilus*, the opercular shows a prominent process towards the pterotic facet of the hyomandibula and also a sensory canal which connects the temporal (or intertemporal) with the preopercular. The opercular of *Gyrinocheilus* does not show these features. Further, the posterior process of the quadrate is disposed laterally to the preopercular in *Garra* and *Crossocheilus* while in *Gyrinocheilus* the process is mesial.

There are three important features in which the hyobranchial apparatus of *Gyrinocheilus* differs from that in the Cyprinidae. There are three pairs of pharyngobranchs and two pairs of hypobranchs in *Gyrinocheilus* whereas in the cyprinids, there are two pairs of pharyngobranchs and three pairs of hypobranchs. The fifth pair of ceratobranchs is slender in *Gyrinocheilus* and is devoid of teeth (Regan, 1911) unlike what is seen in the Cyprinidae. The occurrence of double row of gill-rakers on the dorsal aspect of the branchial arches of *Gyrinocheilus* has already been recorded by Regan. Peculiarly the rakers extend on the median copulae also. In the Cyprinidae, the branchial arches and the copulae are free of rakers.

The first four vertebrae are modified in *Gyrinocheilus* and resemble those in Catostomidae more than those in the Cyprinidae. The fusion of the pleural ribs* of the second and fourth vertebrae by the side of the third centrum leaving a large

* Following the nomenclature of Nelson (1948).

paravertebral space, the absence of dorsal or pleural ribs from the third vertebra and the possession of a horizontal shelf extending over the paravertebral space referred to above and the partial covering of the tripus by the shelf and the occurrence of independent second and third neural arches and spines in *Gyrinocheilus* are all features common to the Catostomidae. But in *Gyrinocheilus* the formation of the 'transverse plate' from the mesial aspect of the fourth pair of pleural ribs is not so complete as in the Catostomidae. In the Cyprinidae, the centra of the second and third vertebrae are fused, there is no extension from the pedicel of the third vertebra in the form of a shelf to cover the large tripus. Further, the transverse processes are really the dorsal ribs (Watson, 1939), a point which I am not able to substantiate in *Gyrinocheilus* as I have not studied its development. Similarly I am not commenting upon the origin of the Weberian ossicles in *Gyrinocheilus*.

Conclusion: In order to assess the systematic position of *Gyrinocheilus*, it is necessary to find out in what characters the skull of the same resembles that in the cyprinoids. In the nature and disposition of the ethmoid, in the general arrangement of the bones of the upper and lower jaws, in the disposition of the sensory canal bones in the orbitotemporal and auditory regions, in the possession of a pre-ethmoid bone and of a subtemporal fossa *Gyrinocheilus* resembles closely the Cyprinidae.

These similarities could not be without significance. Undoubtedly *Gyrinocheilus* must have taken its origin from a cyprinoid ancestor and probably moved parallelly with the Cyprinidae and Catostomidae since the Weberian apparatus in the Siamese species is more catostomid in construction than cyprinid, but it deviated from the parental stock much, and it now exhibits the following differences from the Cyprinidae:

1. The shape of the median rostral is unlike what is generally seen in the Cyprinidae.
2. The premaxilla does not show an elongated rostral process nor a large lateral limb.
3. The palatine while showing an articular facet for the lacrimal (lacrimojugal or lacrimorostral) possesses a long posterior process for the articulation of the entopterygoid.
4. The prevomer shows two elongated anterior processes and posteriorly, it is widened; a posteromedial process is barely indicated.
5. The lateral ethmoid shows laterally a prominent lacrimal (lacrimojugal or lacrimorostral) process while the posterolateral process is reduced; the ventromesial portion extends into the optic foramen.
6. The prootic region exhibits a lateral temporal fossa.
7. The exoccipitals do not bound the foramen magnum nor do they exhibit the lateral fenestra; the basioccipital does not show a large pharyngeal process uniting below the dorsal aorta.
8. The hyobranchial apparatus shows two hypobranchs and three pharyngobranchs and the gillrakers extend on the dorsal aspect of the copulae also.
9. In the upper jaw, the opercular does not show a process towards the hyomandibula as in *Garra* and *Crossocheilus*, nor a sensory canal in it; the posterior process of the quadrate is not lateral but mesial in disposition.
10. The Weberian apparatus resembles more the catostomid type.

