A reassessment of the phylogenetic position of the family Cobitidae (ostariophysi)
Parshall, Alice Margret

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A REASSESSMENT OF THE PHYLOGENETIC POSITION
OF THE FAMILY COBITIDAE [OSTARIOPHYSI]
(TEXT)

Volume I

ALICE MARGARET PARSHALL

A thesis submitted in fulfilment of the requirements
for the degree of Doctor of Philosophy in the
Faculty of Science, University of London.

Summer, 1983
ABSTRACT

The m. adductor mandibulae of members of the Cobitidae and of representatives of other ostariophysean taxa is dissected and a cladistic analysis of the muscle characters is carried out. A peculiar anterior belly of the adductor mandibulae is observed as unique to and shared by the cobitids, the homalopterines and the gastromyzonines. It is concluded that the presence of this muscle belly demonstrates that these three taxa comprise a monophyletic assemblage and this is identified as the cobitoid group. From variation in the anatomy of the adductor mandibulae within the cobitoid group it is hypothesised that, contrary to the traditionally held belief, the botine loaches probably constitute the most phylogenetically advanced lineage of the cobitoids and that the Botini and the Cobitini together form the advanced sister-group of the Noemacheilini, Homalopterini and Gastromyzonini.

The osteology of the two unusual cobitid-like bornean taxa Ellopostoma and Vaillantella is described. A comparative study of cobitoid osteology is carried out subsequent to the myology. It is concluded that Ellopostoma is probably more closely related to the Homalopterini than to anything else and that Vaillantella is probably more closely related to the Noemacheilini than to anything else. It is further concluded that there are no osteological characters to refute unequivocally the novel hypothesis of cobitoid intrarelationships made available from the myological study.
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INTRODUCTION

The systematic position of the cyprinoid family Cobitidae has been the subject of considerable discussion, but despite multivarious suggestions has never been established. A brief review of aspects of this problem is given below by way of introduction to this study. Hensel [1970] provides a more extensive literature review of cyprinoid classification.

Linnaeus [1758] described and differentiated between two genera of carp-like fish - namely the cobitid loach Cobitis and the cyprinid Cyprinus. Cuvier [1819] also recognised the distinct division between these two groups which he identified as "les loaches" and "les carpes".

Regan [1911] followed Sagemahl [1891] and delineated four groups of cypriniform fish namely the Catostomidae, Cyprinidae, Cobitidae and Homalopteridae. Regan also recognised two distinct groups of cobitids which he identified as the Noemacheilinae including the species in which there is no suborbital spine and the Cobitidinae including the species in which such a spine is present.

A more or less immediate affinity between the Noemacheilinae and the family Homalopteridae (which includes both the homalopterid and gastromyzonid groups of fishes) has been proposed by various authors. Hora [1922a and c; 1930] discussed the possibilities for relationship between the cobitids, homalopterids and gastromyzonids, and the psilorhynchids and high-altitude carps. Hora [1932; 1950] developed a theory that the Homalopteridae was a diphyletic
assemblage with the homalopterid and gastromyzonid element of this assemblage more closely related to the cyprinids and to the cobitids respectively.

Nicholls (1938) discussed the interrelationships of the Gobioidae and he followed Takahasi (1925) in concluding that the gobioines and cobitids were related. Nicholls also explored the possibilities for catostomid-cobitid-gobioine relationship. Cobitid-gobioine similarities were considered further by Liu (1940) and Kryzanovskij (1947).

Berg (1940) delineated three separate groups of cobitid loaches, namely the Noemacheilini, Botini and Cobitini the last two groups of which have suborbital spines. These three groups have been recognised subsequently.

Ramaswami (1953) described the osteology of representatives of the three cobitid lineages. In his series of osteological studies of cyprinoid fishes Ramaswami (1952: 1-4, 1953, 1955 a and b, 1957) emphasised the apparent affinity between the noemacheiline cobitids and the members of the family Homalopteridae. Ramaswami (1955a) also suggested that the gobioine Gobiobotia is directly involved with this noemacheiline-homalopterid lineage.

Nalbant (1963) refuted the suggestions of Ramaswami and concluded that there is no immediate relationship between the gobioines and the cobitids. Nalbant suggested that the cobitid loaches probably have their ancestry amongst the South-East Asian cyprinids.

Alexander (1964) concluded that the Cobitidae is probably a monophyletic and, with regard to the cyprinids, a derived assemblage but did not discuss the definitive
characteristics on which this could be established.

Greenwood et al. (1966) pointed out that the distinctions between the gastromyzonids and homalopterids needed further elucidation. They also suggested that the cobitids, gastromyzonids and homalopterids groups were related to one another, and might be derived from some common cyprinoid ancestor near the cyprinids.

Nelson (1969a), from a study of branchial morphology, was lead to conclude in agreement with Greenwood et al. (1966) that the cobitids and homalopterids and gastromyzonids seemed to be closely related groups.

Rass & Lindberg (1971) recognized seven Families within the Cyprinoidei, namely the Cyprinidae, Gyrinocheilidae, Psilorhynchidae, Catostomidae, Homalopteridae, Gastromyzonidae and Cobitidae. These authors concluded that the Cobitidae were the most highly derived of these families and they did not suggest that there was any immediate relationship between the cobitids, homalopterids and gastromyzonids.

Roberts (1973) recognised a distinct separateness of carp-like fishes and loach-like fishes and demonstrated this by dividing his suborder Cyprinoidei into two superfamilies - the Cyprinoidea and Cobitoidea, with the Cobitoidea embracing the cobitids, and the homalopterid and gastromyzonid groups.

Roberts (1972) described the peculiar species Ellopostoma megalomycter which he indicated was generally Noemacheilus-like, with a superficial resemblance to the Kneriidae. Roberts did not further discuss the possible phylogenetic relationship of Ellopostoma to the cobitoid group.
Nalbant & Banarescu (1977) proposed that the cobitid genus *Vaillantella* was quite distinct from all the known species of Noemacheilini, Botini and Cobitini and should be recognised as a fourth lineage of Cobitidae - the *Vaillantellinae*. In this paper these authors made some suggestions on cobitid phylogeny (p.65-8, fig. xixc). Nalbant & Banarescu (1977) made it clear that they recognised the family Cobitidae as a monophyletic assemblage but they did not define its limits, or discuss its possible interrelationships.

Recently Chen (1978, 1980) concluded from a cladistic analysis that the Homalopteridae was a monophyletic assemblage in which is included the homalopterine group on the one hand and the gastromyzonine group on the other. The two subfamilies Homalopterini and Gastromyzonini are recognised in this thesis. Chen did not discuss the possible relationship between the Homalopteridae and Cobitidae.

Wu Xianen et al. (1981) suggested that only five families of Cyprinoidea should be recognised, namely the Catostomidae, Gyrinocheilidae, Cobitidae, Cyprinidae (embracing the Psilorhynchidae) and the Homalopteridae (embracing the Gastromyzonidae). These authors proposed that the Cobitidae was a derived cyprinoid group which is more closely related to the Catostomidae and Gyrinocheilidae than it is to the Cyprinidae and Homalopteridae.

Fink & Fink (1981) reassessed ostariophysean interrelationships on a broad basis. The conclusions of these authors on ostariophysean phylogeny are controversial, but they do at least demonstrate that traditionally held views
on ostariophysean interrelationships have never been tested using the cladistic methodology articulated by Hennig (1966) and that even the major ostariophysean groups lack the synapomorphic definition from which phylogeny can be assessed. Fink & Fink showed very clearly that with the current lack of understanding of ostariophysean phylogeny generally, it is essential that all problems of ostariophysean relationships are not tackled from a preconceived viewpoint without admitting how many and which assumptions have been made. These authors also showed the importance of making extensive outgroup comparisons before making an assessment of the phylogeny, or phylogenetic position of any ostariophysean ingroup.

With this in mind, it is intended in this project firstly to identify a monophyletic assemblage including all or part of the family Cobitidae as currently recognised. At this stage it is intended also to establish particularly whether or not the Homalopteridae are part of the same natural assemblage as the cobitids; since although as described in the introduction, phyletic relationship between the Homalopteridae and cobitids has been frequently proposed, this group has never been given strict synapomorphic definition. In this project, with an ingroup having been established, the second intention is to investigate the cladistic inter- and intra-relationships of that group using the outgroup comparison method as discussed by Watson & Wheeler (1981).

It became evident in the course of this study that the disposition of the m. adductor mandibulae allowed the best definition of an apparently monophyletic assemblage in
which the cobitids were included. Thus the findings from adductor myology are presented first and preliminary hypotheses of cobitid relationships are set up based on jaw muscle characters.

Complete osteological descriptions of *Ellopostoma* and *Vaillantella* are given next, because these descriptions are not available in the literature and both these peculiar taxa feature centrally in this study. Furthermore it is intended that these descriptions should provide a framework for the comparative osteological discussion following.

In the comparative osteology section it has been considered unnecessary to provide complete redescriptions of cobitid osteology. References of sources in literature where specific details of cobitid anatomy are available are given in context. The comparative osteology section here is intended to make it possible to view cobitid osteology in the perspective of the osteology of other Ostariophysi and thus to select characters (sensu Hennig, 1966) with which to test the preliminary hypothesis set up on myological characters.

In order to make comparative analysis possible, representatives of various cyprinoid outgroup taxa were also examined. Furthermore, representatives of the siluroids were dissected as these provided data on the variety of ostariophysean adaptation to a torrential habitat. Without such comparative data it is particularly difficult to assess the systematic significance of the morphological differences between the Homalopteridae and Noemacheilini as most of the species from these two taxa are themselves adapted for
torrential habitat. It was also found to be useful to compare aspects of cobitine and gymnotid anatomy, because both these taxa are peculiarly anguilliform. In order to be able to assess the plesiomorphic ostariophysan condition or precondition and thus to be able to establish the polarity of morphological developments manifest in the cobitoids, aspects of the morphology of characins and gonorrhynchiforms have also been considered.

Since completing the research for this thesis, Sawada [1982] has published a paper entitled "The Phylogeny and Zoogeography of the Superfamily Cobitidae". I have not discussed Sawada's work in this thesis as it was written before Sawada's paper was available to me, but I note that although we have each approached the problem of cobitoid systematics differently, we have come to similar principal conclusions on the issues involved.
MATERIALS AND METHODS

Spirit specimens used for dissection and study of external characters.

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Oronectes platycephalus 1977.2.3:188-188 Hongkong
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Orthrias tchajyuensia 1935.9.12:54-56 Turkey
Parakneria witti 1953.1.26:1-6 Sabi, W. Africa
Pseudogobia esocinus 1907.12.23:144-153 Japan
Psilorhynchus balitora 1932.9.19:4-6 E. Himalayas
Rhamphichthys rostratus 1935.6.4:365-9 Paraguay
Sabanejewia aurata balcanica 1957.12.9:298-307 Transylvania
Sabanejewia conspersa 1964.12.23:5-6 Italy
Sabanejewia larvata collected 23.4.78 Italy
Saurogobio dabryi 1872.4.17:4 N. E. Bengal
Sternopygus virescens 1927.10.4:25-40 Bolivia
Vaillantella flavofasciata 1957.1.23:4-6 Malay peninsula
Vaillantella maasi 1982.3.29:145 Borneo
Vaillantella sp. 1980.10.10:42-46 Malaya

Alizarin and Alcian Specimens

These were prepared using the clearing and differential staining technique discussed by Taylor (1967a & b) and Dingerkus & Uhler (1977).

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Acanthopsis choirorhynchus aquarium specimens Malay peninsula
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Barilius bendelisie 1972.4.17:27 N. India
Botia almorhae 1975.11.21:15-16 Kashmir, India
Botia berdmorei 89.2.1: 1482-91 Manipur, India
Botia geto 93.2.16:63-7 Jamu R. India
Botia histrionica aquarium specimens Bhano
Botia hymenophyse aquarium specimens Singapore
Botia macracanha aquarium specimens Sumatra
Botia modesta aquarium specimens Thailand
Botia sidthimunki aquarium specimens Thailand
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Catostomus comersonii M.C.Z. 56225 Mass. U.S.A.
Cobitis taenia 1976.77:5-13 Bucks, England
Cobitis taenia bilineata collected 20.10.80 Italy
Crossostoma davidii 11633.IV-IX. 926 China
Elllopostoma megalomyctor Sangau
Gastroemyzon borneensis Sarawak
Glaniopsis hanitschi Sarawak
Glyptothorax pectinopterus Bangkok
Gyrinocheilus asymnieri U.P. India
Homaloptera orthogoniata Malaya
Hypopygus lepturus Guyana
Lefus nikonis Japan
Lepidocephalus annandali N. India
Lepidocephalus guntea Darjeeling
Lepidocephalus guntea N. India
Lepidocephalus themalis Sri Lanka
Leptobotia elongata Chungking, China
Leptobotia fasciata Kiu Kiang, China
Misgurnus anguillicaudatus Punnan Lake, China
Misgurnus fossilis Germany
Niwaella delicata

Noemacheilus barbatulus

Noemacheilus barbatulus

Noemacheilus botia

Noemacheilus botia

Noemacheilus corica

Noemacheilus corica

Noemacheilus demisonii

Noemacheilus duaensis

Noemacheilus fasciata

Noemacheilus fasciata

Noemacheilus montanus

Noemacheilus nigromaculatus

Noemacheilus nigromaculatus

Noemacheilus pulcher

Noemacheilus punjabensis

Noemacheilus selangoricus

Noemacheilus stoliczkae

Noemacheilus strauchi

Noemacheilus yarkandensis

Orconectes platycephalus

Orconectes platycephalus

Orthrias tigris

Orthrias tschaiyssuensis

Parakneria witti

Pseudogastromyzon myersi

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1968.11.5:69-72

1969.1.24:374-466

1932.2.20:30

collected 25.10.80

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1889.2.1.1614-7

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1938.2.22:98-107

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1933.8.9:29-31

1978.3.20:225-227

collected 17.10.80

1907.5.4:74-78

1921.7.26:50-58

1935.4.18:11

collected 17.10.80

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collected 11.11.80

1933.7.26:1-3

1889.2.1.1723-5

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1977.2.3:186-188

1935.9.10:54-56

1968.12.13:96-102

1953.1.26:1-6

1974.2.9:6

Japan

Essex, England

Essex, England

Punjab, India

U.P. India

India

Assam

U.P. India

Bombay, India

U.P. India

Sarawak

Sarawak

U.P. India

Yunnan

Yunnan

Canton, S. China

U.P. India

Singapore

Kashmir, India

Issykal

Yarkand

Hongkong

Hongkong

Saroute

Tschaiy, Asia Minor

Sabi, W. Africa

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<td><em>Vaillantella sp.</em></td>
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TERMINOLOGY USED FOR COBITOID GROUPS

In this thesis the various subgroups of the Cobitoidae are identified as below. The names are used for convenience and are not intended to be definitive nomenclature. Steyskal (1980) pointed out that the basinsyms of cobitids in common use are actually inaccurate with regard to the Rules of Zoological nomenclature. Steyskal noted that, for example, the Cobitidae should strictly be called the Cobitididae, and he has been followed in this by Roberts (1982). Steyskal also pointed out that Cobitinae should strictly be called the Cobitininae. I have made use of the terminology which is more commonly known, and in the paragraph below the adjectival form of the names used in this thesis is given in brackets.

The Cobitoidae includes the Homalopteridae [homalopterids] and the Cobitidae [cobitids].

The Homalopteridae [homalopterids] includes the Homalopterini [homalopterines] and the Gastrotronmyzonini [gastromyzonines] following Chen (1980).

The Cobitidae includes the Noemacheilini [noemacheilines], the Vaillantellini [vaillantellines], the Botini [botines] and Cobi tinini [cobitines] following Nalbant & Banareascu (1977).

In most instances it is actually more appropriate to consider the Cobitoidae as divided into the Cobitidinae [cobitidinids] which is the name suggested by Berg (1940) to include the Botini and Cobi tinini which are the spined loaches, and the Noemacheilidinae [noemacheilids] to include all the other cobitoids.
The peculiar species *Ellopostoma megalomycter* is considered as a noemacheilid of *incerta sedis.*
SECTION 1

M. ADDUCTOR MANDIBULAE AND RELATED STRUCTURES
INTRODUCTION AND REVIEW OF PREVIOUS WORK

The m. adductor mandibulae of cobitoid fishes proves to be peculiarly subject to subdivision and elaboration. Only limited studies have been made on the jaw muscles of loaches. Takahasi (1925) included 5 species from the Cobitidae in his work on the cranial muscles of cypriniform fishes, and drew some inferences of the possible relationships his observations might indicate. Chranilov (1928), and Monod & le Danois (1966) looked especially at the parts of the adductor complex associated with operation of the suborbital spine present in cobitine and botine loaches. Monod & le Danois (1966) emphasised the functional and more or less complete anatomical separation of the adductor muscle complex into jaw, barbel and spine operational units. However, the various slips of the adductor muscle involved were named idiosyncratically by them and were not discussed by Winterbottom (1974).

The review of earlier work below is intended to establish a common terminology for, and to clarify the derivation of, the adductor subdivisions found in cobitoid fishes. It also serves to illustrate the variability of the muscle complex in the group, and the problems involved when interpretation is based on an inadequate number of representatives.

Takahasi (1925) described 4 divisions of the adductor complex in cypriniform fishes, which he named the maxillaris, mandibularis, mentalis and preorbitalis parts.

Takahasi denoted maxillaris as that part of the adductor inserting on the maxilla where it may terminate in two tendons crossing each other on the lateral face of that
bone, and also noted that the maxillaris may be connected, via a tendon, with the mandibularis division of the adductor, which lies deep to it, or it may be more or less united with that division. The connecting, internal portion of the maxillaris, which may be entirely tendinous, he called the INT.

In the Cobitidae he examined, Takahasi described the body of the maxillaris as almost completely divided into 2 parts, the upper of which he identified as α and the lower β - reversing the terminology of Vetter [1878] and Dietz [1914]. Takahasi then described the maxillaris of 5 cobitids [Hymenophysa curta, Cobitis taenia, Misgurnus anguillicaudatus, Orthrias oreias and Lefua echigonia] in some detail because he considered the variable form of this muscle indicated the relationships of these species.

Takahasi used Hymenophysa curta (Botia hymenophysa) to represent the Botini. In this species, Takahasi described the α division of the maxillaris as having a double origin, some INT development and "... a remnant of the preorbitalis attached ...". He observed that the β division of maxillaris originated from the articular only and inserted into the rostral cartilage. I find the presence of a distinctive fusiform slip of muscle in this position is characteristic of all cobitoid fishes, but Takahasi's description does not make it clear that in all cobitoids there is a strongly defined upper and lower division of the main body of the maxillaris, the both of which insert on the maxilla via a common tendon, and that the second (dorsal) maxillary insertion of the β portion of the A1 of
Botia hymenophyse as described by him is made by the tendon of another, quite separate fusiform slip of muscle which is derived from the medial surface of the muscle passing into the tissues of the rostrum. Nor is the fragmentation of this muscle passing into the rostrum into three, separate, flat bellies with independent tendons described.

Takahasi (1925) described the \( \alpha \) maxillaris division of Cobitis taenia as two-headed like that of Hymenophyse, but he did not mention the tendency of the upper of these heads to form an additional and deep part. The angular-rostral slip in Cobitis taenia is again identified as the \( \beta \) division of maxillaris. Takahasi described a similar \( \beta \) division in another cobitine, Misgurnus anguillicaudatus but in this species he stated that he observed 3 heads to the \( \alpha \) division; an upper, a lower, and a deep and that the last was the INT-attaching to the mandibularis.

In Orthrias oreis and Lefua echigonia, representing the noemacheiline loaches, Takahasi noted that the \( \alpha \) maxillaris division was again 2 headed. He described the \( \beta \) division in these species as originating from the articular, and inserting onto the maxilla. However, in all the Noemacheilini I have examined, and in cobitoid fishes generally and characteristically, I have found the tendon of insertion of this \( \beta \) slip of Takahasi passes into the tissue of the rostrum, approaches its fellow, and forms a pulley system around the tips of the ascending processes of the premaxillae and the kinethmoid. This muscle slip has a consistent medial relation to the horizontal limb of the premaxilla.
Takahashi described the **mandibularis** division of the adductor as "... characteristically single and lacking in variation in Cobitidae." This division inserts on the dentary and forms a short stout tendon which attaches to the lower jaw immediately posterior to Meckel's cartilage. I observe some variation in the separateness of this last portion which actually inserts onto the coronomeckelian ossification and is identified as the A3 [Winterbottom, 1974]. Takahashi emphasised that the **mandibularis** receives the INT slip derived from the **maxillaris**. I have observed the development of INT to be very variable in cobitoids, but INT is usually only present as a tendinous raphe in the dorsal part of the α division of the **maxillaris** and rarely as an independent muscular body. It is particularly, and notably, well developed as a muscle in *Vaillantella* of the cobitoid species examined in my own study [see p. 37].

Takahashi gave the name **preorbitalis** to a division of the adductor which he considered to be peculiar to *Cobitis taenia* and *Hynenophysa curta* - the 2 spined loaches examined by him. He stated that the **preorbitalis** division originated from the pterygoid bones and from the hyomandibula in the former species, and from the α **maxillaris** division in the latter, and in both inserted on the anterolateral part of the suborbital spine. The muscle derives its name from its insertion, as the cobitidinid suborbital spine is apparently derived from modification of the lateral ethmoid bone [see p. 188] and it is recognised that the preorbital is a part of the lateral ethmoid ossification [Harrington, 1955].

The cobitine *Misgurnus anguillicaudatus* is also a spined
loach, but Takahasi observed that preorbitalis was absent from this species. Takahasi suggested that an evolutionary sequence was indicated, with the botine Hymenophysa representing an intermediate stage in the retrogression of the preorbitalis muscle from a condition like that in the cobitine Cobitis to one like that in the cobitine Misgurnus. He stated that it could be deduced that the muscle was "disappearing" because in many teleostean fishes it did not form an independent structure at all but it was "..... entirely absorbed into the maxillaris, or minimally produced in fibre only." Takahasi concluded that the preorbitalis muscle was a primitive feature, and that it was probably homologous with the 4th division of the levator maxillaris superioris of Amia calva because both the muscles in question were innervated by cranial nerve VII and both inserted onto the preorbital bone.