A comparison of the figures of the dorsal and ventral aspects of *Garra*, *Crossocheilus* and *Gyrinocheilus* reveals at once the differences between the cyprinid genera and the latter; in the shape and disposition of the premaxilla, of the prevomer, of the lateral ethmoid, of the ethmoid, of the nasal, and of the great elongation of the ethmoid region of *Gyrinocheilus* and in the absence of a fontanel bounded by the exoccipital and in the possession of a lateral temporal fossa, *Gyrinocheilus* differs

from *Garra* and *Crossocheilus* in particular and in order to find out the probable progenitor from which *Gyrinocheilus* could have taken its origin, I have searched in vain. The characters appear to be so aberrant that it has not been possible to derive *Gyrinocheilus* from any native cyprinid genus that I have studied. I have not examined any exotic forms and in its modification of the first four vertebrae and in the disposition of the Weberian apparatus, *Gyrinocheilus* resembles more the catostomid of which no representative is found in India and therefore, I could only venture to say, at present, that the probable ancestor of *Gyrinocheilus* may not be an Indian cyprinid.

In view of the overwhelming differences between the cyprinid and *Gyrinocheilus* skulls, there is ample justification for the erection of the family Gyrinocheilidae to accommodate the single genus *Gyrinocheilus* as has been done by Hora (1923).

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Key to lettering.