Chranilov (1928) noted and illustrated the cheek myology of Cobitis taenia. He clearly showed a muscle slip which he named the m. depositor spinae ectethmoidalis extending from the deep dorsal surface of the maxillaris and inserting via a long thin tendon onto the "ectethmoidaldornes" which was the name he gave to the suborbital spine. The ectethmoid is now recognised as included in the lateral ethmoid ossification [see Harrington, 1955], and as Chranilov (1928) himself recognised, the m. depositor spinae ectethmoidalis here is the same muscle as the preorbitalis of Takahasi (1925). However Chranilov refuted the homology of preorbitalis with the 4th division of the levator maxillaris superioris because he noted that this division in Amia originated from
the palatine bone. Chranilov (1928) considered his m. depositor spinae ectethmoidalis to be a specialised development, unique amongst the Teleostei, and derived from the deep part of the maxillaris division of the adductor. I follow this interpretation of Chranilov and note here that I consider the absence of the muscle from Misgurnus species to be the result of particular secondarily loss accompanying extreme reduction of the suborbital spine in this taxon (see p. 194).

Monad & le Danois (1965) detailed the ligaments and muscles operating the suborbital spine and the barbels of the botine loach Botia macracantha. The mechanism they proposed is discussed on page 196. Here only note of their musculature terminology is made. The preorbitalis (Takahasi, 1925) or m. depositor spinae ectethmoidalis (Chranilov, 1928) is described by Monad & le Danois as a weak fibrous band passing between the spine and the posterior part of the flat splint of bone flanking the ethmoid region on each side which these authors call the nasal, and which I interpret as a lachrymal (p. 250). This muscle is not given a name by Monad & le Danois. However, these authors did describe a tendinous "préorbitalis interne", passing between the palatine and the maxilla. I have identified this structure as the palatomaxillary ligament. Monad & le Danois also indicated a "préorbitalis externe" as synonymous with the β maxillaris division of Takahasi (1925), and passing between the mouth border and the maxilla. In fact, as has been discussed, Takahasi used β to denote the slip of muscle passing into the rostrum and the préorbitalis externe of
Monod & le Danois is apparently a separate maxillary division of this β division (see p. 21). Monod & le Danois named the muscle belly passing between the articular and the rostrum the m. labial externe which from its position can be identified as synonymous with the β maxillaris of Takahasi (1925). Monod & le Danois also distinguished a m. labial interne within the fibrous flesh of the upper lip. I cannot find a distinct muscle belly in the fibroelastic tissue of that part.

Winterbottom (1974) established the terminology for the adductor divisions of the Teleostei, and his nomenclature is followed here. The term division A1 is used to denote the parts of the adductor complex lying superficial to the hyomandibular nerve trunk; the A1 usually takes origin from the quadrate, symplectic, preoperculum, hyomandibula and pterygoid bones, and the main part of it inserts on the maxilla. Its origin thus has an ascending or vertical portion, here called the preopercular line, and a horizontal part which here is referred to as the horizontal suspensorial line. The division A1 may subdivide. Winterbottom suggested that the ventrolateral portion of the divided A1 should be identified as A1α and the dorsal remainder of the muscle [tentatively homologised with the levator maxillae superioris of Rosen & Patterson (1969)] should be called A1β. I have not used this α and β terminology so as to avoid implying an homology of adductor parts which is poorly substantiated.

Division A2 extends, typically, from the quadrate, symplectic, meta- and ento-pterigoid bones, hyomandibula and preoperculum, to the coronoid process on the dentary,
and division A3 which is more or less separate from A2, makes its insertion on the coronomeckelian bone. The term AU is used for the fibres which insert in the Meckelian fossa.

Winterbottom (1974) noted that the preorbitalis of Takahasi was peculiar to some Cobitidae and that it passed from the hyomandibula to the lachrymal bone, which appears to have been a misinterpretation of Takahasi's original description.

In the study following here the state of the adductor mandibulae in Cobitidae and the outgroups studied is described and illustrated on the basis of dissections. The muscle complex is discussed in association with the structure and disposition of the underlying suspensorium, and in relation to the suborbital spine and the barbels when these are present. A cladistic analysis of the data is then carried out. Apomorphic features of the adductor complex are selected and cladograms illustrating the hypotheses of relationship proposed are drawn up.

The terminology to be used is as follows:— the division A1 is defined as described by Winterbottom. If two distinct heads of the A1 are separable these are called the A1d (dorsal) and the A1v (ventral) according to their position. The anterior division of A1 consistently present in cobitoid fishes as a fusiform belly originating from the articular, and inserting tendinously onto the rostrum is called the m. rostralis. If m. rostralis subdivides the separate bellies produced are indicated as mr' and mr". Other divisions of the A1 are named according to their insertions. The variable
muscle slip or tendon inserting onto the suborbital spine of Botini and Cobitini is called the A1LE. Dorsal and deep straps of A1d are named as such, and are subsequently indicated as A1dd and A1ddd. Internal connecting fibres between the A1 and A2 are called INT following Takahasi [1925]. Divisions A2, A3 and Aω are recognised as described by Winterbottom [1974].
THE ADDUCTOR COMPLEX AND RELATED STRUCTURES IN THE NOEMACHEILID GROUP

Noemacheilini

In all the species of the subfamily Noemacheilini that I have examined there is a well defined pattern in the adductor complex, despite considerable variation in the position of the mouth and jaws. This variation is illustrated by comparing the mouth of e.g. Noemacheilus nigromaculatus, N. yarkandensis and N. rupecola [fig. ia-c]. In notable contrast there is little variation in the disposition of the barbels and this stable barbel arrangement has been considered sufficiently characteristic of the Noemacheilini to distinguish these from the Botini and Cobitini [see p.84 ]. In the Noemacheilini there are 3 pairs of barbels, 2 rostral, the bases of which are just separated, and one rictal. The barbels vary in length and diameter and there is variation in the extent of the decoration of the labial folds.

The noemacheiline suspensorium varies in the proportions of its individual elements but not in its composition. Notable general features include lack of fenestration [p.148] except for an occasional, small, metapterygoid-symplectic fenestra in N. barbatulus, N. botia, N. corica and Orthrias tschawyssuensis amongst the taxa examined [see fig. ii]. Also typical are the medial reflection of the metapterygoid and entopterygoid to support the eye [p.144]. The lower jaw is edentulus and plesiomorphic [p.153] and a corono-meckelian ossification is consistently present on its medial surface [p.153].
Furthermore, it is typical of Noemacheilini that the infraorbital series is reduced to light tubular ossifications around the infraorbital canal. The frontoparietal canal passes from the frontal bone over the nasal capsule within a short tubular nasal bone. The frontoparietal and the infraorbital canal are both enclosed anteriorly in a short, more or less triangular antorbital ossification (see p.149), posterior to which and between the canals, is a long oval lachrymal bone of variable depth.

Clearly both barbel and jaw morphology are associated with the morphology of the adductor mandibulae. The most usual morphology of the adductor of Noemacheilini is illustrated in fig. iii. The A1 division of the adductor originates along the preopercular line. It has 2 well separated heads between which part of the A2 is exposed. These 2 heads, A1d and A1v converge to form a single tendon. This tendon is a rather conspicuous development in most cobitoids, and for convenience is hereafter referred to as the tendon dv. The A1 inserts via the tendon dv, onto a more or less well-produced bony horn anteroventrally on the maxilla. Thus the A1 is 'V'-shaped with the apex directed anteriorly.

The m. rostralis of all Noemacheilini arises from the angular just anterior to the quadrate-articular saddle joint. Unusually, in Noemacheilus gracilis (fig. iva) the m. rostralis has a second head arising from and mixed with the most anterior fibres of the A1v. The fusiform belly of the m. rostralis passes anterodorsally along the anterior border of A1v, crossing the tendon dv, the maxilla and the
insertion of the palatomaxillary ligament. It forms a slim tendon which inserts onto the rostrum, and the antorbital ossification is related to this tendon laterally.

Amongst the Noemacheilini there is very limited variation in this pattern. In *N. montanus*, *N. notostigma*, *N. rupecola* and *Oronectes platycephalus* (fig. ivc) the A1d is partially pennate. These species are particularly flat headed and the muscle form seems to be associated with the limited vertical space available for its development. The deepest fibres of the A1d, constituting INT, may form either a short tendon passing medially (as in *N. rupecola* and other flat-headed forms) or a long raphe-like fibrous band passing through the medial part of A1d, crossing over the hyomandibular nerve trunk, and inserting on the upper part of the maxillo-mandibulary ligament (as illustrated by *N. stoliczkae*, fig. ivb). A reduction in the angle between A1d and A1V is also generally correlated with flat-headedness, but in *Oronectes platycephalus* a considerable part of A2 is exposed between the two divisions.

There is some tendency for the anterior border of A1v to separate from the main body of the muscle. This is noted in *Lefua nikkonis*, *Oronectes platycephalus*, and especially in *N. stoliczkae* where this border slip is produced as a small, separate and deep belly, originating independently from the quadrate. Its tendon joins the tendon dv.

In a dissection the hyomandibular nerve trunk is very conspicuous as it descends anteroventrally deep to A1, over the surface of A2, and then divides. Its dorsal division follows a characteristic course around the posterior border.
of the maxilla to which it is bound by connective tissue. Distally the ventral division passes over the dorsal border of the angulo-articular and deep into the A2.

The fibres of A2 pass horizontally from the preoperc- cular line to insert on the posteromedial area of the coro- noid process of the dentary. The dorsal part of A2 may extend considerably dorsal to that of A1d as it does in Noemachei- lus rotostigma, N. nigromaculatus, Oronectes platycephalus and Aborichthys elongatus. The A2 is very thin where it underlies A1d but is not reduced to such an extent that 2 heads can be separated.

The A3 adductor division is produced as a thin flat belly on the medial surface of the A2 and its distinct tendon inserts onto the coronomeckelian bone.

A medial view of the lower jaw of a typical noemachei- line shows (fig. iiib) the insertions of the intermandibularis and protractor hyoideus muscles (terminology of Winterbottom, 1974). The intermandibularis is particularly well deve- loped in comparison with that of other cypriniform fishes (Takahasi, 1925) and lies ventrally. The protractor hyoideus is cruciform and does not split at its insertion which is on the dentary posterodorsal to that of the intermandibularis (fig. iiib).

Deviation from this typically noemacheiline condition of the ventral jaw muscles is observed only in a few species. In Aborichthys elongatus a pair of slips separate from the posterior portion of the protractor hyoideus, migrate anteriorly and insert ventrally (i.e. superficially) on the base of the mandibular symphysis.
In *Noemacheilus botia*, as in *Aborichthys elongatus*, the protractor hyoideus has a double insertion but in this case the main body of the muscle is of the form of a pair of parallel bands of fibres and not of a cross. Peculiarly in *N. nigromaculatus* the intermandibularis is absent.

Other noemacheilids

Included here is a selection of non-noemacheiline noemacheilid species (see p.17).

In *Glaniopsis hanitschi* the head is dorsoventrally flattened and thus cheek depth is restricted. The A1d and A1v divisions of the adductor mandibularis (Fig. va) are separated but there is scarcely any space between them. These form a rather long tendon dv. The m. rostralis is large and fleshy with a short tendon, but because of depression of the posterior part of the suspensorium, it is positioned anterodorsally to A1v and does not cross the tendon dv. There is no antorbital ossification in *Glaniopsis*, thus m. rostralis is not flanked by bone laterally. Arising with, but posterior to, and separate from m. rostralis is a thin strap of muscular tissue which crosses the tendon dv and inserts onto the anterior part of the stout oval lachrymal, (lachrymojugal of Ramaswami, 1952:4). This strap is identified here as an A1 lac.

The hyomandibular nerve trunk divides proximal to the A1d dorsal border; its branches follow the courses described as typical for the Noemacheilini. The A2 is fleshy and there is no separate belly or tendon of the A3 discernible. The intermandibularis is a short sliver of muscle which in
Glaniopsis bears the same relation to a fleshy cruciform protractor hyoideus, that it does in noemacheilines.

In *Gastromyzon borneensis* (fig. vb), in which cheek depth is extremely reduced, A1 is only recognisable as two-headed posteriorly. Its body bulges laterally, and it inserts directly onto the anteroventrum of the maxilla—i.e. no tendon dv is formed. The *m. rostralis* arises from the articular but its proximal one third is tendinous. Its middle third is muscular. Its distal third forms a fine tendon which is flanked laterally by the massive, bumper-like lachrymal ossification (the lachrymorostrojugal bone of Ramaswami [1952:3] characteristic of the gastromyzonines. The *m. rostralis* inserts into the rostrum as it does in noemacheilines but is more anteriorly positioned in *Gastromyzon* than it is in a typical *Noemacheilus* and does not cross the tendon dv.

In *Gastromyzon* the A2 has a rather deep, circular area of origin. It inserts on the coronoid process of the dentary. A distinct tendon issues from A3 ventromedially and passes to the coronomeckelian bone. There is a short, wide, horizontally fusiform *intermandibularis* spanning the dentaries. However the space available for protractor hyoideus development is more or less completely obliterated because the pectoral girdle has undergone great modification and expansion, and it lies immediately posterior to the lower jaw. Therefore the layout of the muscles of the floor of the mouth of *Gastromyzon* is not directly comparable with that of e.g. *Noemacheilus*.

In the homalopterine *Balitora brucei* cheek depth is
even more limited than it is in _Gastromyzon_ and the bulk of the adductor complex (fig. vc) is accommodated by horizontal expansion. The A1 is barely separated into 2 heads, even posteriorly. Its fibres course horizontally and unite to form a tendon dv. A short tendinous INT issuing from the internal surface of A1 passes horizontally, dorsal to the dorsal division of the hyomandibular nerve trunk, and inserts onto the maxillomandibulary ligament. 

The _m. rostralis_ is long, and unlike that of _Gastromyzon_ its proximal part is entirely muscular. It arises on the articular. Its distal half passes into a long slim tendon which inserts on the rostrum. The tendon of _m. rostralis_ and part of A1d are both flanked laterally by the lachrymal ossification.

The hyomandibular nerve trunk divides deep to A1 and its two main branches course as they do in a typical _Noemacheilus_. The A2 division of the adductor is visible above the dorsal border of A1 and inserts on the coronoid process of the dentary. Both A2 and A3 are broad, the latter is well-differentiated from A2, and passes to a stout tendon which inserts on the coronomeckelian. In ventral view a very thin, short intermandibularis is seen; its insertion is anteroventral to that of the massive and fleshy _protractor hyoideus_.

In _Ellopostoma megalomycter_ (fig. via) the A1 is almost completely divided. The A1d originates from the dorsal part of the preopercular line and passes forward as a rather shallow strap of muscle. The A1v arises from the anterior part of the quadrate. It is very slim and passes
anterodorsally to join A1d. Tendon dv expands slightly at its insertion on the peculiar, effectively square maxilla. The m. rostralis arises from the articular. Much of its fusiform belly lies along the anterior border of the A1v. It has a double insertion, via both a short tendon attaching to the maxilla anterodorsally and a long very fine tendon inserting on the rostrum. In Ellopostoma the rostrum is truncated and the mouth displaced posteroventrally. The lachrymal bone occupies a relatively posterodorsal position and is not related to the tendons of the m. rostralis.

Deep to A1 the hyomandibular trunk of Ellopostoma can be seen to be distributed like that of a typical Noemacheilus (p.312).

The A2 division of the adductor is expanded at its origin. Its insertion is displaced to the lower part of the posterior border of the coronoid process of the dentary and to the dorsal border of the anguloarticular. In Ellopostoma the coronomeckelian is peculiarly disposed (see p.94) and no separate A3 is discernible.

The dentaries define the sides of an acute isosceles triangle, spanned by a thin and superficial intermandibularis muscle. The protractor hyoideus muscle inserts posterodorsally and deep to the intermandibularis. However, because the dentaries are somewhat compressed together anteriorly the protractor hyoideus of Ellopostoma does not define the shape of a cross, and thus more resembles that of e.g. Noemacheilus botia, than that of most typical Noemacheilus (p.32).

Vaillantella is narrow headed. The A1d division of
the adductor mandibulae (fig. vib) is a strap-like muscle originating from a third of the distance down the preopercular line and is horizontally orientated. A1v is more extensive, arising from the horizontal suspensorial line and joining A1d to form a rather long tendon dv which inserts onto the maxilla. The m. rostralis is well defined, passing between the articular and the rostrum, and crossing over the tendon dv. The lachrymal in Vaillantella is a slim bone situated parallel to the palatine and is not related to the tendon of the rostralis muscle.

Reflection of A1d and A1v of Vaillantella reveals a small and distinctly separate belly of muscle arising deep to A1d mid-dorsally on the preopercular line. This muscle becomes tendinous distally, crosses over the hyomandibular nerve trunk (thus indicating its derivation from the A1) and inserts onto the maxillomandibulary ligament. This muscle is in the position of INT but is more highly developed in Vaillantella than in any other noemachelid species examined in this study. There is also a peculiarly well-developed fibrous tissue connection made between A1d three-quarters anteriorly, and the posterior part of the maxillomandibulary ligament. These fibres arise ventral to the internal part of the A1 and cross over the hyomandibular nerve trunk.

The hyomandibular nerve trunk crosses the long cheek undivided, until it divides immediately posterior to the jaws. Its divisions then follow the typical noemacheilid pattern. The A2 is exposed above A1d and between A1d and A1v, but it is excavated deep to A1d, and is consequently
2-headed. Its dorsal part is a strap-like, and its ventral part a triangular sheet of muscle, and these two parts converge to insert together on the posterior edge of the coronoid process of the dentary. Neither the body nor the tendon of A3 is separately defined in Vaillantella; the coronomeckelian bone is in its plesiomorphic condition.

In ventral view a strap-like intermandibularis and a cruciform protractor hyoideus muscle are arranged in the typical noemacheilid pattern.

THE ADDUCTOR COMPLEX AND RELATED STRUCTURES IN THE COBITIDINID GROUP

Cobitini

There is more variability in the composition of the adductor mandibulae in the Cobitini than there is in the Noemacheilini. In the Cobitini (as also in the Botini) an A1LE division of the adductor is developed in association with the suborbital spine. Furthermore the Cobitini are very narrow-headed which severely restricts the horizontal space available for cheek muscle development. In association with this restriction it seems there is a tendency for the A1d division to differentiate into various separate straps of muscle with horizontally dispersed fibres. The A1v is restricted to a band of muscle fibres arising from the quadrate immediately posterior to the quadrate-articular joint.

As in the case of the noemacheilids there are features of jaw and barbel morphology of Cobitini which are obviously involved with the morphology of the adductor
mandibulae. It is notable that the suspensorium is fenestrated in all the Cobitini I have examined [see fig. viib] except *Mugurnus anguillicaudatus* [fig. viia].

The pterygoid series is fragile and is not produced medially onto a shelf of bone under the eye. The entopterygoid is reduced to a more-or-less nail-like shaft of bone. A very distinctive feature of the cobitine lower jaw is that the coronomeckelian is absent from the medial face of the lower jaw [see p.154-5].

Vertical cheek space is restricted from below by the ventral position of the mouth, and from above by the erectile suborbital spine which features in all Cobitini. The space immediately below the spine is occupied by the anterior invasion of an hypertrophied *adductor arcus palatini* muscle. Gosline (1975) compared the disposition of this muscle and the action of the palatine, as a mechanical strut, with the situation in catfish where it operates the barbels, and in *Cobitis* where it abducts the suborbital spine [Chranilov, 1928].

As in the Noemacheilini there are 3 pairs of barbels in the Cobitini. In the Cobitini these are rostral, mid-maxillary and maxillomandibulary in position [fig. ie and f].

The lachrymal bone of the Cobitini is more posterodorsally positioned than that of noemacheilids. In Cobitini it is a slim shaft of bone which lies between the anterior end of the frontoparietal, and the infraorbital sensory canals and posteriorly almost contacts the anterior condyle of the suborbital spine, in the operation of which it partici-
pates as a lever (see p.193).

The basic arrangement of the cobitine adductor complex is demonstrated in Cobitis taenia. The A1d is present as a broad horizontal band originating from the dorsal half of the preopercular line. Its dorsal fibres have a deeper origin more posteriorly and anteriorly curve over the dorsal border of the more ventral fibres. The A1v is restricted. The A1d and A1v converge to form a short tendon dv which inserts on the maxilla anterodorsally. The rostralis is very slim. It originates from the articular, becomes tendinous in its distal half, crosses the tendon dv and passes to the rostrum. The A1LE lies deep to A1d. It has an oval belly originating from the preopercular line and it passes anterodorsally to become a slim tendon the distal part of which is visible above A1d and which inserts on a nubbin on the anterolateral part of the suborbital spine.

The hyomandibular nerve trunk crosses the cheek deep to the A1LE, dividing into maxillary and mandibular divisions deep to A1d which follow the same courses as in noemacheilines. A substantial proportion of A2 is exposed between A1d and A1v and its dorsal margin extends to the base of the A1LE. A2 narrows to make a rather short insertion on the posterior of the coronoid process of the dentary. The thin A3 has a fine tendon passing to a tiny nubbin of bone raised on the dorsal border of the angulo-articular.

The intermandibularis lies superficial to the anterior insertion of the cruciform protractor hyoideus.
The arrangement of the jaw muscles in Sabanejewia aurata balcanica is essentially the same as in Cobitis taenia except that in the former species A1d is considerably deeper. The anterior profile of the maxilla in Sabanejewia is sigmoidal and as the whole sheet of the A1d attaches to this border, it tends to form a longer strap A1dd and a shorter, more ventral strap A1d. A1d is joined by A1v. The rostralis insertion is displaced ventrally from relation to these maxillary insertions of A1. The depth of A1d reduces the exposure of A2 and the distal production of both this and the A3 are rather more extensive than in Cobitis taenia.

Misgurnus fossilis, M. anguillicaudatus, M. mizolepis and M. dabryanus were dissected (fig. viii). Misgurnus fossilis (fig. viiiia) has a deep A1d with a double insertion, the 2 tendons of which are separated by the maxillary attachment of the palatomaxillary ligament. The body of this A1d is partially divided and defines the shape of a long 'Z'; its most dorsal fibres have a deeper origin. The A1v is very restricted and the rostralis is very long and slim, just crossing the insertion of A1. The A1LE is small but muscular and passes into a distinct tendon inserting onto the tiny suborbital spine.

Much of the A2 is exposed between A1d and A1v. The A2 makes a rather extensive insertion onto a triangular area on the medial aspect of the coronoid process of the dentary and onto the dorsal part of the narrowest part of the anguloarticular immediately posterior to this. No A3 is differentiated.
In *Misgurnus anguillicaudatus* the separation of A1d and A1dd muscle portions is complete, and the palatomaxillary ligament can be clearly seen between the two anterior insertions of these. The A1v division is rather less restricted than in *M. fossilis* and the rostralis muscle forms a rather more distinct belly. Its tendon crosses both that of A1, and the palatomaxillary ligament. The most notable feature is the complete absence of A1LE, although the suborbital spine is present, fully developed albeit delicate. A triangular area of A2 is exposed laterally and this muscle inserts expansively onto the lower jaw as in *M. fossilis*. A flat A3 with an independent tendon is produced on its internal surface.

The situation in *M. mizolepis* (fig. viiiib) is like that in *M. anguillicaudatus*, i.e. there is no trace of an A1LE, although there is a tiny suborbital spine present. The A3 is present as a slim tendon only.

In *M. dabryanus* (fig. viiic), A1d, a partial A1dd and a clearly defined A1dddd are present but there is no trace of A1LE.

The hyomandibular nerve trunk, and the intermandibularis and protractor hyoideus muscles are distributed in all the *Misgurnus* species examined, in the same way that they are in *Cobitis taenia*.

In *Acanthophthalmus semicinctus* (fig. ixa) the A1 has three insertions on the maxilla. A1d and A1dd are completely separated. A1v is present as a band of muscle arising from the quadrata. It crosses the tendon of A1d obliquely, and inserts independently between A1d and A1v.
on the anterior part of the maxilla. This cross-over of
tendons is not per se unique (see p. 55). The m.
rostralis in Acanthophthalmus runs parallel to the A1v and
crosses the insertion of A1v. The A1LE is well-developed
and other features are as in Cobitis but A3 is completely
absent.

Somileptes gongota (fig. ixb) resembles Acanthophthalmus
semicinctus in the crossing of the tendons of A1d and A1v
and in the essential composition of its adductor mandibulae.
However, in this species the insertion of the A1v has
encroached dorsally to monopolise the anterodorsal surface
of the maxilla, and the insertion of A1dd which is well-
defined has migrated to a flange raised on the antero-
dorsolateral part of the preethmoid bone. The rostralis is
very fine. The A1LE is particularly large, and its origin
is unusually wrapped by a splitting of the internal
posterior part of A1d. Other features are the same as in
Cobitis; no A3 is differentiated.

Niwella delicta (fig. xa) is rather short cheeked, and
is of interest because it demonstrates an unusual, hyper-
trophied condition of its A1dd division. That division
forms a broad band of muscle, completely separate from A1d
and extending ventrally so that the palatomaxillary
ligament does not lie between the insertions of A1d but
attaches to the anterodorsal edge of the maxilla, and
furthermore a large proportion of A1d in N. delicta is
flanked laterally by A1dd. Other features in this species
are as in Cobitis.

In Acanthopsis choiorhynchus (fig. xb) the A1dd is
so expanded that it and its tendon flank the whole of A1d, with the result that A1v can be seen passing deep to it. The origin of A1dd monopolises the dorsal two-thirds of the obliquely orientated preopercular line. The A1d has a deep origin, its dorsal fibres originate in part from the orbitosphenoid bone. The A1d [lying deep to A1dd] and the A1v join at their maxillary insertion, passing to a rather long tendon dv. The rostralis muscle reflects the peculiar elongation of the ethmoid region of this species, and its distal half is tendinous. A1LE also has a rather long tendon, which passes deep to A1d and to A1dd to insert onto the lateral ethmoid spine.

Only a very small area of A2 is exposed between A1dd and A1v. The fibres of A2 pass horizontally and insert onto the posterior border of the dentary coronoid process. A reduced A3 is present.

The protractor hyoideus is a narrow muscle but it and the intermandibularis are arranged as in Cobitis. Lepidocephalus guntea, L. thermalis and L. annandali were dissected. In L. guntea [fig. xia] A1d is broad. Fibres from the dorsal border of A1d form a shallow separate belly A1dd, and A1d and A1dd are separate throughout their entire lengths. Division A1v and the belly of the rostralis are well-defined. Reflection of the upper part of A1 reveals a strap of muscle lying deep to it, occupying the same position as the deep strap described as A1ddd in Misgurnus dabryanus. However in Lepidocephalus guntea this strap can be traced to a tendon inserting independently on the antero-ventral part of the maxilla.
This deep strap A1ddd in *Lepidocephalus guntea* could be interpreted as an A1d which has come to lie deep (as a similar strap does in *Acanthopsis choirorhynchus*) and has shifted its tendon confluity with the tendon of A1v to that of A1dd which lies laterally to it. A1ddd would then be the dorsal division of A1dd. Alternatively the deep strap could be interpreted as an enlarged, internal development of INT, homologous with the INT fibres present in many *Noemacheilus* species (and especially in *Vaillantella*), which in some of the Cobitini including *L. guntea*, has extended anteriorly to insert on the maxilla rather than onto the maxillomandibulary ligament; this solution was adopted by Takahasi [1925]. Thirdly the A1ddd here could be a neomorphic development of A1.

In *L. guntea* the A1LE lies medial to, and proximally is partially embraced by, the deep muscle strap A1ddd described above. The tendon of A1LE passes to the suborbital spine.

The hyomandibular nerve trunk and the A2 muscle of *Lepidocephalus* is typically arranged. There is a small tendinous extension from A2 inserting onto the anguloarticular. It is interesting to record that in *L. guntea* (and also in *L. caudofurcatus*) the coronomeckelian bone appears to be a sesamoid ossification in A2, and thus does not provide for the insertion of the A3 adductor division unless it is proposed that A3 is not distinct from A2.

The arrangement of the division A1 in *L. thermalis* is essentially the same as in *L. guntea* except that the rostralis muscle is fleshier. The attachment of the A2
on the lower jaw is also similar.

In _L. annandali_ (fig. xib) the dorsal strap A1d is present, but a division A1ddd is not developed.

In all 3 species of _Lepidocephalus_ the disposition of the _intermandibularis_ and _protractor hyoideus_ is as it is in _Cobitis taenia_.

**Botini**

Elaboration of the _adductor mandibulae_ in the Botini takes place in the anterior portion of the muscle and this elaboration characteristically involves the _rostralisis_ division.

In the Botini the 2 pairs of upper lip barbels are joined at their bases and are produced as a tuft of 4 barbels on the rostrum (fig. xxxiie). In correlation with this, i.e. to support this tuft of barbels, it is noted that Ramaswami (1953) reported that the botine _premaxillae_ differed from those of the Cobitini and Noemacheilini because they had "... a more or less developed anterior projection ..." (see p.156-7). In the Botini, as in the other Cobitidae, the third pair of oral barbels is rictal in position.

Apart from the _premaxillae_ the condition of the suspensorium in Botini is plesiomorphic; it is rather short and robust and lacks fenestration (fig.xxxviic). The lower jaw is also plesiomorphic and a triangular coronomeckelian ossification applied to the internal face of the coronoid process of the dentary is a constant feature. The head is not wide in Botini, but there is much less limited cheek
breadth in this group than in the Cobitini, and in all botine fishes there is some medial reflection of the pterygoid series of bones to form a shelf under the eye. Vertical cheek depth is restricted by the presence of a massive erectile suborbital spine. Immediately anterior to the spine there is a large strong oval lachrymal ossification (see p. 249).

As discussed on page 72-3, 2 genera of Botini are currently recognised, namely Leptobotia and Botia. Botia is divided into 3 subgenera, namely Botia s.str., Hymenophysa and Sinibotia (Fang, 1936). Hymenophysa has been subsequently divided into Hymenophysa and Modesta species groups (Taki, 1972). The adductor complex of a representative of each of these categories has been dissected, and it is noted that there is extreme variability in the arrangement of the peculiar anterior divisions of the adductor of Botini.

In Leptobotia pratti [fig. xii.a] the division A1d is a deep band of muscle with horizontally disposed fibres. It is joined by the division A1v which is a rhomboidal block of muscle, originating from the larger part of the horizontal suspensorial line. The tendon dv is long. The rostralis division arises from the articular and passes anterodorsally. The belly of the rostralis is double for its entire length, i.e. both m. rostralis and m.r' are developed and these two bellies have independent tendons inserting onto the rostrum. The m.r' division is identified as the deeper of these 2 bellies; it makes a second tendinous insertion onto the anterior part of the
lachrymal bone which is in lateral relation to the tendons of rostralis passing to the rostrum and to the tendon dv. There is also a strap of dense connective tissue extending between the quadrate and the posterior part of the lachrymal, which is therefore rather firmly strapped to the side of the snout.

Running through the A1d division internally of Leptobotia pratti, and of all Botini, there is a strongly developed tendinous band of fibre. This is in the position of the INT (Takahasi, 1925) and is referred to as such here, although in L. pratti it passes onto the tendon dv anteriorly, while INT of most cobitoids inserts onto the maxillomandibulary ligament. This INT division in Botini provides the origin of the A1LE division. A1LE is a short, very strong, partly muscular and partly fibrous band of tissue passing dorsally at right angles from the anterior part of INT. It inserts onto the extension of the suborbital spine anterior to the ascending process of that bone.

In L. pratti the A2 division is exposed above the A1d posteriorly as a curved crest of muscle fibres. It is also exposed between A1d and A1v. The fibres of A2 converge as they pass anteriorly and insert on a rather small area on the posterior part of the coronoid process of the dentary. The A3 is clearly defined as a fusiform belly of muscle on the internal surface of the A2. It passes an independent tendon to the coronomeckelian bone.

In L. pratti the hyomandibular nerve trunk and the intermandibularis and protractor hyoideus muscle resemble
those of a typical noemacheiline.

In *L. fasciata* the division A1 [fig. xiib] resembles that of *L. pratti* except that the slip of muscle formed along the anterior border of the A1v division in *L. pratti* is developed as a thin flat more independent belly of muscle in *L. fasciata*. It originates from the articular and inserts tendinously onto the medial face of the mr'. In *L. fasciata* the m. rostralis and mr' share a single tendon of insertion into the rostrum. In other features *L. fasciata* resembles *L. pratti*.

In *L. elongata* [fig. xiic] the arrangement of the A1d and A1v is the same as in *L. pratti*, with a clearly defined belly of muscle formed along the anterior border of the A1v. However in *L. elongata* the tendon of this belly crosses laterally over, and then inserts into the dorsal edge of, the tendon dv. Anteriorly to this both the rostralis and mr' are developed. The arrangement of the INT and A1LE in *L. elongata* is also the same as it is in *L. pratti*, except that in the former species there is additionally a distinct bond of muscle fibres produced from the medial face of the A1 which pass internally and insert onto the maxillomandibulary ligament. The other features of *L. elongata* are also the same as in *L. pratti* except that the protractor hyoideus splits at its insertion and embraces intermandibularis posteriorly.

*Botia macracantha* [fig. xiiiia] is included in the subgenus *Botia* s.str., but is in some ways peculiar [see Taki, 1972 and p.341]. In the adductor complex the A1d and A1v divisions are similar to those of *Leptobotia*. 
There are 2 bellies in the position of the rostralis. The more lateral of these two does not insert into the rostrum but passes a cylindrical tendon to a small nubbin on the maxilla anterodorsally. This portion of the adductor muscle is called the m. rostralis max [m.r.max]. The more medial belly inserts tendinously into the rostrum and is thus identified as the m. rostralis. The A1LE and INT divisions are arranged as they are in Leptobotia. The fibrous band of tissue between the quadrate and the posterior end of the lachrymal is notably well defined. In other features B. macracantha resembles Leptobotia. However, B. macracantha is unusual in that in this species the dentaries appose anteriorly and form a long symphysis. As a consequence of this inter-mandibularis is posteriorly displaced, and the protractor hyoideus inserts on the posteroverntral edge of the dentary.

B. almorhae is the type species of Botia s.str. The arrangement of the divisions A1d, A1v, INT, A1LE and the myofibrillar band of tissue between the quadrate and the lachrymal is similar to Leptobotia and this arrangement can be considered as the typical botine condition. In B. almorhae the m.r. max. division is present. Anterior to this there are 3 more bellies of muscle which insert into the rostrum. These 3 bellies are identified as the rostralis, the m'r and the m''r. Two of these bellies lie deep to, and one lies superficial to, the m.r.max. ["sdd": p77]

Unusually, in B. almorhae, the insertion of the protractor hyoideus on the dentary is anteroverntral to that of the intermandibularis.
Botia geto is also included in Botia s. str. In this species the major portion of the adductor is typical. The m.r.max. division is present. Anterior to this there are 2 bellies of muscles of which one lies superficial and the other lies deep to the m.r.max.

Botia hymenophyssa and B. berdmorei represent the Hymenophyssa species group of the botine subgenus Hymenophyssa. In the anterior part of the adductor of both of these species the m.r.max. division is clearly defined. Anterior to this there are 3 bellies of rostralis (rostralis, mr' and mr''), of which two are superficial and one is deep to the m.r.max. [ssd' p77]

The Modesta species group of Hymenophyssa is represented by Botia modesta and B. robusta. In B. modesta (fig. xiiib) the divisions m.r.max, rostralis, mr' and mr'' are present. Of the 3 bellies of rostralis, one is superficial and two are deep to the m.r.max.

The protractor hyoideus splits at its insertion on dentary, and the intermandibularis, which is unusually short, makes its insertion between the two heads formed.

In B. robusta the m.r. max. division is formed; anterior to this there are only 2 bellies, identified as the rostralis and mr'. One of these lies deep, and the other superficial to the m.r.max.

Botia superciliaris (fig. xiiiic) is the representative of the monotypic subgenus Sinibotia. In this the m.r.max, rostralis, and mr' are present, and these are arranged as they are in B. robusta.
USE OF THE ADDUCTOR COMPLEX AND RELATED STRUCTURES IN REPRESENTATIVES OF OSTARIOPHYSEAN OUTGROUPS

In a cladistic assessment outgroup character states must be estimated in order to be able to deduce which [if any] of the myological features found in the ingroup, which here includes the cobitoid fishes described above, are apomorphic and are thus available for use as characters sensu Hennig [1966] in erecting a hypothesis of relationship.

The practice of ingroup-outgroup analysis in cladistic assessment is discussed by Watson & Wheeler [1981] and the method of these authors will be followed here.

In this study outgroup representatives have been selected because they fulfill at least one of the two criteria below:- either the group represented has been indicated in the literature as likely to be more or less closely related to members of the cobitoid group, or the representative is more or less highly adapted for a habitat similar to a habitat also exploited by a member of the cobitoid group.

From the ingroup study it is evident that attention should be focussed on conditions of the adductor complex in outgroups which could predispose fragmentation of the A1 division of that muscle, and especially which could predispose the formation of the m. rostralis division which appears to be characteristic of cobitoids.

It is also noted that the disposition of the hyo- mandibular nerve trunk and the intermandibularis and
The protractor hyoideus muscles is very similar in all members of the cobitoid group.

*Barilius bendelisis, Barbus ticto, and Aulopyge huegelii* were dissected to demonstrate the form of the adductor mandibulae which is plesiomorphic amongst cyprinid fishes.

In *Barilius bendelisis* (fig. xiva) although not in all species of *Barilius* (see Howes, 1980) a small rictal and a maxillary barbel is produced on each side of the mouth. In the adductor there is an unsubdivided A1 which is a triangular sheet of muscle originating from the preopercular line and inserting tendinously onto the maxilla. The divisions A2, A3 and Aω are also present and these insert onto the coronoid process of the dentary, onto the coronomeckelian bone, and onto the meckelian fossa of the lower jaw respectively.

In *Barbus ticto* there are no oral barbels which Howes (1981) considered to be the result of secondary loss. The adductor resembles that of *Barilius* except that the Aω division is absent.

*Aulopyge huegelii* is superficially rather loach-like, having long, pouched cheeks, a ventral mouth and well developed rictal and maxillary barbels. Heckel (1841) suggested that *Aulopyge* was probably an aberrant barbine. Its adductor complex resembles that of *Barilius*; the A1d and A1v divisions do not develop from the A1.

In the 3 cyprinid species above the hyomandibular nerve trunk does not bifurcate conspicuously in the way that it does in cobitoid fishes. Most notably the large
wandering maxillary division of the nerve is not produced. It is also noted that the *intermandibularis* muscle is absent. The *protractor hyoideus* splits and makes a double insertion on the dentary on each side.

*Abbottina rivularis* and *Pseudogobio esocinus* represent the family Gobiinae. A conical, rictal barbel is present in all members of this taxon.

In the adductor of *Abbottina* (fig. xivb) the A1 is completely divided into A1d and A1v portions. The A1d arises from the preopercular line. Its fibres are horizontally orientated. It inserts via a long tendon onto the maxilla anteroventrally. The A1v arises from the central part of the horizontal suspensorial line. Its fibres are anterodorsally orientated. It passes a narrow tendon across the tendon of the A1d and inserts onto the maxilla independently, anterodorsally. There is no further tendency for the A1 to fragment.

The A2 is extensive. It is visible above the A1d and between the A1d and the A1v. It inserts onto the posterior border of the coronoid process of the dentary. A small A3 is developed.

The hyomandibular nerve trunk pierces through the dorsal portion of the A2 and then courses anteroventrally between A1 and A2. The maxillary division of this nerve is small and does not wander around the posterior border of the maxilla.

In *Pseudogobio* (fig. xivc) divisions A1d and A1v are formed as in *Abbottina*, and a portion of the A2 is exposed between A1d and v. However, in *Pseudogobio*, A2 is
excavated deep to A1d, and a separate band of A2 is present dorsal to A1d, which apparently is derived from the part of A2 dorsal to the perforation made in this muscle by the hyomandibular trunk in Abbottina; the dorsal part of the A2 (A2d) formed in Pseudogobio actually lies superficially to the hyomandibular nerve trunk. The A2d and A2v divisions pass to a single tendon which inserts onto the coronoid process of the dentary. A thin A3 division is present.

In both the gobioine species above the intermandibularis is absent. The protractor hyoideus is present as a pair of parallel bands of muscle - i.e. it is not cruciform. It splits at its insertion and makes a double insertion on the dentary on each side.

Takahasi (1925) suggested that of the cyprinid fishes examined by him Pseudogobio appeared to be the most closely related to the Cobitidae because the crossing over the tendons of the A1 of Pseudogobio on the lateral face of the maxilla appeared to him to be reminiscent of the form of the anterior part of the adductor of cobitids. In fact this crossing-over of two tendons of A1 occurs in many cyprinids, e.g. Puntiollites, Amplyrhynchos, Cyclocheilichthys, Aspidoparia and Cosmocheilus (Howes pers. comm.), and in Catostomus, Acanthophthalmus, Somileptes and Ellopostoma amongst those species examined here. The 'crossed tendons' arrangement of A1 appears to be an adaptive development associated with a bottom feeding habit.

The relationships of the aberrant hill-stream
cyprinoid Gyrinocheilus have not been established. Smith [1945] considered that the monotypic family, the Gyrinocheilidae, occupied a systematic position between the families Homalopteridae and Cobitidae, while Ramaswami [1952:1] suggested that Gyrinocheilus was probably more closely related to the Catostomidae than it was to anything else. Gyrinocheilus completely lacks barbels and has an extraordinarily modified lower jaw. The head is depressed, and the cheek is very shallow and very broad.

The peculiarity of the Gyrinocheilidae is emphasised by the anatomy of the adductor complex. The adductor of Gyrinocheilus aymonieri (fig. xva) comprises 4 more or less fusiform bellies of muscle originating in horizontal sequence. The most lateral of these arises from the preopercular line and inserts onto a very strongly produced horn on the anteroventral part of the maxilla. This division is identified as an unsubdivided A1. Of the 3 deeper bellies the lateral inserts into the dentary in a gutter positioned lateral to the coronoid process of that bone. The middle division inserts onto the posterior border of the coronoid process. The 2 divisions are apparently both derived of the A2. The most medial division of the adductor passes to the coronomeckelian and is identified as the A3.

The hyomandibular nerve trunk courses between the A1 and the A2. It divides and unlike in cobitoids the small maxillary division produced courses straight across the lateral face of the maxilla. In Gyrinocheilus there is no intermandibularis
and protractor hyoideus finds no insertion on the peculiar lower jaw.

The systematic position of the cyprinoid hill-stream fish Psilorhynchos is also obscure. Hora (1920) emphasised the separateness of Psilorhynchos from a Noemacheilus-gastromyzonine-homalopterine group, and he suggested that Psilorhynchos was associated with the cyprinids Garra and Labeo. Jordan (1923) actually included Psilorhynchos in the family Cobitidae. Ramaswami (1952:2) suggested that the family Psilorhynchidae "... probably branched off from cyprinoid stock later than Gyrinocheilus ..." and that it had homalopterid and noemacheiline affinities. There are no barbels on Psilorhynchos but rictal barbels are present in Parapsilorhynchos (Hora, 1921). The head is very flat.

In the adductor complex of Psilorhynchos balitora [fig. xvb] the A1 is tripartite. The largest of these 3 divisions is a fleshy triangular sheet of muscle extending between the preopercular bone, and the anteroventral part of the maxilla. There is a completely separate deeper dorsal strap of the A1 which passes parallel to the above. The third part of the A1 is ventral in position. It originates from a lateral tubercle on the quadrate bone, and from the anguloarticular and passes a fine tendon which joins the insertion of the other parts of the A1 on the maxilla. This ventral division cannot be interpreted as equivalent to the m. rostralis per se, because it does not insert into the rostrum. However, it originates from the same bones as the m. rostralis of cobitoids and its presence and position in Psilorhynchos are of interest in
this context. This is further discussed on p. 79.

The hyomandibular nerve trunk of *Psilorhynchus* courses and divides in the same way that it does in *Gyrinocheilus*. The intermandibularis muscle is absent; the *protractor hyoideus* makes a single insertion on the dentary.

Little is known of the relationships of the predominantly North American family Catostomidae. Nicholls [1943] put forward a hypothesis that the Gobioinae were "supercessory" to the Catostomidae in China, where the latter group are now represented only by *Myxocyprinus*. Ramaswami [1957] listed features in which he considered the Catostomidae resembled *Gyrinocheilus*. Weisel [1960] emphasised that the catostomids should be considered as derived over, and not primitive to, the cyprinids and this view was endorsed by Uyeno & Miller [1965] who indicated a tetraploid origin of the karyotype of catostomids from the genome of a "cyprinid-like ancestor".