amr., anterior process of median rostral; *amy.*, anterior myodome; *an.*, angular; *apv.*, anterior projections of the prevomer; *aq.*, articular facet for lower jaw; *aq'.*, articular facet for quadrate; *asc.*, sensory canal in the angular; *atf.*, anterior opening of the trigeminofacialis chamber; *bh.*, basihyal; *bo.*, basioccipital; *bp.*, pelvic bone; c_1, c_2, c_3, c_4, centrum of the first, second, third and fourth vertebrae; cb_1, cb_2, cb_3, cb_4, cb_5, ceratobranchials 1, 2, 3, 4, 5; *ch.*, ceratohyal; *cl.*, claustrum; *cle.*, cleithrum; *co.*, coracoid; cop_1, cop_2, cop_3, cop_4, copulae 1, 2, 3, 4; cop_2', a median ossification posterior to copula 2; *d.*, dentary; *dlp.*, dorsolateral process of median rostral; *dmp.*, dorsomedian process of median rostral; *dpp.*, dorsal premaxillary process of maxilla; eb_1, eb_2, eb_3, eb_4, epibranchials 1, 2, 3, 4; *ecp.*, ectopterygoid, *enp.*, entopterygoid; *eoc.*, exoccipital; *eor.*, exoccipital roof of the sinus impar; *ep.*, esophageal process; *epi.*, epiotic; *ept.*, epiotic articulation of post-temporal; *et.*, ethmoid; *fhy.*, articular facet in pterotic and sphenotic; *fma.*, articular facet in the maxilla; *fr.*, frontal; hbr_1, hbr_2, hypobranchial 1, 2; hh_1, hh_2, hypohyal 1, 2; *hp.*, bony plate for attachment of horny pad; hp_3, horizontal projection from third vertebra; *hy.*, hyomandibula; *ic.*, intercalarium; *iop.*, interopercular; *ite.*, intertemporal region; *iv.*, intervertebral foramen; *jf.*, jugular foramen; l., laçrimorostral; *le.*, lacrimorostral projection of lateral ethmoid; *les.*, lateral extrascapular; *let.*, latera lethmoid; *lf.*, the reminiscent lateral fenestra between the supraoccipital and exoccipital; *li.*, ligament; *llm.*, lateral process of maxilla; *llp.*, lateral limb of premaxilla; *lpm.*, lateral projection of premaxilla; *ltf.*, lateral temporal fossa; *m.*, median articular facet of pelvic bone; *ma.*, median preethmoid articular facet of palatine; *max.*, maxilla; *mco.*, mesocoracoid; *mp.*, metaptérygoid; *mr.*, median rostral; *n.*, nasal; *n'.*, sensory canal in nasal; na_1, neural arch of vertebra 1 in fig. 15 and vertebra 2 in fig. 14; na_2, neural arch of vertebra 2 in fig. 15; na_4, neural arch of vertebra 4; na_{23}, neural arch of vertebra 3; ns_4, neural spine of vertebra 4; ns_{23}, neural spine of vertebra 3; *ocl.*, outline of claustrum; oeb_1, oeb_3, oeb_4, outline of epibranchials 1, 3, 4; *of.*, optic foramen; *oio.*, outline of interopercular; *oma.*, outline of maxilla; *op.*, opercular; *opa.*, outline of palatine; *opb.*, outline of pharyngobranchs 3, 4; *ope.*, outline of pre-ethmoid; *opr.*, opercular process towards hyomandibula; *oqp.*, outline of quadrate process; *os.*, orbitosphenoid; *osa.*, outline of sesamoid angular; *oss.*, projection of os suspensoria; *pa.*, parietal; *pah.*, pterotic articular facet of hyomandibula; *pal.*, palatine; *pam.*, palatine process of maxilla; *pas.*, parasphenoid; pb_1, pb_2, pharyngobranchs 1, 2; pb_3, united pharyngobranchs 3, 4; *pc.*, cartilaginous remnants between the bones of the hyobranchial apparatus; *pcl.*, postcleithrum; *pet.*, pre-ethmoid; *php.*, pharyngeal process; *plr.*, pleural rib; *pls.*, pleurosphenoid; *pmr.*, posteromedian process of median rostral; *pmx.*, premaxilla; *pmy.*, posterior myodome; *pop.*, preopercular; *ppr.*, pterotic process; *ppt.*, pterotic limb of post-temporal; *pr.*, winglike process of the median rostral; *pro.*, prootic; pr_2, pr_4, dorsal ribs of vertebrae 2, 4 in fig. 14 and pleural rib in fig. 15; *pt.*, post-temporal; *pte.*, pterotic; *pv.*, prevomer; *pvm.*, prevomerine process of maxilla; p_3, projection from the neural complex of third vertebra; *q.*, quadrate; *qp.*, posterior process of quadrate; *r.*, radials; *ra.*, retroarticular; *rpm.*, rostral process of maxilla; *sa.*, sesamoid angular; *sah.*, sphenotic articular facet of hyomandibula; *sc.*, scaphium; *sca.*, scapula; *scd.*, sensory canal in dentary; *scl.*, supracleithrum; *sco.*, sensory canal in opercular; *se.*, supraethmoid portion of ethmoid; *seo.*, opening of the sinus impar in the exoccipital; *sm.*, symphysis meckelii; *so.*, supraoccipital; *so.*, orbitosphenoid in figs. 4, 6; so_2, so_3, so_4, so_5, so_6, suborbitals 2, 3, 4, 5, 6; *soc.*, supraorbital sensory canal; *sop.*, subopercula; *sp.*, sphenotic; *spo.*, sensory canal in preopercular; *spr.*, sphenotic process; *ste.*, supratemporal region; *stf.*, subtemporal fossa; *suo.*, supraorbital; *sy.*, symplectic; *tf.*, trigeminofacialis chamber; tp_1, tp_2, dorsal ribs of vertebra 1, 2; *tr.*, tripus; *tra.*, posterior portion of tripus; v_5, fifth vertebra.

* This paper was not accessible to the author.