The Catostomidae develop no barbels. The suspensorium and the lower jaw are plesiomorphic. The adductor complex is simpler in composition than it is in *Psilorhynchus* and *Gyrinocheilus*, and in some ways is simpler than it is in its pleisiomorphic cyprinid form.

In *Catostomus* ([fig.xvc] A1) A1 is an extensive unsub-divided triangular sheet of muscle originating from the preopercular line. This single A1 has 2 tendons of insertion; the tendon of the arteroventral fibres extends anterodorsally, crossing over the tendon of the remainder of the muscle which passes horizontally to the antero-
ventral part of the maxilla. There is a well-developed band of fascia extending between the basal portion of A1 and the lachrymal bone which in Catostomidae is a robust oval ossification resembling that of the Noemacheilini [see p.251].

The A2 division is also an extensive triangular sheet of muscle; it inserts on the posterior of the coronoid process of the dentary. There is no trace of the A3 division although a well-developed coronomeckelian ossification is present.

The hyomandibular nerve trunk courses between A1 and A2. It does not produce a maxillary division of the cobitoid-type. However, in Catostomus there is a large and superficial intermandibularis muscle present. The protractor hyoideus lies deep to this, its body is cruciform and it makes a single insertion on the dentary dorsal to insertion of the intermandibularis. The layout of these 2 muscles should be noted as being very similar to that in cobitoids.

DISCUSSION

A hypothesis of the relationships of the cobitoid group can now be erected, based on those features of the adductor complex and related structures of cobitoids which, from comparison with the same developments in outgroups can be deduced to be synapomorphies sensu Hennig [1965].

Firstly, it is possible to recognise a monophyletic assemblage on the basis of the presence on a rostralis
division of the adductor. This assemblage includes all noemacheilid and all cobitidinid species, and it is proposed that these together comprise the cobitoid group which can be referred to as the Cobitidae. Since the m. rostralis is not found outside the cobitoid group, the presence of the m. rostralis appears to be a good character by which to define the Cobitidae.

The m. rostralis appears to be involved with the operation of the cobitoid-type oral barbels. Gosline [1973] suggested a mechanism of barbel movement which he considered was widespread throughout the cyprinids. This involved simple downward and forward movement of the barbels with the maxilla as the mouth is opened. With regard to this the development m. rostralis can be interpreted as an apomorphy. The origin of this muscle is consistently disposed over the base of the rictal barbel, with these two more or less cylindrical soft structures maintaining a slightly spiralled relation to each other. The insertion of the m. rostralis into the tissue of the rostrum and the pulley system formed by its tendons across the rostrum presumably allow more extensive and more controlled movement of the upper lip barbels than would be possible without discrete muscular control.

In the Noemacheilidini an A1LE division of the adductor is never developed. This allows the Noemacheilidini to be separated from the Cobitidini in which this muscle is found. The Noemacheilidini are therefore proposed as the primitive sister group of the Cobitidini [fig. xvi].
Within the Noemacheilidini it is convenient now to consider 2 groups somewhat separately; although neither group at this stage can be adequately defined. The noemacheilines are those species traditionally included in the cobitid subfamily Noemacheilini. The other noemacheilids include the gastromyzonines, homalopterines and Glaniopsis, Vaillantella and Ellopostoma, the relationships of which to be Noemacheilini are in need of elucidation.

Not only does the Noemacheilini lack adequate phylogenetic definition, but also the a-level systematics of this group are currently in a state of extreme confusion and apparent inflation and a world-wide review of the group is badly needed in order at least to coordinate nomenclature. The short review following here is intended only to outline the problem.

Banarescu & Nalbant (1964) suggested that the one hundred or more nominal species included in Noemacheilus as generally recognised could be classified into 10 genera. These genera are distinguished from each other on e.g. the relative positions of the dorsal fin and oral soft anatomy.

Banarescu & Nalbant (1968) reorganised the Noemacheilini into only 3 genera, namely Noemacheilus, Oronectes and Aborichthys. Oronectes (Gunther, 1866) embraces Lefua (Herzenstein, 1888) and its synonym Elixis (Jordan & Fowler, 1903). Aborichthys (Chaudhuri, 1913) is maintained following the recommendations of Hora (1925). Noemacheilus (van Hasselt, 1823) however has effectively no definition and Banarescu & Nalbant stated that it
contains "at least 4 distinct phyletic lineages". This
classification of Banarescu & Nalbant (1968) was followed
by Jayram (1981), in his handbook of the fresh-water
fishes of India, Pakistan, Bangladesh and Sri Lanka,
and generally, and neither the phyletic ranking, nor indeed
the nomenclature of the subgroups of Noemacheilus has been
satisfactorily established.

The problem of noemacheilin classification is com-
plicated by additional monotypic genera which have been
erected from time to time, to accommodate aberrant new
species. These include Enoemacheilus
embracing Noemacheilus brevis only in which the mouth is
peculiarly terminal, Turchinoemacheilus (Banarescu &
Nalbant, 1964) embracing N. kosswig only, and a new genus
proposed but not named by Jayram (1981) to embrace N.
paguensis in which the dorsal fin is peculiarly positioned.
No estimation of the systematic position of these nominal
genera in relation to other noemacheilines has been made.

It is in itself interesting that resolution of
noemacheilin phylogeny is not made possible by study of
the adductor complex. As has been noted (p.31) there is
a characteristic lack of variation in the disposition of
the jaw muscles in the Noemacheilini.

It appears to be most appropriate to illustrate the
few noemacheilin species in which the form of the
adductor differs slightly from that described as typical
(p.30) as forming an unresolvable polychotomy on a
branching diagram (fig.xvi). In Noemacheilus gracilis
the m. rostralis has a two-headed origin. In this it
illustrates one possible mechanism by which the m. rostralis might have been derived, i.e. by migration of the anterior "border-slip" portion of the A1v division anteriorly, across the quadrate-anguloarticular joint. However, the condition of the m. rostralis in N. gracilis can equally be interpreted as derived, with the muscle having secondarily secured additional posterior origin.

*Noemacheilus stolickzae* is interesting because, in addition to a typical m. rostralis division, a deep slip of muscle along the anterior border of the A1v is unusually well-developed. This offers an alternative interpretation of the mechanism of derivation and elaboration of the m. rostralis, involving lateral rotation of the posterior part of the lower jaw and of the muscles associated with it. Such lateral rotation would result in an increase in the area of the mouth floor and could be linked with the formation of the cobitoid type intermandibularis muscle. It is thought that the adductor mandibulae of catfish is complexed by rotations in the suspensorium.

Other variations occurring in the jaw muscle morphology of Noemacheilini include the absence of the intermandibularis muscle in *N. nigromaculatus* which is narrow jawed, and the double insertion of the protractor hyoideus in *Aborichthys* and in *N. botia* which are both rather deep bodied. I do not consider it is possible at this level to ascribe phyletic significance to these variations or those of *N. gracilis* and *N. stolickzae*. Variation in the development of the INT division of the adductor in Noemacheilini is discussed on p.31.

The species described as other noemacheilids are now
considered in relation to the typical noemacheilines.

There is no development in the adductor muscle to justify the phyletic separation of *Gastromyzon*, *Balitora* or *Glaniopsis* from the Noemacheilini. It is therefore proposed that the family Homalopteridae with *Glaniopsis* and the Noemacheilini are included in the monophyletic assemblage which is referred to as the Noemacheilidini (fig. xvi); it is noted that the form of the adductor of the other noemacheilids differs little from that of the Noemacheilini.

The condition of *rostralis* in *Gastromyzon borneensis* where the proximal portion of this muscle is tendinous, is interpreted as an autopomorphy (fig. xvi). It is probably associated with the extreme depression of the head in this species.

A note is made of the strongly defined A1lac division in *Glaniopsis* which also appears to be an autapomorphy (fig. xvi). The significance of this is discussed further on p.67 p77.

The phyletic position of *Ellopostoma* in relation to the other noemacheilids is not clear (see fig. xvii). In *Ellopostoma* both the divisions A1d and A1v are present. Additionally there is a fusiform belly of muscle arising in the position of the *rostralis* division of a typical Noemacheilus. However this belly in *Ellopostoma* makes its main insertion onto the maxilla; the muscle also passes a second, very fine tendon across its maxillary insertion, and this second tendon inserts into the rostrum. On the one hand the state of this belly of muscle in *Ellopostoma*
can be interpreted as representative of a stage in the
development of the typical cobitoid state of the muscle.
It can be proposed that 2 tendons of the A1 have crossed
on the lateral face of the maxilla in the way discussed
on page 55, and that the rostralis-type belly then has
separated from the anterior of the A1v and become
associated with the rostrum. *Ellopostoma* then can be related
to all the other cobitoids as shown in fig. xviiia. On the
other hand the condition of the muscle belly in *Ellopostoma*
can be interpreted as derived from a typical cobitoid-type
rostralis condition, with *rostralis* having surrendered the
larger portion of its rostral; for a maxillary insertion.
I consider the truncated profile of the rostrum of
*Ellopostoma* makes the second of these alternatives the more
likely and it is proposed that *Ellopostoma* is included
in the Cobitoididae, and may be related to the other members
of this group either as illustrated by fig. viib or fig.
viic.

The maxillary insertion of the *rostralis*-like muscle
in *Ellopostoma* must be considered in the light of the
development of the *rostralis max.* division in the
Botini [p.50], and of the peculiar slim anteroventral A1
division formed in *Psilorhynchus*, which also inserts on
the maxilla [p.57].

The adductor complex of *Vaillantella* essentially
resembles that of a *Noemacheilus*, and *Vaillantella* is
therefore clearly a member of the cobitoid group. However
*Vaillantella* differs from a typical *Noemacheilus* in that
it has a peculiar development of the INT portion of the A1,
and this is discussed below.

The diagrammatic figures [fig.xviii] have been redrawn from the work of Takahasi [1925]. They show that Takahasi considered that the INT portion of the adductor present in many Noemacheilini was homologous with the second maxillary insertion from the A1d made in many Cobitini. I have identified the feature in the Cobitini as the A1dd division, and not as homologous with the INT. I have included a diagram of the adductor of Vaillantella on fig. xviii for comparison with Takahasi's figures. This shows that on a gradual basis Vaillantella lies between the Cobitini on the one side and the Noemacheilidini on the other. The hypothesis to be tested is whether the morphology of the INT actually suggests in cladistic terms, that Vaillantella is more closely related to the Cobitini than are the Noemacheilidini.

On the one hand it can be proposed that the INT of Vaillantella does represent a stage in the development of the internal portion of the cobitine adductor. This requires the assumption that Takahasi was correct in considering the portion of the adductor identified as A1d here, was homologous with INT. The development of the A1d from the INT involves migration of the insertion of INT from the lower jaw and the maxillomandibulary ligament onto the maxilla. The insertion of the division A1 is considered to have made this migration at least once during teleostean evolution [Schaeffer & Rosen, 1969].

Alternatively, as the INT development in Vaillantella originates in the same position as the A1LE division of
Cobitini, it can be proposed that the INT of Vaillantella represents a developmental stage in the production of the cobitine type of A1LE. The development of the A1LE would require that the tendon of insertion of the INT in Vaillantella has migrated posteriorly from the lower jaw to pass to the lateral ethmoid suborbital spine. This is an attractive hypothesis; it proposes Vaillantella is the sister group of the Cobitini. However, no representative of an intermediate condition is known; in no cobitoid does an INT division insert on the lachrymal bone which is situated between the maxilla and the lateral ethmoid. When fibres from A1 do attach onto the lachrymal bone, as they do in e.g. Glaniopsis (p.33) and some of the Botini (p.50), they are derived from the lateral, and not from the internal surface of the A1.

It can also be proposed that the INT development of Vaillantella predisposes the development of the botine type of the A1LE, because it provides a fibrous base in a position from which connecting fibres can develop between the A1, and the lateral ethmoid (see p.48). There is strong superficial resemblance between the relations of the anterior part of the INT, to muscle fibres of the A1d passing to A2 and to the coronary process of the dentary in Vaillantella and Leptobotia elongata. This proposal would suggest that Vaillantella is more closely related to the Botini than it is to any other group.

I do not consider that any of these hypotheses of relationships of Vaillantella is substantiated on the basis of INT morphology. Clearly there is a great deal of
variation in the form of the INT development of cobitoid fishes. I am led to conclude that the connections made between the A1d and the A2 divisions of cobitoid fishes generally develop too multivariably to be useful as indicators of relationship, and that the INT division of Vaillantella must therefore be interpreted as an autapomorphic feature.

With this in mind, two possible hypotheses of the relationship between Vaillantella and the other cobitoids are put forward for testing (figs. xixa and xaxb). Neither of these hypotheses is preferred at this stage. Nalbant & Banarescu (1977) suggested that Vaillantella was "between the Botini and Noemacheilini", and shared no characters with the Cobitini. These authors surmised that the Noemacheilini, Vaillantella and the Botini represented one lineage or subdivision of the Cobitidae, and the Cobitini a second. This third hypothesis of the relationships of Vaillantella is illustrated by fig. xixc. The investigation of the INT above has neither substantiated nor refuted this hypothesis. These 3 hypotheses are considered further on page 333-4.

The significance of the form of the adductor in the Cobitini is now considered.

The Cobitini are usually identified as the most structurally peculiar, and by implication derived, group of the Cobitidae. This view was supported by e.g. Chranilov (1928), Rendahl (1933), Ramaswami (1953), Nalbant (1963), Alexander (1964), Bacescu (1965, 1970, 1972) and Nalbant & Banarescu (1977). However, the interrelationships of the Cobitini have never been clearly
demonstrated, nor assessed from a cladistic viewpoint.

The intrarelationships of the group are equally ill-understood. It has been proposed that the Cobitini are not a monophyletic assemblage. Ramaswami (1953) stated that "in the Cobitini the members show such extraordinary variation in the skull structures that it must be concluded that they are polyphyletic". Ramaswami concluded there are 2 phyletic series within the Cobitini, of which one includes _Acanthopsis_, _Acanthophthalmus_ and _Lepidcephalichthys_ (_Lepidocephalus_) and the other _Cobitis_, _Somileptes_ and _Misgurnus_. Nalbant (1963) also considered that "the cobitine phylectic series is not unitary". He discerned "three directions of evolution each starting from a somewhat different level of organisation". Nalbant proposed that the first of these directions is taken by _Misgurnus_, the second by _Cobitis_, _Sabanejewia_, _Niwaella_ and probably _Somileptes_, while the third direction is illustrated by the _Acanthopsis-Acanthophthalmus_ line.

Nalbant's (1963) "phylogenetical scheme" of the relationships of the Cobitini and Botini is reproduced (fig. xxv). He proposed 12 genera of Cobitini in this 1963 paper, but it should be emphasised that both the genera and their interrelationships were apparently defined on a mixture of shared primitive and derived characteristics.

The study here of the _adductor mandibulae_ makes it possible to properly define the Cobitini and to establish the interrelationships of this group within the Cobitidae.

The Cobitini share with the Botini the possession of an A1LE division of the adductor passing to the lateral
ethmoid suborbital spine which is itself characteristic of these two groups (fig. xvi). The nature of the A1LE is different in the Botini and the Cobitini and allows distinction to be drawn between the two groups.

The Cobitini are separated from the Botini by the nature of the m. rostralis. This is always a single belly of muscle in the Cobitini, resembling that of the Noemacheilini, while the rostralis of the Botini is always subject to some elaboration.

The Cobitini are thus indicated as a monophyletic assemblage by the characteristic morphology of their A1LE division. Furthermore it is characteristic of the Cobitini for the A1d division to tend to elaborate, producing the A1dd and A1ddd divisions. The pattern of development of these straps actually provides little elucidation of the intrarelationships of the Cobitini.

On analysis it appears that the A1dd and A1ddd portions, while per se derived features have probably been similarly elaborated more than once within the Cobitini. For instance, in Misgurnus mizolepis there is an A1dd division but no A1ddd develops, while in M. dabryanus both the A1dd and A1ddd are present; Misgurnus can be delineated in other characters (see p.339). Likewise, in Lepidacephalus annandali a strap of muscle in the position of the A1ddd is present, but there is no A1dd, while in other species of Lepidacephalus there are both the A1dd and the A1ddd divisions. Like Misgurnus, the genus Lepidacephalus can be effectively delineated on other characteristics. Thus it seems that the patterns of the A1dd and A1ddd
described in cobitine species do not constitute characters sensu Hennig [1966], and cannot be used to demonstrate phylogenetic relationship. They may however indicate the evolutionary direction, or polarity of otherwise defined lineages.

With this said a preliminary hypothesis of cobitine intrarelationships is put forward in fig. xx. This hypothesis proposes one lineage of cobitines, including Cobitis, Sabanejewia, Acanthophthalmus, Somileptes and Misgurnus, which is loosely defined on the capacity to usually produce only an A1dd division. This group can be further resolved about a polychotomy contributed by the distinctiveness of:-

- Somileptes, which demonstrates an autapomorphic condition in which the A1dd inserts onto the preethmoid bone.

- Misgurnus, in which, except in M. fossilis, the A1LE muscle has apparently been secondarily lost.

The crossing of the tendons of the A1d and A1v divisions seen in Somileptes and Acanthophthalmus is recognised as a derived but as discussed on p. 55 a far from unique, condition.

Of the other cobitines, Niwaella and Acanthopsis both show, and may or may not strictly share, a peculiarly extensive A1dd which has enlarged and come to lie lateral to the A1d. The broken lines on fig. xx. show that this condition can be interpreted as another derived state of the A1d, or as a stage in the development of the A1ddd. The second of these alternatives would suggest that
Acanthopsis and Niaella are more closely related to Lepidocephalus in which A1ddd does develop, than are the other Cobitini.

The preliminary hypothesis of cobitine relationship put forward here in fig. xx little resembles the hypotheses of either Ramaswami (1953) or Nalbant (1963). However study of the adductor has allowed definition of the Cobitini as a monophyletic albeit disseminated group. Moreover the position of the Cobitini in relation to the other Cobitidae is clarified, and it is apparent that they are less discrete from the other loaches than is proposed by Nalbant & Banarescu (1977). Cobitine intrarelationships will be further investigated using osteological data (p.336-9).

The significance of the form of the adductor in the Botini is now investigated. The traditionally and generally held view appears to be that the Botini are the most primitive of the Cobitidae. Nalbant (1963) pointed out that the Botini more closely resemble typical cyprinids than do the other loaches, and that the Botini should therefore be considered as more primitive than the other loaches. The same general conclusion was reached by Rendahl (1933), Ramaswami (1953), Nalbant (1963), Alexander (1964), Taki (1972) and Nalbant & Banarescu (1977).

Within the Botini the genus Leptobotia has been usually recognised as the primitive genus (see e.g. Fang, 1936) because in Leptobotia the preopercular region is "garnished" with small scales, of the cypriniform type,
while other botine fishes are scaleless in this area, as are cobitids generally. Occasionally *Leptobotia* has been defined to include only those botine species in which one suborbital spine has a single barb, with *Botia* then including the species in which the spine was bifid [see Hora, 1922a]. Currently *Leptobotia* is rather loosely defined on the squamation characteristic [Kobayasi, 1956].

The intrarelationships of *Botia* have been the subject of some considerable discussion. Fang (1936) proposed the phylogeny for the species of *Botia* reproduced in fig. xxi. Fang considered that *Hymenophysa* was the primitive subgenus of *Botia* and within *Hymenophysa* a *Hymenophysa* species group was evolutionarily advanced over a Modesta group because the former group uniquely developed the peculiar aperture between the ascending processes of the premaxilla discussed on p.159. Fang interpreted *Sinibotia* as the most advanced subgenus of *Botia*; *Sinibotia* is distinguished by the absence of a cranial fontanelle.

Taki (1972) reassessed the phylogeny of the species of *Botia*, and his conclusions are reproduced in fig.xxii. Taki recognised *B. macracantha* as definitely distinct from the other *Botia*. He stated that "*B. macracantha* has followed its own southward dispersal route ... and retained the primitive *Botia* characteristics ..." Taki tentatively suggested that *Leptobotia* might be more advanced than *Botia* because of the absence of cranial fontanelle in some species of *Leptobotia*. 
This traditional understanding of the systematics of the Botini is inadequate for two main reasons. Firstly, while both Nalbant (1963) and Taki (1972) state that Botia is probably monophyletic, in neither of these papers, nor elsewhere, is the actual characteristic definition of either Botia or of the Botini discussed. Secondly, the morphological characteristics which are used to interpret botine phylogeny in the papers reviewed above can all be shown to be of plesiomorphic distribution throughout the Ostariophysi.

Developments in the adductor mandibulae of the Botini allow a better understanding of the phylogenetic systematics of that group. I observe that the Botini are characterised by the polymerised condition of their \textit{m. rostralis}. On this character they are interpreted as the derived sister group of all other cobitoids.

The Botini share possession of an A1LE adductor division with the Cobitini and the Botini thus indicated as more closely related to the Cobitini than they are to the Noemacheilidini, with the Botini and Cobitini together comprising the group referred to as Cobitidini (fig.xvi).

Recognition that Botini are the most derived sub-family of the Cobitidae clearly contrasts with the traditionally held view on the systematics of not only the Botini, but also of the Cobitidae as a whole.

The degree of polymerisation of the \textit{m. rostralis} in some botine species is shown in the table (fig.xxiii). The character states resulting from the variable degree of elaboration of the \textit{m. rostralis} are considered as good
indicators of the relationships of the group (see fig. xxiv).

In *Leptobotia* as recognised here the m. rostralis is always more elaborate than it is in any noemacheilid or cobitine, but in *Leptobotia* the m.r.max. division of the rostralis is never wholly developed. Full development of the m.r.max. division is characteristic of *Botia*. On this basis I interpret *Leptobotia* as the primitive sister group of *Botia*.

Within *Leptobotia* (fig. xxiva) in *L. fasciata* the rostralis is elaborated into 3 bellies. The larger two of these pass a common tendon into the rostrum. The more posterior of these 2 bellies originates from the quadrate, i.e. posterior to the quadrate-articular joint, and the arrangement of this position of the rostralis of *L.fasciata* resembles that seen in *Noemacheilus gracilis* (see p.30). The third belly of the m. rostralis of *L. fasciata* lies deep and its tendon passes into the medial face of the larger two bellies, and in this portion the m. rostralis of *L. fasciata* superficially resembles that of *Noemacheilus stoliczkae* (see p.31).

In *L. pratti* the rostralis has 2 bellies, and in addition a strongly defined slip of muscle forms along the anterior border of the A1v. It is not possible to suggest whether the state of the rostralis of *L. pratti* is more or less derived than that of *L. fasciata*, and these 2 species are not phylogenetically separable on a cladogram [fig. xxiv].

In *L. elongata* the rostralis has 3 bellies; the larger 2 of these pass independent tendons into the rostrum;
the third and more posterior belly of the *rostralis* also has an independent tendon, but this tendon crosses over, and then inserts into the dorsal edge of the tendon *dv*. This can be interpreted as an incipient development of the *m.r.max.* division of *Botia*. Thus a hypothesis is put forward that *L. elongata* is more closely related to *Botia* than are the other members of *Leptobotia* [see fig. xxiv].

The genus *Botia* is defined on its possession of a fully developed *m.r.max.* division, and that division is present in all the species of *Botia* examined in this study. The number and disposition of the bellies of *rostralis* present in addition to the *m.r.max.* are then used to suggest the phyletic dissemination of the genus *Botia*. Figure xxiv shows that of the species examined in this study, *B. macracantha* alone has a single *m. rostralis*. In *B. geto*, *B. robusta* and *B. superciliaris* there are 2 bellies of the *rostralis*. In *B. hymenophysa*, *B. modesta* and *B. almorhæ* the *rostralis* has 3 bellies.

If *Leptobotia* is employed as a functional outgroup to *Botia*, it can be proposed that a double condition of the *m. rostralis* is pleisiomorphic to Botini. It can then be proposed that *B. macracantha* on the one hand and the *Botia* species developing three bellies of *rostralis*, represent character states which have been derived from a double condition of the *rostralis* by consolidation and elaboration respectively. These could be illustrated forming a trichotomy as a cladogram.

However, it is tentatively further proposed that the *Botia* species with 3 bellies in their *rostralis* division
probably do not represent a monophyletic assemblage. These species fall into 2 natural groups determined by the arrangement of the three bellies of the rostralis in relation to the m.r.max. There is no reason why the species with the "ssd" [see p.50-7], or "add", triple form of the rostralis should be more closely related to each other than either of them should be to the botine species with two bellies of the rostralis. Thus 4 discrete lineages of Botia are proposed which at this stage are shown forming a polychotomy on a cladogram [see fig.xxiv].

A note is added on the development of A1 lac. In many species of Botia a fibrous or partially muscular strap-like A1 lac division is present, passing from the lateral surface of the A1 to the lacrhythal bone. A well developed A1 lac is also described in the noemacheilid Glaniopsis. The A1 lac is not unique to these cobitoid species. In some gymnotid electric eels the whole of the A1 division inserts onto the lacrhythal.

Outgroups

An outgroup representative here refers to a member of a taxon outside the Cobitoidae as defined on the presence of the rostralis division of the A1. Thus it is evident that the adductor complex in outgroup representatives is investigated primarily in order to look for a morphological predisposition to form rostralis [see p.27].

The adductor complex in Barilius, Barbus and Aulopyge demonstrates the plesiomorph cyprinid layout of that muscle. The division A1 is not subdivided and
neither the rostralis nor any differentiation of muscle fibres situated on the anterior border of the A1 is produced. The intermandibularis muscle is absent.

In the species of Gobiinae examined the A1 is subdivided into the A1d and A1v and these tendons of these portions cross. However in neither Abbottina nor Pseudogobio is there any predisposition to form the rostralis and in neither species is the intermandibularis muscle present. Consequently I conclude that there is no development in the jaw muscles to substantiate the hypothesis put forward by Takahasi [1925] that the Gobiinae are more closely related to the cobitids than are any other cyprinids. It is noted that in both Abbottina and Pseudogobio the protractor hyoideus muscle makes a single insertion at the lower jaw as it usually does in cobitoids rather than a double insertion which is the more common condition amongst cyprinids. It is suggested that a reduction in the insertion of the protractor hyoideus is an accompaniment of a straight ventral body profile and of the bottom habit.

The study of the adductor mandibulae has not elucidated the phylogeny of the hill-stream cyprinid, Gyrinocheilus. However there is no tendency for the A1 to subdivide into A1d and A1v portions in this species, nor for a division in the position of the rostralis of cobitoids to develop. It is concluded that despite its hill-stream habitat Gyrinocheilus, or the "sucking-loach" as it is commonly known is not immediately related to either the cobitids or the homalopterids, despite suggestions made in the
literature (see p. 56).

The adductor of *Psilorhynchus* is not readily interpretable. In *Psilorhynchus* the A1 is subdivided horizontally rather than vertically, and produces 2 bellies which from their positions can be identified as an A1m (medial) and A1l (lateral). In addition to these bellies there is a tiny slim fusiform anteroventral division of the A1 produced, the tendon of which joins that of A1m and A1l.

Lauder (pers. comm. fig. xxvi) suggested that the small anteroventral belly of the A1 of *Psilorhynchus* was a modified rostralis which had secondarily assumed a maxillary rather than a rostral insertion. He suggested that the A1d of *Psilorhynchus* was equivalent to the A1d and the A1v of cobitoids, and that the A1m of *Psilorhynchus* was the homologue of the A1dd division which is characteristic of cobitine cobitids. Lauder proposed that *Psilorhynchus* was a derived cobitine cobitoid.

An alternative interpretation would be that the A1d and the anteroventral A1 divisions of *Psilorhynchus* are homologous with the A1d and the A1v of cobitoids, and that the A1m division of *Psilorhynchus* is a unique feature which has resulted from expansion of the cheek in the horizontal plane. Under this interpretation *Psilorhynchus* is excluded from the Cobitoidae, which is the more commonly held view of the systematic position of this taxon.

The small anteroventral belly of the A1 of *Psilorhynchus* does, as pointed out by Lauder, originate
from the same position as does the rostralis of cobitoid fishes. However, a hypothesis that *Psilorhynchus* is a derived cobitine loach requires either that the suborbital spine and the structures associated with it have all been secondarily lost from *Psilorhynchus* or that *Psilorhynchus* is conceived as the primitive sister group of all the spined loaches. The first of these two hypotheses is prohibited on the principle of parsimony expounded by Nelson (1970). The second hypothesis suggests that *Psilorhynchus* occupies a phylectic position between the Cobitidini and Noemacheilidini and may be more or less closely related to *Vaillantella*: A hypothesis of relationship between *Vaillantella* and *Psilorhynchus* is attractive. At this stage it may be noted that the INT division of the A1 of *Vaillantella* is in a similar position to the A1m division of *Psilorhynchus*.

The organisation of the adductor mandibulæ in *Catostomus* is simple. The A1 is unsubdivided; it inserts onto the maxilla via 2 tendons which cross each other. There is no indication of any tendency to form a rostralis division, and in the form of A1 there is little resemblance between *Catostomus* and any cobitoid. However, the intermandibularis and protractor hyoideus muscles of *Catostomus* are disposed in the same way that they are typically in cobitoids. Lauder (pers. comm.) suggests that this arrangement of the intermandibularis and protractor hyoideus may be characteristic of a monophyletic lineage embracing the Cobitoidea and the Catostomidae. If this is the case the Catostomidae must be
interpreted as the plesiomorphic sister group of all
the loaches and it must be assumed that the catostomids
have the potential to develop the rostralis from the
anteroventral portion of their A1 (which inserts onto
the anterodorsal part of the maxilla).

Alternatively it can be hypothesised that the
similar morphology of the intermandibularis and protractor
hyoideus muscles in the loaches and the suckers reflects
similarities between the feeding mechanisms of these 2
groups, and is not a valid indicator of relationship at
this level. The possibility of relationship between the
catostomids and cobitoids is further explored from an
osteological viewpoint [see p.141 -330 ].
Barbels develop in all cobitoid fishes, but the value of the presence or nature of these barbels in both the ingroup, and outgroup systematic analysis of the group is not easy to assess.

Fink & Fink (1981) discussed the problem of attributing any phylogenetic significance to the distribution of ostariophysean barbels generally. They pointed out that the capacity to produce a barbel is evidently a characteristic shared by cypriniforms and siluroids, but that the barbels have apparently been independently evolved in these two groups. Fink & Fink emphasised the particular lability of cypriniform mouthparts, and suggested that evolution of barbels has probably been a frequent occurrence at all levels in this taxon.

Historically the disposition of barbels and of other oral soft tissues has been considered as of extreme significance in providing an understanding of cyprinoid systematics. However, it is now appreciated that a more or less highly developed barbel at the rictus of the mouth is a plesiomorphic character at the cyprinoid level, and thus the presence of a rictal barbel is of limited phylogenetic significance in the group. Furthermore the development of barbels on the upper lip appears to be extremely labile amongst cyprinoids. Gilbert & Bailey (1972) discussed the reliability of barbels in cyprinid systematics, and these
authors concluded that in cyprinids barbels may be present or absent in members of otherwise clearly related groups, and may vary interspecifically, and even bilaterally on the same individual. Moreover they pointed out that as such oral features as barbels are highly adaptive, and subject to repeated development or loss depending on selective environmental forces, they must be interpreted as heterogeneously disposed, and polyphyletic in origin, and their elaboration, and enhancement with sensory structures seen as providing adaptive advantage to groups which emphasise senses other than vision in food getting.

In cobitoids a rictal barbel is invariably present. It is innervated by the lower division of the hyomandibular trunk, and liberally endowed with chemoreceptors (fig.xc) identified from Raffin-Peyloz [1955]. However, clearly the presence of this barbel does not suggest that the cobitoids necessarily have any particular cyprinid relationships. The basal association of the rictal barbel with the m. rostralis by which the cobitoid group is defined is reiterated [see p.60 ].

It is characteristic of Cobitidae that there are, as well as the rictal barbel 2 pairs of barbels on the upper lip. The differential arrangement of the 3 pairs of barbels, in Cobitidae and the development of additional oral soft decorations, e.g. mental lobes and buttons, and labial furrows and grooves is central to the current α-level interpretation of the family. Discussion of this is beyond the scope of this thesis. However, as pointed out in the
myology section here, the pattern of cobitid barbel arrangement has also been used to define the intra-relationships of this taxon at the subfamily level, and this is discussed below.

It is pertinent to consider, with regard to cobitoid intra- and inter-relationships, the level of universality at which 2 paired upper lip barbels are derived, and the possible subsequent transformations and elaborations which may be imposed on these.

Nalbant (1963) emphasised that all members of the Cobitidae have 3 pairs of barbels. He pointed out that the 4th and 5th pairs, which have sometimes been described in the genus Misgurnus (fig. i.e) are actually only exaggerated mental lobes, although the histological difference between these two structures does not ever appear to have been defined. Nalbant delineated 2 cobitid barbel patterns. The first, according to him is that demonstrated by the Botini (fig. xxxi.e) and Noemacheilini (fig.i, and xxxii) where the 4 rostral barbels issue together as a tuft with some basal separation in the Noemacheilini. The second pattern is demonstrated by the Cobitini (fig.ie) where the 4 upper lip barbels are completely separated from each other. Nalbant concluded that these patterns are stable, and provide a good phylogenetic criteria for recognising the cobitid subfamilies. He further concluded that "the ancestral form of the loaches ought to have retained some cyprinoid characters", and that 2 or 3 pairs of barbels of which 2 pairs have a distinctly rostral
position is such a character.

I can see no reason why such an arrangement should be interpreted as primitive for Cobitidae, and in a cladistic analysis gradual morphological sequences are not recognised as demonstrating phylogeny. Thus I do not agree with Nalbant (1963) that the Botini and Noemacheilini are indicated as primitive Cobitidae on barbel characteristics. Furthermore, I do not share the conclusion of Nalbant & Banarescu (1977) that, because in Vaillantella the 4 rostral barbels spring from a common base somewhat resembling the arrangement of the barbels in Botini (see fig. xxxiia), Vaillantella must be more closely related to Botia than Noemacheilus. The cobitid phylogeny proposed by Nalbant & Banarescu (1977) relies heavily on barbel characteristics. These authors suggest that the Cobitini "having only one pair of rostral barbels" are separated from all the other loaches. I interpret the position of the barbels of cobitoids as correlated with the form of the m. adductor mandibularis, and from this (p.46 ) it appears that tufted rostral barbels as of the Botini represent a derived condition amongst cobitoids.

In the non-noemacheiline noemacheilids there are sometimes, but not invariably 3 pairs of barbels. In Glaniopsis there are 3 pairs of barbels which are rictal, maxillary, and rostral in position. In this species the inner edge of the lower labial fold also produced as a barbel-like loop. This oral morphology led Hora & Jayram (1951) to propose that Glaniopsis probably occupied
a systematic position between the Cobitidae and gastro-
myzonines.

The disposition of the barbels in Ellopostoma as
pointed out by Roberts (1972) does not conform to the
cobitid pattern. I have emphasised similarity between the
external oral anatomy of Ellopostoma and some homalop-
terines [fig. xxvii, p. 97]. However, the phylogenetic
significance of homalopterine oral morphology has not been
established. Fang (1935b) considered that homalopterine
evolutionary advance principally involved modification of
external mouthparts, which indicated 3 levels of organisation
within the group. Fang identified a primary series of 4
conical upper lip barbels as are present in Vanamenia
stenosoma as demonstrating the ancestral cobitid-type of
homalopterine oral morphology. Between these primary barbels,
secondary and tertiary series of barbels may develop
producing in fullest expression a tentacular fringe of 13
barbels as on the upper lip of Crossostoma. While the
hypothesis of Fang is very attractive it should be said
that there is no corroboration for a hypothesis that barbel
multiplication and elaboration necessarily accompanies
evolutionary advance within the homalopterines.

I conclude that drawing any inference of cobitoid
relationships from superficial barbel anatomy should be
undertaken with caution. However it may be noted that as
phylogenetic significance of the presence of a rictal barbel
in cobitoids and in other Ostariophysi cannot be assessed
on barbel characters alone there is no reason why the
Cobitoids should be considered as more closely related to the cyprinids than are e.g. the siluroids, as the *m. rostralis* is just as unique to the cobitoids as is the modified maxillary support of the catfish barbel to this taxon (see Alexander, 1965). Furthermore, as the 3 pairs of barbel arrangement is found in no ostariophysean group outside the cobitoid assemblage, I suggest that the whole cobitoid assemblage can be characterised by a potential to develop 2 pairs of upper lip barbels operated by *m. rostralis* which develops in association with these.

Within the Cobitoidas the potential to multiply, elaborate, and transform the 2 pairs of upper lip barbels may be a homalopterid character, but clearly a character of potential is inaccessible. Although the oral anatomy of *Ellopostoma* resembles that of some homalopterids it is only actually possible to draw the same conclusion from the oral morphology of *Ellopostoma* as from the myology (p.65) i.e. that *Ellopostoma* is either the plesiomorph sister group of the whole cobitoid lineage (with the upper lip barbels not fully represented) or that the valve-like mouth of this (p.91) is a highly derived condition. The instability of upper lip decoration in the homalopterids may itself be used to suggest that *Ellopostoma* is more closely related to these than to Cobitidae. The contrastingly stable development of 3 pairs of barbels in all Cobitidae is noteworthy. However, because 3 pairs of barbels are present in some non-cobitid cobitoids, it is tautological to attempt to define the Cobitidae on this
character, which apparently defines a polyphyletic group, and is here interpreted as a plesiomorphic cobitoid condition.

I recognise the position of the barbels in Botini as a derived condition. Within the Botini the premaxillary aperture of the Hymenophysa subgenus is a further derived development promoting carriage of the tufted rostral barbels further anteriorly [p.159].
SECTION 2

DESCRIPTION OF ELLOPOSTOMA MEGALOMYCTER
This peculiar small fish from Borneo was first described as *Aperioptus megalomycta* by Vaillant (1902: p. 145), who proposed a provisional new genus *Ellopostoma*, or 'sturgeon mouth' to accommodate the species within the Cobitidae.

An amended description of the same material was given by Roberts (1972) but because the specimens had deteriorated, few details could be ascertained. Radiographs showed post-cranial bony capsules, which led Roberts to conclude that *Ellopostoma* was probably more closely related to the noemacheiline cobitids than to any other group, but as he found no oral barbels, he concluded that it differed considerably from all other known cobitids. Barbels are in fact present (see below). Roberts tentatively suggested features of the caudal skeleton of *Ellopostoma* which could indicate that it, the Kneriidae, and Cobitidae are in some way related.

The following description is based on new material collected by Roberts, six specimens of which were deposited in the B.M.(N.H.) collection (1981.4:13:20-26).

**External Oral Features** (fig. xxviia)

The mouth is inferior, positioned below the unusual broad rostrum described and illustrated by Roberts (1972). The oral opening is bordered by well-defined upper and lower labial folds, neither of which is cleft. The upper labial fold bears a blunt, triangular protruberance in the
mid-line, and on each side of this, mid-laterally, there is a longer fleshy cone of tissue which I interpret as a short maxillary barbel. The lower labial fold is raised into two tubercles, one on each side of the mid-line, and these fit between the structures on the upper lip, thus producing a valvular seal for the mouth. These oral features are not described by Vaillant (1902, fig. 43) nor Roberts (1972, fig. 2). There is also a fleshy median thickening, or mentum, on the lower lip, behind the mandibular symphysis. Just medial to the rictus a fold of skin produces very limited mental lobing. These features are recorded by Roberts (1972). A short maxillomandibular barbel develops at the rictus of the mouth on each side; this was identified as a maxillary barbel by Vaillant (1902). Roberts (1972) states that both oral and preoral barbels are absent.

There is no nasal barbel, but a small leaf-shaped flap of skin is associated with the anterior nasal opening.

The oral anatomy of Ellopostoma rather closely resembles that of the homalopterines Travaricoria sp. and Bhavania australis (fig. xxvib). The mouthparts of Ellopostoma described above may function as Hora & Law (1942) suggested they did in these homalopterines. These authors proposed that the more or less fringe-like developments on the upper lip of homalopterids are used for testing the purity of water to be inhaled. They further proposed that the lower labial arrangement allowed water to enter at the sides of the middle part of the lower or posterior lip and that the mental lobing, which is also
indicated as sensory, is pro- or retracted to open or close this channel. Thus in the homalopterine above the oral modifications are thought to be primarily associated with the reorganisation of an effective respiratory current in a hill-stream environment, while in Ellopostoma the modifications may be associated with the production of a suitable feeding current [see p.115-6].

**Suspensorium and opercular Series** (fig. xxxvic)

The suspensorium of Ellopostoma is modified overall to accommodate the large eye. Its components are flattened sagittally, and it is effectively limited to the vertical plane. The more dorsal elements are shallow and the more ventral ones deep.

The hyomandibula is long and anteroventrally orientated. Proximally it forms two heads. The posterior head articulates into a socket formed with one third on the pterotic, and two thirds on the sphenotic; the anterior head articulates with the sphenotic only. The upper part of the hyomandibula is broad and rectangular. On the posterior border of the bone there is a condyle one-sixth ventrally which articulates with the operculum, and mid-ventrally there is a flange which articulates with the ascending part of the preoperculum. The distal third of the hyomandibula is narrow. Its cartilage capped end articulates with the interhyal.

The symplectic is quite short and slim, tapering anteriorly. Both ends are cartilage tipped.

The quadrate has an unusual low triangular body. The
long edge of this is angled posteroventrally and has a synchondrotic union with the metapterygoid. The posterior process of the quadrate is long and slim. The articulation between the quadrate and the lower jaw is through a simple saddle joint.

The metapterygoid is an irregularly shaped plate of bone. It is minimally produced towards the hyomandibula posteriorly. The metapterygoid is not produced medially into a shelf within the orbit. It makes simple buttress articulations with the symplectic ventrally, and with the ectopterygoid dorsally.

There is no suspensorial fenestration.

The ectopterygoid is leaf-shaped and lies medially to the quadrate, anguloarticular and coronoid process of the dentary. The short flat dorsal surface of the bone supports a strong ligament to the palatine.

The entopterygoid is a short rectangular plate of bone. It articulates loosely over the anterodorsal border of the metapterygoid. Its anterior end is gently concave and this makes a loose articulation with the palatine.

The operculum has a low anterodorsal process for the insertion of m. dilator operculi. The posterodorsal angle of the operculum is raised to support the dorsal portion of the gill opening and the posterior edge of the bone is longer than the anterior one.

The suboperculum is massive and rectangular.

The preoperculum is a broad falciform bone. Its ascending limb is longer than its horizontal part. It bears the preopercular sensory canal which produces three
branches within the bone.

The interoperculum is deep and is raised posteriorly where it articulates against both the operculum and the suboperculum. The interoperculum extends slightly anteriorly to the anterior end of the preoperculum.

**Lower Jaw (fig. xxxviiiic)**

The anguloarticular is particularly short and its body is rectangular.

The retroarticular is attached synchondrotically to the anguloarticular ventrally and passes the ligament between the interoperculum and the deep ventral ligamentous process of the dentary.

The edentulous dentary is long, and has a tall coronoid process with a concave posterior border raised on its dorsal edge two-thirds anteriorly. The coronoid process is underlain medially by the ectopterygoid. The dentaries curve medially and flare slightly at their symphysis, but this articulation is not elaborated. The dentary sensory canal is not contained within the bone. Meckel's cartilage is large - half the total length of the dentary.

The coronomeckelian bone is peculiarly positioned. Half of it protrudes above the dorsal border of the anguloarticular and it actually articulates against shallow ridging on the external face of this bone. This migration of the coronomeckelian seems to be associated with consolidation of m. adductor mandibularae parts A2 and A3. In some species of the cobitine *Lepidocephalus* the
coronomeckelian is entirely free from the anguloarticular, and is present as a sesamoid ossification in the adductor muscle (see p.155).

The Upper Jaw (fig. xxxixd)

The horizontal limb of the premaxilla is extremely short and deep and effectively square. The ascending process of the premaxilla tapers. It is twice the length of the horizontal limb and set at an oblique angle of about 125° to it. The ascending processes of the premaxillae are bound to the kinethmoid dorsally, and they support the ventral portion of the oblique rostrum.

The maxilla of Ellopostoma is also highly modified. The main body of the bone is a square plate. This has a long fine rostral process directed ventrally behind the ascending process of the premaxilla. Anterodorsally the maxilla is thickened into a preethmoid buttress which is directed posteriorly. The maxilla is effectively excluded from the border of the mouth by the horizontal limb of the premaxilla.

The palatine is the connecting element between the upper jaw, suspensorium, and ethmoid. It is a short, twisted cylindrical bone. Anteromedially the palatine forms a cup which embraces the cartilage-capped head of the vomer. The palatine is produced as a strong horn anteriorly to which is attached the palatomaxillary ligament. With twisting of the palatine shaft, the palatine-enteropterygoid articulation is disposed almost vertically. A lateral ridge on the palatine shaft pro-
vides attachment for the strong ectopterygoid-palatine ligament.

**Ethmoid Region** (fig. xxviii)

In dorsal view the supraethmoid portion of the ethmoid complex can be seen to have an expanded, horizontal, anterior border, and posteriorly to make a short straight suture with the frontal on each side of a mid-line notch in its posterior border.

The mesethmoid is produced into the laterally concave medial walls of the nasal capsule. Anteriorly these parts of the mesethmoid curve laterally beyond the supraethmoid, and contribute to an extraordinary vertical fan-shaped wall of bone which extends across the anterior of the ethmoid region and supports the dorsal portion of the oblique rostrum. It appears that the medial part of this anterior vertical wall is formed by the anterior part of the supraethmoid. There is a small flange raised on each side of the wall, against which rests the ossification enclosing the anterior termination of both the frontoparietal and infraorbital sensory canals (see p. 105). The posterior portion of the mesethmoid narrows to form a short nasal septum. In ventral view the mesethmoid is visible as a small block, expanded posteriorly and forming a synchondrosis with the lateral ethmoid of each side.

The vomer is 'T'-shaped and forms a weak syndesmotic articulation with the anteroventral surface of the mesethmoid. The anterior part of the vomer curves ventrally. Each limb of the vomer has a detachable cartilage cap which
articulates with the palatine. This cap is interpreted as an unossified second preethmoid, PE2 [see p.169-70]. The kinethmoid is accommodated in a concavity between the limbs of the vomer. The posterior process of the vomer is flat, narrow and extends slightly posteriorly to the ethmoid base. It is received into a groove on the anteroventrum of the parasphenoid.

The kinethmoid is a simple cylindrical bone. Its rounded dorsal end is bound to the tips of the ascending processes of the premaxillae, and its ventral end lies in the kinethmoid notch of the vomer. The kinethmoid is anterodorsally orientated when the mouth is closed.

The preethmoid (PE1) is not ossified. It is present on each side as a short cylinder of cartilage intervening between the cartilage vomerine heads posteriorly, and the preethmoid buttress of the maxilla anteriorly.

In possessing preethmoids and a kinethmoid Ellopostoma is indicated as a cypriniform species [as by the same characters are the cobitoid fishes]. It is extremely unlikely that the similarities between the Kneriidae and Ellopostoma which were pointed out by Roberts [1972] are actually anything other than superficial.

The lateral ethmoid bones are large in accordance with the large orbital cavity. Each lateral ethmoid consists of a wide anteriorly convex coronal plate, which constitutes the anterior orbital wall. Dorsomedially this plate is produced into a cone of cartilage which articulates under the frontal. Ventromedially it is produced to a prong of bone which extends, dorsal to the parasphenoid,
towards its fellow. The ventral horizontal border of the coronal plate of the lateral ethmoid is excavated medially over the palatine, and laterally over the tubular infraorbital canal ossicles. A small flange extending from the anterior of the coronal plate articulates with the first infraorbital bone and this flange is identified as a short lachrymal process of the lateral ethmoid. This process forms the lateral wall of the nasal capsule, and its base is pierced by a foramen for the superficial opthalmic nerve.

Anterodorsomedially the lateral ethmoid is produced into a peduncle of bone which extends to support the mesethmoid dorsally. It is noted that this articulation is not developed in any cobitid. Below this the medial portion of the lateral ethmoid of *Ellopogstoma* is convex laterally where it forms the lateral wall of the nasal foramen.

The basal portion of the lateral ethmoid is rectangular. Medially it forms a broad synchondrotic articulation with the mesethmoid base, and has effectively no relation to the orbitosphenoid base.

**The Sphenoid Series**

The orbitosphenoid bone is formed dorsally into a 'U'-shape; each limb supports the frontals and extends anterodorsally to form a synchondrotic articulation with the mesethmoid. The ventral portion of the orbitosphenoid forms a complete short deep interorbital septum. Anteriorly it is produced onto a small horizontal shelf of bone which
interlocks with the posterior border of the mesethmoid. The horizontal ventral edge of the orbitosphenoid rests in a groove on the parasphenoid shaft. Posteriorly the orbitosphenoid articulates with the pterosphenoid bones and is excavated here around the anterior border of the optic foramen.

The pterosphenoids are peculiarly disposed. They appear to have been displaced as a result of expansion of the orbital cavity, and they lie effectively coronally across the postorbital wall [fig. xxixb]. The pterosphenoids fail to meet each other dorsally. They contribute to the walls of the optic foramen and below this just meet each other ventrally where they appose a small sagittal plate raised from the dorsum of the parasphenoid. Each pterosphenoid bridges over the posterior myodome, extending between the parasphenoid plate above in the mid-line, and the prootic laterally. The pterosphenoid-prootic suture is interrupted by the anterior trigeminofacial foramen. Laterally the pterosphenoid forms a vertical synchondrosis with the sphenotic, and it is roofed in this part by the frontals.

The sphenotic is short and forms the dorsal postorbital angle. It articulates with the prootic, pterotic and pterosphenoid and is partly hidden from dorsal view by the frontal and parietal. Laterally the sphenotic has a strong flat process which extends the orbital wall posterolaterally.
Otic Series (fig. xxixa and b)

Each prootic is wider than it is long. In the mid-line the pair provide the dorsal wall of a shallow posterior myodome. Peculiar digitiform projections from the parasphenoid and basioccipital bones extend onto the ventral surface of the prootic.

The prootic contributes to the formation of a deep subtemporal fossa. The fossa is elongated anteriorly, with the prootic and pterotic forming its long walls and the exoccipitals bearing a small ventral depression to complete it posteriorly. The prootic forms a synchondrosis with the sphenotic. However, it is noted that it makes no contribution to the socket for the anterior hyomandibula head.

The anterior part of the prootic is reflected dorsally as a result of expansion of the orbital cavity, and meets the pterosphenoid in the postorbital wall. This suture is interrupted by the anterior trigemino facial foramen. The posterior trigemino facial foramen is wholly enclosed within the prootic. The anterior saccular recess does not invade the prootic.

The pterotic adds to the posterolateral orbital wall. Its dorsal surface is almost completely covered by elements of the dermal skull roof and is visible only anteriorly at its articulation with the sphenotic and posteriorly where it produces a short curved spinous process. Ventrally the pterotic contributes to the formation of the long lateral wall of the subtemporal fossa as described above, and it is perforated by a small nerve foramen in this
portion.

An intercalar is present as a flat fragment of bone articulating with the pterotic only.

The opisthotic is absent.

**Occipital Series**

The epioccipital is a small round bone situated in the posterodorsal braincase. It is exposed in dorsal view. The epioccipital is produced into a round horizontal shelf posteriorly, onto which the posttemporal articulates.

The supraoccipital is shield-shaped. Anteriorly it is produced into short limbs which contact the sphenotic below the parietal on each side. The anterior border of the supraoccipital is excavated around the posterior margin of the posterior cranial fontanelle, and the transverse occipital sensory canal can be seen passing in the skin over this part. Dorsally the bone is raised into a ridge which supports the epaxial musculature.

Posteriorly the supraoccipital meets the exoccipitals; it just fails to be excluded from the foramen magnum by these bones. At the junction of the exoccipitals with the supraoccipital there is a round socket in the midline into which articulates a condyle formed on the anterior element of the neural arches modified over the Weberian apparatus [fig. Lviiia]. The formation of a second vertebral-cranial articulation is extremely unusual amongst Ostariophysi (p.312).

The dorsal portion of each exoccipital bone is reduced; the pair just fail to meet each other in the
dorsal mid-line where they join the supraoccipital to form the peculiar articular socket described in the paragraph above. There is no lateral occipital fenestra.

The exoccipital bones descend as coronal plates and contribute the major part of the borders of the large foramen magnum between them. The ventral wall of each exoccipital features a single large perforation through which cranial nerves IX, X, XI and the jugular vein exit together. This perforation, and much of the ventral surface of the bone, are covered by fine bony ramifications derived from peculiar cribiform plating which extends from the basioccipital.

The basioccipital is massive and extraordinary. Bony, net-like processes issue from its ventral periphery. This bony netting underlies the parts of the prootic and exoccipital adjacent to the basioccipital, and expands dorsally onto the exoccipital as thin, cribiform plates. These plates are supported posterodorsally on a tiny triangular "pharyngeal process" of the basioccipital, between which is enclosed the aortic canal. This "pharyngeal process" is extremely reduced. Roberts [1972] described anteriorly directed lateral processes of the basioccipital of Ellopastoma. These were probably the proximal portions of the cribiform plates described above. Roberts also recorded the absence of cyprinid-type pharyngeopophyses in Ellopastoma.

The parasphenoid is extremely unusual; it is spatula-shaped, being narrow anteriorly and wider and effectively square posteriorly (fig. xxixa). Its anterior tip is
bifurcated and enclosed between the mesethmoid and the posterior process of the vomer. The shaft is considerably expanded below and between the orbits. The parasphenoid has fine bony projections which extend over its articulation with the prootic.

Roberts [1972] recorded that the posterior portion of the parasphenoid of Ellopostoma was divided as it is also in Cobitidae and Kneriidae. I note that the parasphenoid terminates in an oblique and linear - i.e. undivided - edge which lies under the basioccipital.

Immediately posterior to its articulation with the pterosphenoid bones the parasphenoid is perforated by two vascular foraminae on each side (see p.237-8).

The Dermal Skull Roof

The supraethmoid has been described with the mesethmoid (p.96).

The nasal is reduced to a tubular ossification carrying a portion of the frontoparietal canal over the nasal capsule on each side.

The frontals form straight sutures with the posterior border of the supraethmoid on each side of a small anterior cranial fontanelle. Each frontal (fig.Lxiv) is narrow over the orbit and forms a narrow brow. The frontal expands around the posterodorsal margin of the orbit, but leaves the larger part of the dorsal surface of the sphenotic exposed so that this bone completes the orbital margin in this position. The frontals appose each other at a straight suture. They are separated
posteriorly by the anterior part of the posterior cranial fontanelle.

The parietals are simple and more or less square. The frontoparietal suture is straight. The parietals are completely separated from each other by the cranial fontanelle.

The supratemporal is a long rectangular plate-like ossification lying lateral to the parietal on each side.

The posttemporal is a horizontal rectangular plate of bone suturing with the posterior of the supratemporal [fig. Lxiia].

There is no ossification in the wall of the anterior part of the lateral line. The lateral line passes anteriorly over the supracleithrum, and then through the posttemporal into the supratemporal, where it divides. Its medial branch passes through the posterior part of the parietal and then crosses over the supraoccipital in the skin. The preopercular canal originates from the anterior branch of the lateral bone and descends to enter into the preoperculum. There is no suprapreopercular ossification.

A tubular ossification attached to the dorsal surface of the sphenotic carries the cephalic canal system to the posterior margin of the orbit where it divides. Its frontoparietal division passes through the frontal and into the tubular nasal ossification.

The circumorbital bones are reduced and fragmented to form a series of 7-9 tubular ossifications and the infraorbital canal passes through these. Anteriorly the frontoparietal, and infraorbital canals converge and are
both enclosed within a triangular ossification which is identified as an antorbital (see p.249).

The lachrymal is present as a long oval plate of bone. It articulates with the lateral ethmoid, and does not enclose a sensory canal.

An oval supraorbital bone is present.

**Pectoral Girdle** [fig. Lxivc]

The pectoral girdle articulates with the skull via an unusually long, rectangular posttemporal, the medial part of which lies on the epioccipital, on a small horizontal plate on that bone. The posttemporal contains the proximal part of the lateral line and anteriorly it articulates with the supratemporal.

The supracleithrum is a falciform bone. Proximally it forms a loose ball-and-socket articulation with the posttemporal and has effectively no ascending part. Distally the supracleithrum overlies laterally the upper four-fifths of the ascending limb of the cleithrum.

The ascending limb of the cleithrum is almost twice as long as the horizontal limb. The posterior, lateral and anterior laminae (terminology of Brousseau, 1976) are developed on its ventral portion.

The horizontal limb of the cleithrum is broad. A well-developed lateral lamina extends from this as a triangular flange which curves slightly ventrally at its apex. The horizontal medial lamina is also extensive and is deeply notched where it becomes continuous with the anterior lamina. This notch accommodates the dorsal part
of the inferior-pharyngeal bone.

The pectoral symphysis is deep and simple.

There is no postcleithrum.

The scapula is small. It forms a synchondrotic articulation with the posterior borders of the coracoid, and of the cleithrum. The scapula has a tall broad ascending spine and surrounds a large foramen. It is raised to form half the mesocoracoid pedestal. The glenoid cavity of the scapula is quite deeply cupped.

The coracoid is broad. It forms synchondrotic articulations proximally with the scapula and with the cleithrum, and distally against the internal face of the cleithrum immediately posterior to the pectoral symphysis. The coracoid contributes half the mesocoracoid pedestal. Laterally to this it is reflected ventrally and forms a narrow triangular flange which is a reduced vertical lamina of the coracoid.

No coracocleithral foramen develops in Ellopostoma.

There are three proximal pterygDSPheral elements. The first, or most lateral of these articulates with a facet formed on the scapula posteroinerally. The second and third pterygiophores abut the scapula and mesocoracoid contributions to the mesocoracoid pedestal respectively. There are four radial menisci, of which only the first is ossified.

The pectoral fin of Ellopostoma has twelve rays and of these the fourth ray is the longest. The first dorsal ray \( (R + 1) \) makes a saddle articulation with the glenoid cavity of the scapula via a semicondylar medial head and
a slightly longer lateral process. The proximal end of R + 1 also has a triangular ascending process and a low ventral buttress which articulates with the first radial meniscus. The remaining R + rays are fine with small spatulate heads. The R-pectoral fin rays have hammate heads and the first five of this series are slightly flattened.

No manifestation of sexual dimorphism has been recorded on the pectoral fin of Ellopostoma (see p.269-70).

Pelvic Girdle

The pelvic girdle consists of a pair of archipterygial plates each of which is bifid anteriorly. The plates are produced into strong ischial processes posterior to a short symphysis, and immediately anterior to the symphysis they enclose a pear-shaped median aperture. Each archipterygial plate is concave dorsally. As a result of this, ventrally the pelvis is formed into a pair of runners or stands, which are supported by the ischial processes posteriorly. This pelvic arrangement is frequently developed in bottom living Ostariophysi.

The pelvic fin has 9 rays. Three radial elements, lateral, mid, and medial in position separate the dorsal and ventral ray series. The medial radial or ischial element is large; it is wedged between a small shelf projecting from the internal surface of the archipterygial plate laterally and the ischial process medially.

A lateral pelvic spine is present.
Dorsal Fin

The dorsal fin of *Ellopostoma* has 19 rays of which the anterior 3 are unbranched.

The fin is supported on 15 proximal radials which articulate with the neural spines of V8-19 inclusively. There are 13 medial radials and 15 pairs of distal radials. A small posterior stay piece is ossified.

Anal Fin

The anal fin of *Ellopostoma* has 9 rays of which the anterior 3 are unbranched. Roberts (1972) quotes the anal fin ray number of 5-6 for the types examined by him. The fin is supported on 6 proximal radials which articulate with the haemal spines of V24-27 inclusively. There are 4 medial radials and 6 pairs of distal radials. A triangular posterior stay piece is ossified.

Caudal Skeleton [fig. xxxa]

The following description of the caudal skeleton differs considerably from that of Roberts (1972), which was of necessity "interpretative" because of the poor quality of the old material available to him.

The caudal fin of *Ellopostoma* is deeply forked; its principal ray count is \((1 + 9)(9 + 1)\) and there are approximately 9 dorsal and 7 ventral procurrent rays. There are 5 hypurals of which HU1 and as was hitherto undeterminable HU2 are fused to the complex ural centrum. It is noted that HU2 is free from the ural centrum in kneriids. A hypural foramen is well-developed. The parhypurapophysis is present only as a very low triangular
flange. Both the parhypural and the flattened haemal spine of the first preural vertebra are autogenous.

The urostyle is broad and strong. The single epiural is also broad. There is a single uroneural element present in cartilage only.

The comparative series of drawings (fig.xxx) shows that the caudal skeleton of Ellopostoma more closely resembles that of e.g. Noemacheilus botia than it does, as Roberts (1972) suggested, that of the Kneriidae (here represented by Parakneria). In kneriids HU1 fails to reach, and HU2 is not fused to, the complex ural centrum. Both these articulations are made in Ellopostoma and in the Ostariophysi, and Roberts' suggestion that caudal anatomy might indicate a relationship between Ellopostoma and the Kneriidae is refuted. However, given the apparently mosaic distribution of caudal osteological features throughout the Otophysi and Anotophysi, the use of caudal characteristics to indicate relationships at this level must be questioned (Rosen & Greenwood, 1970; Taverne, 1974).

It is interesting to note that in Ellopostoma the intermuscular bones flanking the caudal peduncle are hypertrophied as they are also in many cobitids (p.315).

Axial Skeleton

V1-4: modifications associated with the Weberian apparatus (fig. xxxi)

Both Vaillant (1902) and Roberts (1972) recorded ossifications around the anterior chamber of the swim-
bladder of *Ellopostoma* which they consider to be strongly reminiscent of the postcranial capsules of Noemacheilini. The structures in *Ellopostoma* consist of a bony sphere situated on each side of the anterior vertebral column, and communicating with its fellow posteriorly via an incompletely formed bony canal. A chain of Weberian ossicles is associated with each of these spheres, demonstrating that *Ellopostoma* is unequivocally an Otophysean (Rosen & Greenwood, 1970), and that its resemblance to the Kneriidae is indeed only superficial. It appears that the bony spheres, as well as the Weberian ossicles, are derived from parts of V1-4.

The centrum of VI is reduced to a short platycoelous disc. It has long digitiform lateral processes.

The centra of V2 and 3 are fused into a single amphicoelous element referred to as V2 + 3. No zygoepophyses are formed on this complex vertebrae. It bears a small facet just anterior to its waist on each side, against which the medial limb of the tripus articulates. Dorsolaterally V2 + 3 supports a pair of plates which are identified as the remains of the neural arch of the third vertebra (NA3).

The lateral processes of V2 (P2, see Alexander, 1964) are fused to the anteroventrum of V2 + 3. Proximally these processes are expanded and form scallop shaped flanks on each side of the centrum. Distally P2 becomes incorporated into the swimbladder capsule.

The centrum of V4 is long and amphicoelous. The parapophysis of V4 is fused to its centrum, and the
pleural rib of 4 (P4) articulates at a synchondrosis below this. P4 is expanded in its distal portion and it, and the osseous suspensoria of 4 become incorporated in the capsule walls. V4 supports a well-developed neural arch.

The dorsal elements derived from V1-4, which surround the neural canal are shown in the diagram (fig. xxxia). The claustrum on each side is well-developed. It articulates below a mid-dorsal shield-shaped plate which is identified as the second supraneural (SN2). This supraneural element is produced into a condyle anteriorly, and this condyle articulates into the unusual socket on the occiput (see p.101). Each plate identified as NA is raised into a very low ridge dorsal to the Weberian chain.

The neural complex is large. Its sagittal plate extends as far anteriorly as the anterior limit of SN2, and posteriorly it meets the flattened neural spine and neural arch of V4. A single large free supraneural ossification is present posterior to NA4. The neural spine of V5 is slightly flattened but V5 itself is a typical axial vertebra carrying a parapophysis which is fused to it laterally, and which articulates with an unmodified pleural rib.

The formation of the capsule around the anterior parts of the swimbladder appears to be as follows.

P2 is produced into a strong horizontal falx of bone called P2H, which expands laterally and contributes the anterodorsal portion of the capsule. A descending part of P2 (P2D) is apparently developed only as a curved ridge of bone raised on the medial part of the anterior
capsule wall. However, as there are no sutures in this portion of the capsule, the precise identity of its components cannot be established.

It appears that P4 contributes most of the capsule walls. Lateral to its articulation below NA4 it expands into a horizontal plate of bone and this forms the roof of the capsule. Proximally the tripus emerges from below the anterior edge of P4. This aperture through which the tripus pauses is enlarged medially by excavations in NA2 and NA4 where they lie adjacent to P4H. Distally P4 sutures with P2H, and curves ventrally to form the anterior wall of the capsule. P4 appears to recurve posteriorly to form the floor of the capsule leaving huge apertures in the lateral aspect of the capsule. Above and especially below these apertures P4 is produced into a shelf of bone, and apposes the body wall.

It is notable that there is no anterolateral aperture in the capsule wall; an anterolateral aperture is a very characteristic feature of the typical noemachelline capsule (see p. 191).

Of the Weberian apparatus the tripus is reduced; its posterior limb is truncated and the transformator process is absent. The ossicle is almost 'V'-shaped. The medial limb of the tripus is broad and articulates with V2 + 3 as has been described above. The anterior limb of the tripus is also broad and this passes the interossicular ligament anteriorly. The intercalarium is present as a quadrilateral sesamoidal nodule of bone in this ligament. Anteriorly the ligament is attached to a
well-defined, ascending process raised on the apex of the small cup-shaped scaphium. Neither the anterior nor the articular process of the scaphium is defined at all; this ossicle fails to articulate with the centrum of V1.

The morphology of the modified V1-4 in Ellopostoma contrasts with that of a typical Noemacheilus in some major features; in no noemacheiline is the Weberian chain exposed as it is in Ellopostoma, while paired antero-lateral (as well as lateral) apertures are present in all Noemacheilini. Both these differences are consequential to the disposition of P2 in Ellopostoma which is distinctly different from that of a typical Noemacheilus (see p.289).

The Posterior Axial Skeleton

The vertebral column consists of 34 elements of which the first 4 are modified into the Weberian apparatus and the post cranial capsule described above. The posterior vertebral element is the complex ural centrum.

There are 7 pairs of rather round-headed pleural ribs which articulate under short square parapophyses fused to V5-11. The proportion of ribs to vertebrae here is low in comparison to other loaches which reflects that the thoracic region of Ellopostoma is peculiarly short and deep. The neural spines of V5-8 are slightly flattened sagittally.

The first haemal arch is completed on V16. Thus there are 17 caudal vertebrae.

The intermuscular skeleton is well-developed. Its terminal components reinforce the caudal peduncle. Both the dorsal and the ventral series are forked and form
strong latticing above and below the vertebral column over the flanks. The ossifications become weaker and wispy anterior to the level of the dorsal fin. The ventral series is represented anteriorly up until the posterior rib, and the dorsal series up until V8. It is noted that the dorsal series does not become associated with the Weberian apparatus, and that there are no epicranial ossifications developed.

Branchial Skeleton

The hyoid skeleton includes ventrally a short, shallow urohyal which is notched anteriorly and posteriorly and greatly expanded laterally. Dorsal to this there is a 'Y'-shaped basihyal. Between the urohyal and basihyal there is a stout sublingual bone lying wedged between the anterior hypohyals [fig.Lxxxiiiib]. The posterior hypohyals are small quadrilateral bones. The ceratohyal is rather short and is deeply waisted. The epihyal is short and square. A cylindrical interhyal bone is positioned between the internal face of the epihyal, and the hyomandibula and symplectic.

There are 3 branchiostegal rays. The first of these is falciform and the second somewhat broader. These articulate on the internal and external face of the waisted portion of the ceratohyal respectively. The third branchiostegal ray is spatulate and articulates over the ceratohyal-epihyal junction.

In the basibranchial skeleton there are 3 ossified basibranchials of which the first is peculiarly
'T'-shaped with a very short stalk.

There are 3 pairs of hypobranchials ossified. The first of these has an anterior elongation which articulates with the posterior hyohyal on each side.

The ceratobranchials are wide and strongly curved bones. Proximally ceratobranchials 1-4 have ventral flanges. Ceratobranchials 2, 3 and 4 carry combs of long strong gill rakers as described by Roberts [1972].

The fifth ceratobranchial (CB5) is a slimmer bone. It is modified into the inferior pharyngeal bone along which there is a single row of approximately 35 low conical teeth. Ventromedially there is a long, strong digiform process produced on the bone for the insertion of the pharyngeal retractor muscle.

The four epibranchial ossifications are shallow and stout [fig.Lxxxviib]. Epibranchial 3 (EB3) has a spinous dorsal process. EB4 is widely flared in its dorsal portion; it has no dorsal process. The inferior pharyngeal bone makes its dorsal articulation with CB4 via chondrified ligamentous tissue.

There are 2 large, quadrilateral infrapharyngobranchial ossifications, which are identified as IFB2 and IFB3, of which IFB3 is the larger. The infrapharyngobranchials are rather discrete from each other and are positioned anterodorsally to EB2 and EB3 respectively.

The modifications apparent in the branchial morphology of Ellopostoma, especially the exaggerated gillrakers, can be correlated with an unusual feeding habit. It appears that Ellopostoma feeds by branchial straining which is a
feeding habit unknown in the Cobitidae.

The significance of the anatomy of Ellopostoma and the possible relationship of Ellopostoma to the cobitid and cobitoid group which have been discussed in the comparative review (p.332-3), in light of the hypotheses of the relationships of Ellopostoma which has been assembled from adductor myology (p.64-5; fig.xvii).
SECTION 3

DESCRIPTION OF VAILLANTELLA
Vaillantella was first collected from Kalimantra (Borneo) and described as *Noemacheilus euepiptera* (Vaillant, 1902). The fish is readily distinguished from all other *Noemacheilus* known, because of the great elongation of its dorsal fin. In a footnote Fowler (1905) proposed *Vaillantella* as a new genus of Cobitidae.

*Vaillantella maasi*, from Sumatra, was described by Weber & de Beaufort (1916) from a single specimen, separable from *V. euepiptera* on median fin ray counts.

<table>
<thead>
<tr>
<th>dorsal</th>
<th>anal</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>64</td>
<td>7</td>
<td><em>V. euepiptera</em></td>
</tr>
<tr>
<td>73</td>
<td>15</td>
<td><em>V. maasi</em></td>
</tr>
</tbody>
</table>

A third species, *V. flavofasciata* was described from Kuala Tahanin, the Malay peninsula, by Tweedie (1956). According to Tweedie this species is "... very close to *V. maasi* ..." and the 2 species are only distinguishable from each other on median ray counts.

<table>
<thead>
<tr>
<th>dorsal</th>
<th>anal</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>63-70</td>
<td>12-13</td>
<td><em>V. flavofasciata</em></td>
</tr>
</tbody>
</table>

Nalbant & Banarescu (1977) reexamined the material available, and proposed the *Vaillantellinae* as a new monogenic subfamily of Cobitidae, including the three species above, definitively separable from each other on median fin ray counts as below:

<table>
<thead>
<tr>
<th>dorsal</th>
<th>anal</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>3/52-60</td>
<td>2/5</td>
<td><em>V. euepiptera</em></td>
</tr>
<tr>
<td>3/68-71</td>
<td>2/10-13</td>
<td><em>V. maasi</em></td>
</tr>
<tr>
<td>3/61-67</td>
<td>2/0-12</td>
<td><em>V. flavofasciata</em></td>
</tr>
</tbody>
</table>

[Upper bracket = unbranched rays]
Nalbant & Banarescu make a particular note that the only specimen of *V. flavofasciata* known from Malaya is more similar to the single specimen of *V. maasi* known from Borneo, than it is to *V. maasi* from Sumatra, despite the geographical closeness of Malaya and Sumatra.

The median fin ray counts of six specimens available for this study here, from South Nerus, Malaya are given below. Only in specimen 1, an aliziran preparation, was it possible to be sure of the unbranched ray count, so for specimens 2-6 the total apparent count is given.

<table>
<thead>
<tr>
<th>Spec. No.</th>
<th>S.L. [mm]</th>
<th>Dorsal</th>
<th>Anal</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>60</td>
<td>2/62</td>
<td>64</td>
</tr>
<tr>
<td>2</td>
<td>59</td>
<td>63</td>
<td>11</td>
</tr>
<tr>
<td>3</td>
<td>40</td>
<td>62</td>
<td>12</td>
</tr>
<tr>
<td>4</td>
<td>68</td>
<td>63</td>
<td>11</td>
</tr>
<tr>
<td>5</td>
<td>54</td>
<td>65</td>
<td>11</td>
</tr>
<tr>
<td>6</td>
<td>37</td>
<td>63</td>
<td>13</td>
</tr>
</tbody>
</table>

These specimens can therefore apparently be ascribed to *V. flavofasciata* (Tweedie).

The anatomy of *Vaillantella* is described below. Osteology is described from the aliziran-alcian transparency preparation of specimen 1.

**External Oral Features**

In *Vaillantella* (fig. xxxiia) the mouth is sub-terminal, and is bordered by smooth upper and lower labial folds, neither of which is cleft, furrowed, or decorated.
There are two pairs of short rostral barbels, joined at their bases, and a single, longer maxillomandibular barbel at the rictus of the mouth on each side. There is some fleshy skin folding over the ventral surface of the lower jaw, but no mental buttons are developed. The nasal "barbel" is produced as a fleshy leaf associated with the anterior nasal opening.

Nalbant & Banarescu [1977] cite this barbel arrangement as characteristic of the botine Cobitidae ... "and equally so of some primitive noemacheilines, e.g. Noemacheilus s. str., although in this the lips are always at least a little furrowed." They do not provide specific examples, but consider the presence of four rostral barbels to indicate relationship between the Botini, Noemacheilini, and Vaillantella. I have not found a tuft of rostral barbels overlapping at their bases, like those of the Botini in any of the Noemacheilini I have examined. Although in Noemacheilini the four upper lip barbels may be arranged together on a well-defined rostral skin fold there is always some separation of the median pair. For comparison with the barbel arrangement of Vaillantella, I have illustrated the external oral features of Noemacheilus poonensis [fig. xxxiiib] and N. pulcher [fig. xxxiic] which Banarescu & Nalbant [1968] include in Noemacheilus s.str., N. corica [fig. xxxiid] which Jayram [1981] indicates as a member of this subgenus, and a botine [fig.xxxiie].

I consider that there is actually no evidence to substantiate a hypothesis that a rostral tuft of barbels is the primitive cobitid condition. The significance of
barbel arrangement in the Cobitidae is discussed on p. 82-8.

**Suspensorium and opercular Series** (fig. xxxvid)

The suspensorium of *Vaillantella* is long, shallow and not particularly robust.

The hyomandibula is a broad rectangular bone. Dorsally its small convex anterior head articulates in a socket on the sphenotic and pterotic and is well separated from a longer, flat posterior head, which articulates with the pterotic only. Articulation with the operculum is made via a condyle a quarter down the posterior edge of the hyomandibula, which below this is grooved to receive the ascending part of the preoperculum. Ventrally the hyomandibula is excavated over the interhyal.

The symplectic is long and slim, with cartilage capping both ends.

The quadrate has a triangular body and its posterior margin is joined synchondrotically to the anterior border of the metapterygoid. The symplectic is accommodated in an invagination over the posterior process of the quadrate, which is long, slim and spinous.

The main body of the metapterygoid is a long triangular, sagittally orientated plate. Posteriorly it is produced into an unusually long, cylindrical hyomandibular process which is capped with cartilage. The dorsal border of the metapterygoid is reflected medially to form a shelf under the eye.

The small, boot-shaped ectopterygoid is applied along the anterior quadrate edge; it supports the entopterygoid
dorsally, and does not extend to underlie the coronoid process of the dentary, or the anguloarticular.

The entopterygoid is large. Its dorsal part is reflected medially, and this portion articulates with, and continues anteriorly, the shelf of the metapterygoid. The entopterygoid is supported on the dorsal borders of the meta- and ecto-pterygoids, and is produced as a descending flange partially underlying these. The entopterygoid extends forward to the anterior margin of the ectopterygoid, and is produced into a condyle articulating with the palatine.

There is no suspensorial fenestration.

The operculum is triangular with a horizontal dorsal border. The anterodorsal dilator operculi process is low. Anteroventrally there is very slight digitiform production of the operculum, and this lies over the dorsal margin of the suboperculum.

The suboperculum is a long oval plate, applied under, and extending just anterior to, the operculum.

The preoperculum is a long slim faix with a very short ascending part; it does not enclose the preopercular sensory canal, which can be seen passing through the skin superficial to it.

The interoperculum is also long and slim, deepening posteriorly, where it abuts against the suboperculum only. It extends anteriorly as far as the anterior limit of the preoperculum.
The Lower Jaw [fig. xxxviiid]

The anguloarticular complex is triangular, its apex ascending below the coronoid process of the dentary. In medial view it displays a short meckelian chondrification, and dorsal to this a low, triangular coronomeckelian ossification. Posteriorly it forms a wide simple saddle joint with the quadrate. The retroarticular is joined synchondrotically to, and protrudes from, the anterodorsal ventrum of the anguloarticular. Each dentary bears a rectangular coronoid process three-quarters back on its dorsal border. The two dentaries form a half-hoop joined anteriorly through a slightly expanded, but simple mental symphysis. The dentary sensory canal is not contained in the bone, but can be seen passing through the skin along its ventral border.

The Upper Jaw [fig. xxxixc]

The paired premaxillae are 'L'-shaped. The horizontal limb of each is slightly longer and thicker than the ascending process, and excludes the maxilla from the mouth border. The ascending processes taper, and are bound to the kinethmoid at their lips.

The body of the maxilla is rectangular. Anterodorsally it is extended to flank the kinethmoid; this part bears a strong, cartilage-tipped, descending rostral process, which touches its fellow behind the ascending premaxillary limbs. Posterodorsally the maxilla is formed into a buttress against which the preethmoid and prepalatine bones articulate. Posterodorsally it is
extended beyond the horizontal limb of the premaxilla. This part is firmly bound to the coronoid process of the dentary by the tissue of the maxillo-mandibular ligament and does not contribute to the mouth border.

The palatine is a cylindrical shaft-like bone. Anteriorly a narrow prolongation articulates with the prepalatine ossification. Anteromedially the palatine loosely embraces the vomer. Posteriorly it is produced into a broad condyle which articulates with the entopterygoid. The palatine is not expanded medially into a shelf below the nasal capsule.

The Ethmoid Region [fig. xxxiii]

The ethmoid block is extremely narrow. A separate supraethmoid is not represented, except perhaps as part of the tiny wings present on the dorsum of the mesethmoid, which itself is reduced to a sagittal plate of bone. The ethmoid articulates posterodorsally in a notch between the two frontals, and is supported by a cartilaginous peg issuing from its posterior face, which lodges under the frontal on each side. Posteroventrally the ethmoid is produced into a pair of short peduncles which articulate synchronodrotically with the base of the lateral ethmoid of each side; immediately dorsal to this articulation each bone forms a small, horizontal and semicircular plate, which is accommodated in a flat notch on the anteroventrum of the orbitosphenoid. Anteriorly the ethmoid extends to attach to the oblique ligament of the kinethmoid, but is considerably distant from the kinethmoid ossification.
The body of the vomer is shield-shaped, and is firmly attached to the ethmoid ventrum. Anteroventrally it is produced on each side, to form a facet for the preethmoid. Laterally it is embraced by the palatine. Its posterior process is extremely long and fine, and is tightly held in a groove on the ventral surface of the parasphenoid shaft. The form of the posteroventral orbitosphenoid-ethmoid articulation is particularly noteworthy in light of the mobile, rotating-shelf joint here which is characteristic of the Cobitini [see p.186 ]. In _Vaillantella_ movement at this point is limited primarily by the parasphenoid-vomer lock.

The kinethmoid ossification is slightly expanded dorsally where it is bound to the tips of the ascending premaxillary processes. It is a small rectangular plate in lateral view, but bears midventrally, well-defined lateral shoulders to which attach the ligaments passing to the rostral processes of the maxilla. The ventral end of the kinethmoid is attached to the anterior ethmoid tip by an oblique ligament.

Both a preethmoid and a prepalatine ossification are present. The preethmoid is cylindrical, lying between the anterior vomerine facet and the maxillary buttress. The prepalatine is a shorter cylindrical bone, positioned dorsolateral to the pre-ethmoid, between the palatine and the maxillary buttress.

The lateral ethmoid is small. Its basal part forms a synchondrosis with the orbitosphenoid and is approached by small peduncles from the posterior part of ethmoid. It
is interesting that this articular part of the lateral ethmoid is convex, and that the orbitosphenoid is produced towards it, receiving it in a round, flat socket which is devoid of articular cartilage. The vertical plate of the lateral ethmoid is concave posteriorly, and is supported by small digitations which it extends onto the orbitosphenoid. It forms a small anterior orbital wall. Laterally there is a long, slim and poorly ossified lachrymal process of the lateral ethmoid produced anteriorly. The lachrymal process lies lateral to the palatine, medial to the infraorbital canal and parallel to the lachrymal bone.

The Sphenoid Series

The orbitosphenoid is 'U'-shaped, supporting the anterior part of each frontal dorsally. Posteriorly it forms a straight synchondrosis with the pterosphenoid, thus completing the orbital septum. Ventrally it lies in a groove on the parasphenoid. Its articulation with the lateral ethmoid is described above. A small horizontal split between the orbitosphenoid, pterosphenoid, and parasphenoid bones provides an exit for the optic nerve of each side.

The pterosphenoids are a pair of well-separated, rectangular plates each extending between the frontal above and the parasphenoid below. Posteriorly the pterosphenoid articulates with the sphenotic, and via small peduncles with the prootic. The posterior edge of the bone is evacuated between this and its parasphenoid
articulation, forming the anterior wall of the anterior trigemino-occipital foramen. This foramen is notably large.

The sphenotic is a small oval bone in the lateral wall of the braincase. It articulates synchondrotonically with the pterotic, epioccipital, pterosphenoid, and prootic, and dorsally is only partly covered by the frontal and parietal.

The Otic Series

The prootics are square bones in the braincase floor. The pair meet in the midline, dorsal to the parasphenoid, and contribute the walls of a very shallow posterior myodome. The anterior border of each prootic contributes to the border of the anterior trigemino-occipital foramen, and the posterior trigemino-occipital foramen is wholly enclosed in the body of the prootic. The posterior edge of the prootic is excavated to form a conical anterior saccular recess. A shallow depression formed in the region of the junction between the pterotic, exoccipital, and pterotic bones is a minimally defined subtemporal fossa.

The pterotic is a triangular wedge in the postero-lateral braincase wall. Its association with the hyomandibula fossa formation have been described [p.127]. It carries a small spinous process directed posteriorly. Dorsally the pterotic is partially overlain by the parietal. There is no temporal opening.

The occipital is absent.

The Occipital Series

The epioccipital is the round postero-dorsolateral
element of the braincase. It provides most of the articular area for the posttemporal, but its surface is peculiarly smooth around this articulation. Small crests on the posterior of the epioccipital support the epaxial musculature.

The supraoccipital is a long, shield-shaped bone with limbs extending anterolaterally to suture with the sphenotic. It articulates with the pterotic, epioccipital and the exoccipital on each side. Its outer surface is convex and smooth, except for a tiny triangular ridge behind the parietals. Its anterior border has no excavation as there is no posterior cranial fontanelle in Vaillantella.

The exoccipitals form a short suture in the dorsal mid-line and thus wholly enclose the huge foramen magnum. Their dorsal plates are limited, and there are no lateral occipital foraminae enclosed within them. There is a notch in the posterior border of each exoccipital. The ventral exoccipital walls bear separate perforations for the ninth cranial nerve (Cr. IX) anteriorly, Cr X together with the jugular vein, and for Cr XI posteriorly.

The basioccipital is a narrow pentagonal bone; posteriorly it articulates with the first vertebra, and ventrally it bears a pair of small, slightly flared divergent plates, which are greatly reduced pharyngeal processes.

The parasphenoid is an unusual shape in Vaillantella. The anterior third is very narrow, and its top is held tightly between the ethmoid and the posterior process of the vomer. It is grooved dorsally and ventrally where
it accommodates the orbitosphenoid and the posterior vomerine process respectively. The middle third of the parasphenoid between the optic foramen and the anterior trigemino facial foramen is expanded. The posterior third between the prootics is again narrow. The parasphenoid terminates in a clear fork underlying the basioccipital. The conformation of the parasphenoid, and the elongation of the pterosphenoid bones suggest that elongation in the skull of Vaillantella has taken place from this central part.

The Dermal Skull Roof

The supraethmoid is, as noted above [p.124] greatly reduced.

The nasals are reduced to traces of ossification round the laterosensory canal.

The frontals [fig.Lxie] are narrow anteriorly, and expanded posteriorly. The pair meet at a wavy suture in the mid-line, uninterrupted by a fontanelle. They are notched anteriorly, to accommodate the extremely narrow ethmoid, and expand slightly at the level of the lateral ethmoid of each side. A small semicircular plate extends ventrally over the dorsal part of the orbitosphenoid-pterosphenoid suture on each side, but does not reach the parasphenoid. The frontal sensory canal is not contained within the bone, but can be seen running free in the skin over it.

The parietals are square, meeting the frontals anteriorly, and each other in the mid-line, at straight
sutures. The sphenotic, pterotic and supraoccipitales are partly overlain by the parietales, thus completing the cranial roof.

There is a small square, dermosphenotic present free from, and overlying the sphenotic.

In *Vaillantella* there is no distinct supratemporal ossification. This part of the cephalic sensory canal system is in the skin.

The posttemporal is a long, slim, oval, bone, proximally lying on the epioccipital adjacent to its articulation with the pterotic, and distally articulating with the supracleithrum.

The infraroarial bones are reduced to tiny and occasional patches of ossification in the infraroarial canal wall. The fronto-parietal, and infraroarial canals converge anteriorly. They open towards each other terminally, although no commissure is apparent. The lachrymal is a long, slender splint-like bone lying between, and not containing the canals above and below it. It is adjacent and parallel to the lachrymal process of the lateral ethmoid. The temporal canal forms posterior to the orbit, and can be clearly seen in the skin flanking the braincase. It crosses the posttemporal and the supra- cleithrum, and becomes the lateral line in the wall of the anterior third of which are patches of ossification. The origin of the transverse occipital canal can be seen where the temporal canal crosses the epioccipital. The origin of the preopercular canal is invisible, but the canal itself can be seen in the skin coursing over the preopercu-
lum. There is no supraorbital bone.

The Pectoral Girdle

The pectoral girdle makes its dorsal articulation via the posttemporal as described above (p. 130).

The supracleithrum is an irregular oval bone of the same length as the posttemporal. Its upper half is overlain by the latter, and has the proximal part of the lateral line associated with, but not attached to it. A blunt process medially serves as the point of attachment for Baudelot's ligament.

In describing the pectoral girdle the terminology of Brousseau (1976) is used. The ascending limb of the cleithrum is two-thirds as long as the horizontal limb. Its upper third has a gutter laterally, accommodating the ventral supracleithrum tip, and posteriorly it is slightly expanded into a curved lamina. The lateral limina of the cleithrum is present only on the horizontal limb, and is increasingly emphasised anteriorly. Medially the horizontal limb has a flat surface. The oblique lamina is represented only as a ridge with which the proximal coracoid articulates. This encloses the anterior foramen posteriorly. The cleithra expand slightly at the simple pectoral symphysis.

The scapula is quadrilateral in outline, enclosing a very small scapula foramen. It is synchronondrotically joined to the posterior face of the cleithrum, and bears a small triangular ascending process at the dorsal end of this articulation. It also forms a synchronondrosis with
the coracoid, adjacent to which the scapula is raised into part of the mesocoracoid pedestal. The glenoid cavity in the scapula is shallow.

The coracoid is expanded proximally, where a broad oblique lamina of the coracoid meets the cleithrum, thus excluding the scapula from the posterior border of the anterior foramen. The coracoid is raised against the scapula and forms the larger part of the mesocaracoid pedestal. There is no accessory coracoid foramen. The vertical lamina of the coracoid is rectangular, and there is no descending prong. The coracoid shaft is long and slim, bounding the anterior foramen laterally. It is cartilage tipped and articulates with the cleithrum under a ridge which is all that is present of the horizontal medial lamina.

The pectoral fin attaches via four slim and rectangular proximal radials, the first of which articulates with the scapula, the second with the scapula-coracoid junction, and the third and fourth with the posterior coracoid margin. Distally, 7 or 8 cartilaginous menisci lie between the radials and the fin rayheads. There are ten rays. The dorsal head of the first \([R + 1]\) is modified to contribute to the glenoid saddle joint via a semicondylar lateral head, and a longer medial head. It also bears a triangular ascending process, and a triangular ventral flange which overlaps \(R - 1\). Ventromedially \(R + 1\) bears an articular buttress which contacts the first radial meniscus. The remaining rays are slim and simple.
The Pelvic Girdle ([fig. xxxiv)

This consists of a pair of archipterygial plates, each of which is deeply bifid anteriorly, producing spines which are long, very slim and closely apposed. The plates expand posteriorly, and a small triangular median aperture is enclosed between them. Posteriorly a pair of huge ischial processes develop, meeting in the mid-line extending, and reinforcing the pelvic symphysis. Each ischial process has a central cribiform area.

A well ossified ischial or medial radial element is present, inside the angle between the ischial process and the posterior edge of the archipterygial plate against which the pelvic fin rays articulate. There are 8 pelvic fin rays, the dorsal and ventral heads of which are separated by the medial radial element above, and also by a mid- and lateral radial meniscus on each side. The archipterygial surface is not raised into a articular condyle for the fin, nor for the fin muscles internally [dorsally] or externally [ventrally], although the plate surface is somewhat rugose over these areas. A lateral pelvic spine is present.

Dorsal Fin

As has been discussed (p.118-9) the number of rays in the median fins has been considered as of primary importance in separating the species of Vaillantella. In the specimen studied here, there are 64 dorsal fin rays, of which the first 2 are unbranched. These rays articulate with 63 paired distal radials, 61 medial radials and 63
spine-like proximal radials, the anterior of which are without medial radials. The proximal radials of this extraordinarily elongated dorsal fin articulate with the neural spines of V11-48. There is a tiny posterior ossified stay piece.

**Anal Fin**

In this specimen there are 14 anal fin rays, of which the anterior 3 are unbranched. These rays are supported on 11 paired distal radials, of which the anterior 3 are unbranched, 9 medial radials, and 11 spine-like proximal radials, the anterior two of which are without medial radials. The proximal radials of the anal fin articulate with the haemal spines of V36-42, and a minute, elongate and slim posterior stay piece is present.

**The Caudal Fin** [Fig. xxxivb]

The caudal fin of *Vaillantella* is forked. The principal ray count is \((1 + 9) - (8 + 1)\). The compound ural centrum is surmounted by a tall, broad urostylar process anterior to which there is a well-ossified epural. Distal to the urostylar process a single cartilagenous uroneural is present. The urostyle is broad and spatulate, and articulates with hypurals 3-6, which support the upper ray series. The hypurals are long, slim and rectangular. Hypurals 1 and 2 are fused to the ural centrum. The parahypural is expanded and plate-like, supporting the lower ray series. No parahypural pophysis is raised. The parahypural and the haemal spine of the second preural vertebra are autogenous. There are only
4 upper, and 3 lower procurent rays, and despite the length of the dorsal fin, the caudal fin is discrete. There are no elaborated intermuscular elements flanking the caudal peduncle, which contrasts with the usual noemacheilinete condition (p.315).

Axial Skeleton [fig. xxxv]

V1-4: modifications associated with the Weberian apparatus

The anterior swimbladder chamber of *Vaillantella* is partially encapsulated. Nalbant & Banarescu (1977) describe this capsule as uniquely consisting of two distinct lateral plates, and differing from the type of air bladder encapsulation characterizing the Noemacheilini where only the medial pairs are ossified. They consider this reminiscent of the Botini, especially *Leptobotia fasciata* and *Botia modesta*, and indicative of relationship between *Vaillantella* and the Botini.

The posterior portion of the airbladder is very long, free and divided into two cylindrical chambers by a coronal constriction. Nalbant & Banarescu (1977) consider that in this *Vaillantella* resembles certain, mostly high altitude, Noemacheilini.

The centrum of the first vertebra is short and platycoelous, with a round anterior profile forming the occipital articulation. Dorsally it supports the claustrum of each side, and lateral to this a small condylar process of the scaphium articulates with it. A pair of stout, curved lateral processes arises from the centrum ventrolaterally, to the tips of which attach ligaments passing
to the supracleithrum.

The centra of the second and third vertebra are fused and form a long, biconical and amphicoelous element. Lateral processes identified as those of V2 (P2) issue from below the anterior part. They are produced anterodorsally, and extend anterolaterally to partially flank and provide zygodontal support for the first centrum. Each process is bifid distally. The upper part (P2H) is a broad horizontal prong angled posteriorly, crossing over, but free from P4H. The lower part (P2D) descends as a broad falx on each side, curving posteriorly below P4H; it encloses a nerve foramen basally, and is produced as a horizontal spur laterally, which may include the distal part of P4H fused with it (p.239). Along its medial edge P2D meets P4D; the two bones constitute the partial anterior, ventral, and medial walls of the swimbladder on each side. The articular limb of each intercalarium impinges on V2 + 3 anterodorsally and there are indentations for the articular limb of the tripus of each side just posterior to the waist of this compound centrum.

The centrum of V4 is long, biconical and amphicoelous. Its pleural rib articulates in a cartilage lined apophysis on each side. Each rib expands as a horizontal plate (P4H) partially roofing the anterior part of the capsule and also lying over the tripus, which passes from below it anteriorly, over P2. Laterally P4H descends as a slim shaft spanning the angle between P2H and P2D, thus enclosing a small triangular and anteroventrally directed aperture. The descending part of P4H fuses to P2D and
may contribute to the lateral part of the wall formed from P2D. The part called P4D issues from beneath the parapophyses of V4 which are not fused to the centrum. P4D flares laterally and descends as a curved plate apposing P2D, and posteriorly is produced as an os suspensorium, which is concave posteriorly, and meets its fellow in the mid-line at a wavy suture.

The fifth vertebra is unmodified. It bears a slim pleural rib articulating with a low parapophysis which, like those posterior to it, is fused to its centrum.

Associated with the neural canal over V1-4 there are paired claustra, resting on the first centrum dorso-laterally, and suturing above with a mid-line shield-shaped element called SN2 following Fink and Fink (1981). SN2 articulates posteriorly with the base of the neural complex, and it is noted that cartilage is absent from this suture. The neural complex itself is long and rhomboidal in outline. The neural arch of 3 (NA3) forms synchondrotic articulations with the neural complex behind and with the claustrum in front, and rests on the anterior of V2 + 3. The NA3 lacks lateral production. It is excavated posteriorly leaving a dorsal aperture against the deep base of NA4. The neural spine of V4 is rather low and expanded.

On each side the Weberian chain consists of the os suspensorium, claustrum, scaphium, intercalarium and the 'Y'-shaped tripus, which has a long curved transformator process attached to fibres in the tunica externa. The tripus has a broad cartilage capped articular limb, and
a narrower anterior limb from which the interossicular ligament extends to the lateral end of the horizontal limb of the intercalarium, which lies at right angles to the spinous articular limb of that bone. The intercalarium is thus 'L'-shaped. Medially it contacts V2 + 3. The scaphium is cup-like. It has a small cartilage capped articular process, a slim spinous anterior process and a low blunt ascending process. The anterior border of each scaphium lies inside the foramen magnum, accommodated by lateral expansion of the foramen.

An intermuscular splint is associated with the base of the fourth and fifth neural arches: these are the most anterior representatives of the dorsal series of intermuscular bones.

The Posterior Axial Skeleton

Posterior to the Weberian apparatus the axial skeleton comprises 51 elements, plus the ural centrum. Twenty pairs of pleural ribs articulate with parapophyses which are fused to V5-24. The posterior ribs are very reduced. The abdominal vertebrae have poorly defined zygapophyses. The first haemal arch is completed on V28, thus there are 27 caudal vertebrae, characterised by rather long neural processes and prezygapophyses, and low posteriorly directed haemal spines.

The intermuscular skeleton comprises weakly ossified fine splints. The dorsal epicentral series extends from the caudal to V4. The ventral series is represented from the caudal peduncle to the ribs. The splints do not fork
and do not define an interlocking matrix.

**Branchial Skeleton**

The hyoid arch is short and deep, and the paired elements are narrowed to plates. The basal support of the hyoid consists of a urohyal, a simple basihyal, and dorsal and ventral paired hypohyals. There is no sublingual ossification in *Vaillantella* (see p.318). Each ceratohyal is short, and marked by two concave excavations ventrally. The first and second branchiostegal rays articulate with its lateral surface. The epihyal is also short, and triangular, and supports the third branchiostegal ray laterally. The three branchiostegal rays are flattened and filiform. The base of the interhyal shows a shallow bifurcation, and straddles the epihyal distally.

In the fragile basibranchial skeleton there are only 2 ossified basibranchial elements. Hypobranchials 1, 2 and 3 ossify. The first is slightly elongated anteriorly, and forms a loose saddle articulation in a concavity under the ventral hypohyal.

There are four long, slim and simple ceratobranchials. The fifth ceratobranchial is modified as the inferior pharyngeal bone. Its shaft is long, slim and curved and bears a single line of 7 simple conical teeth on a small, round, mid-distal expansion. Thus an independent tooth plate is not present. The inferior pharyngeal bone bears a ventrolateral digitiform process two-thirds distally for the attachment of the levator muscle.

The upper part of the branchial skeleton consists
of 4 slim epibranchials, which lack dorsal processes. The fourth epibranchial has a double proximal articulation with both the fourth ceratobranchial and the upper end of the inferior pharyngeal bone. Two infrapharyngobranchials ossify. The anterior of these [number 2] is round, placed between the second and third epibranchials, while the posterior [number 3] is long, spanning the second and third epibranchial, and extending towards the fourth epibranchial, to which it is linked with loose ligamentous tissue.

The significance of the anatomy of Vaillantella and the possible relationship of Vaillantella to the cobitid and cobitoid groups are discussed in the comparative review [p.333 - p334], in light of the hypothesis of the relationships of Vaillantella which has been assembled from adductor myology [p.65-8, fig. xix].
SECTION 4

DISCUSSION OF THE COMPARATIVE OSTEOLOGY OF COBITOIDES
SUSPENSORIUM AND OPERCULAR SERIES

Suspensorium and Lower Jaw [fig. xxxvi]

Howes (1981) points out that "in general there is uniformity of the suspensorial elements in the Cyprinidae; the variation is one of degree usually involving elongations, deepening, or medial depression of the bones". Similar variations of proportion are demonstrated by the suspensoria of cobitoid fishes.

In the Noemacheilini the hyomandibula is somewhat expanded and vertically disposed. Of its two dorsal articular heads, the anterior [sphenotic] abuts the pterosphenoid anteriorly, posteriorly lodging in a socket formed on the sphenotic and sometimes the prootic as well, while the posterior [pterotic] head articulates with the pterotic and sphenotic. The two hyomandibular heads are usually separated from each other, but are not so in Noemacheilus barbatulus, N. botia, Orthrias tscheiissuensis and N. nigromaculatus of those examined in this study. The significance of this separation is discussed by Howes (1980) with regard to the bariliine cyprinids and he notes that the condition of separation of the hyomandibular heads is derived, and is apparently correlated as much with vertical, as horizontal elongation in the suspensorium. Howes' conclusion seems also to apply to the cobitoids.

The hyomandibular-opercular articulation is a well-defined ball-and-socket joint involving a round condyle on the posterior border of the hyomandibula which is proportionally more ventrally positioned in the more flat-headed
noemacheilines. Ventrally the hyomandibula is grooved over part of the preoperculum. The groove is deep in flattened species, and especially so in _N. rupecola_. The pph [hyomandibular facet towards the preoperculum] of Ramaswami (1953) is the terminal projection of this groove. Ramaswami considered that its development in _Glaniopsis_ [fig. xxxvib] as well as in many noemacheilines, suggested relationship between these taxa (Ramaswami, 1952.3). I consider this hypothesis is refuted by the frequent appearance of this articulation throughout the Ostariophysi and also in _Parakneria_ and I consider that it should be interpreted as a plesiomorphic otophysean development.

The symplectic tends to be long in _Cobitidae_. Typically in the _Noemacheilini_ the symplectic is a rather slim, tapering bone. Occasionally, and markedly in _Lefua nikkonis_, its dorsal border is sculptured, where it articulates with the ventral border of the metapterygoid.

Amongst the _Noemacheilini_ the body of the quadrate varies from triangular to quadrilateral in shape, and has an invagination posterovertrally to accommodate the anterior tip of the symplectic. The posterior process of the quadrate is typically elongated, flattened and robust in _Noemacheilini_ and it is formed into a groove over the anterior end of the preoperculum.

The metapterygoid is usually not excavated, [see p.147-9] although as illustrated by _Orthrias_ [fig. iia] a small suspensorial fenestra is not unknown in the _Noemacheilini_. The metapterygoid is reflected medially to provide a shelf of bone under the eye. The production of the posterior part
of the metapterygoid, flanking the hyomandibula, is scarcely developed in Noemacheilini. In some species, e.g. *N. fasciatus*, there is a small cap of articular cartilage here.

The ectopterygoid is a simple flat plate of bone, directly proportional in length to the length of the jaw. It forms an overlapping plane articulation with the anterior border of the body of the quadrate. It also usually extends over the medial surface of both the anguloarticular bone and the coronoid process of the dentary.

The entopterygoid is large in Noemacheilini and has a well-developed medial reflection. It articulates firmly with the metapterygoid and with the quadrate. It makes an unusual kind of articulation with the palatine. Anteriorly the entopterygoid is formed into a strongly concave cup which is partially bordered by an inverted "U" of bony thickening. Thus limited ball-and-socket type movement is apparently possible between the palatine and entopterygoid.

Considered as a unit, the noemacheiline suspensorium is well-integrated, consolidated and robust.

The other noemacheilids show some variation from the typical neomacheiline suspensorium morphology. In *Glanioptus* (fig.xxxvib) the posterior process of the quadrate is highly developed, and both the metapterygoid and its posterior process are long and large. The metapterygoid is minutely fenestrated on its ventral border. By contrast, the entopterygoid is extremely reduced, and nail-shaped. The suspensoria of gastromyzonines and homalopterines were discussed by Ramaswami (1952: 3 and 4) who reported the
presence of a strong posterior metapterygoid process (pmp) in these two groups. In typical homalopterines and gastromyzonines the entopterygoid is large and usually, as also in the noemacheilids, interdigitates with the metapterygoid to some extent.

The jaw of *Vaillantella* (fig. xxxvid) is much longer than that of any other noemacheilid. In *Vaillantella* the posterior process of the quadrate is slim and spinous. The posterior process of the metapterygoid is long, and cartilage capped.

The suspensorium of *Ellopostoma* (fig. xxxvic) is peculiarly short. The preoperculum is stabilised by a flange on the posterior part of the hyomandibula, but there is effectively no posterior production of the metapterygoid, and no horizontal metapterygoid shelf on the floor of the massive orbit.

The suspensorium of the Cobitini contrasts with that of the noemacheilids. The typical cobitine suspensorium (fig. vii) is fragile and fenestrated. The hyomandibula heads are small. The anterior head, which never extends to articulate with the pterosphenoid, is usually round, and the posterior head is well-separated from it, and flatter. The hyomandibular-opercular articulation is usually no more than one-third ventral on the posterior hyomandibular border, but in *Cobitis* and *Sabanejewia* it is half ventral, although these are no more flat-headed than other Cobitini. The hyomandibula forms a shallow groove over the pre-operculum. The symplectic is very long and slim. The body of the quadrate is deeply excavated by the suspensorial
fenestra. The posterior process of the quadrate bone is long and slim.

The metapterygoid of some cobitines may be extremely reduced, for example in *Acanthophthalmus muraeniformis* in which it is no more than a Y-shaped strut of bone around the suspensorial fenestra. In the Cobitini the metapterygoid never develops a medial reflection. It may extend posteriorly as a process lying internal to the hyomandibula but a posterior process ([p.121]) does not develop. In *Acanthopsis choirocrynchus*, there is a spinous process directed anteriorly on the posterodorsolateral part of the metapterygoid. This process appears to be an autapomorphy associated with the peculiar condition of the adductor mandibulae in this species (see p.44).

In the Cobitini the ectopterygoid is usually reduced. It does not extend as far as the coronoid process anteriorly. The ectopterygoid is more or less produced posteriorly where it articulates with the dorsal border of the body of the quadrate, and is frequently an L-shaped bone.

The entopterygoid is reduced to a slim shaft of bone with a small concave cup anteriorly, which articulates with the palatine. This extremely reduced condition of the entopterygoid is characteristic of all cobitine species.

In the Botini the state of the suspensorium resembles very much that described as plesiomorphic for cyprinids by Howes [1980, 1981], and shows few peculiarities. Howes [1980] discussed a lateral flange of the hyomandibula as a synapomorphy uniting the bariliine genera in which it occurs, despite its occasional appearance elsewhere in the
Ostariophysi [Howes, 1978, Forey, 1975]. The presence of this flange in Botia macracantha of the cobitids examined here seems to emphasise the interpretation of Fink & Fink [1981] that this is actually a plesiomorphic feature [see fig. xxxviia and b]. In Botia modesta, B. almorhae and B. sidthimunki [see fig. xxxviic] there is a strong lateral prong of bone issuing laterally from the concave cup of the entopterygoid, with which the palatine articulates anteriorly. The presence of this prong reinforces the hypothesis derived from myology [p.76-7] that these species form a natural group from which B. hymenophysa and B. berdmorei are excluded.

There are only a few features in which the suspensoria of cobitoids differ from the plesiomorphic ostariophysean condition of that portion. The symplectic in Ostariophysi is seldom as long as in the noemacheiline, and especially cobitine cobitids. Howes [1980] described a comparatively long symplectic in the cyprinids Opsariichthys, Zacco and Barilius group A and Luciosoma and suggested that this was the common, and by inference, plesiomorphic cyprinid condition. It appears that the same polarity of symplectic length occurs in the Cobitidae. The symplectic in the Botini is short in comparison to the condition of that bone in the Noemacheilini and the Botini are here interpreted as the most derived cobitids. The extensive symplectic elongation in the Cobitini is, however, also apparently a derived condition.

The significance of fenestration in the ostariophysean suspensorium is not established. Fink & Fink [1981] noted the occurrence of a fenestra in the suspensorium in "most
primitive Ostariophysi" and cited it as a "primitive oto-
physan character", which is present in cyprinids and
characins and absent from ostariophysan outgroups to these.
These authors suggested a hypothesis of independent loss of
the fenestra from derived representatives of various
ostariophysan lineages can be substantiated by the "double-
headed axe profile of the metapterygoid in many of the
cyprinids from which the fenestra is absent". Fink & Fink
considered that this hypothesis is simpler and more
parsimonious than one of independent acquisition of the
fenestra in [many) primitive members of both cyprinid and
characin lineages. The last view is in support of that of

Howes (1978) concluded that the fenestra "is certainly
a functional device" serving either to relieve stresses by
directing forces generated in the lower jaw around the peri-
meter of the pterygoids and into the cranium, or perhaps more
importantly to act as a type of hinge which enables the
pterygoids to undergo lateral rotary movements. He pointed
out the correlation in characins, between reduction in
fenestration and reduction in the complexity of the dental
symphysis. Howes also indicated that when the skull is wide
the metapterygoid is often displaced towards the parasphenoid
thus providing additional space to accommodate the adductor
mandibulae, and that in the broader-headed cyprinids and
characins, the fenestra is usually absent.

A functional hypothesis for the development of a
suspensorial fenestra is substantiated by the cobitoids.
Typically in the noemacheilids, which are generally
broad-headed the fenestra is small or absent. In *Vaillantella* which is a narrow headed noemacheilid the medial reflection of the metapterygoid can provide the space to accommodate the adductor mandibulae muscle and in this species the fenestra is absent. In the Cobitini, which are narrow headed, horizontal cheek space is severely limited (p.38). The fenestra is present in all the Cobitini except *Misgurnus*. In *Misgurnus* the suborbital spine is vestigial, and the horizontal cheek space is less limited than in other cobitines.

In the Botini there is a massive suborbital spine, the head is not particularly wide, and the suspensorium does not develop a fenestra. However, the study of the adductor mandibulae muscle has emphasised that, in the Botini, most of the mobility takes place anteriorly, involving the complex rostralis muscles (p.46).

I am in agreement with Howes (1978) that suspensorial fenestration is a plesiomorphic ostariophysean character, the "potentiality for development of which has been realised in several lineages and under a variety of necessary combinations of selective pressures". The distribution of the fenestra within an ostariophysean lineage cannot therefore serve to indicate phylogeny, and I do not agree with suggestions that the distribution of this fenestra elucidates cobitid phylogeny (see e.g. Ramaswami, 1953).

The relations of the palatine, ento- and ectopterygoid bones are distinctive in cobitoids. Howes (1978) noted variation in the state of this articulation in cyprinids according to head width. He showed that, in cyprinids, the
joint is usually formed by a right-angled indentation in the ectopterygoid, and that the articular end of the palatine is usually simple, but may be sloped, and partially overlapped by the entopterygoid. In the cobitoids the palatine-entopterygoid articulation takes the form of a more-or-less complete ball-and-socket joint. Typically in the case of the noemacheilids, and especially the Noemacheilini, it appears that lateral rotation is possible between the palatine and entopterygoid. The development of this articulation is probably a prerequisite to development of the mobile suborbital spine of the Cobitidini. In the Cobitidini the ball-and-socket type of joint between the palatine and the endopterygoid becomes involved at least synergistically in the lever system operating the spine [see p.193 ].

Reduction of the ectopterygoid bone to the degree shown by some cobitines, e.g. *Acanthophthalmus muraeniformis* is unusual, as is the production of the posterior (quadrate) process of the ectopterygoid in the Cobitini generally, which is not observed outside this group. However, the form of the cobitine ectopterygoid seems to be correlated with lengthening of the suspensorium in this group, and within the group all degrees of modification of the bone are seen, which renders its form ineffective for use as a character.

**The Opercular Series** [see figs. ii, vii & xxxvi]

In the Noemacheilini (fig. ii and xxxvi) the operculum is quadrilateral, variably produced anteroventrally and usually longer than high.
In the Cobitini [fig.vii] the operculum is a fragile plate and strongly anteroventrally produced so that it is more or less triangular in form. Fink & Fink [1981] suggested that triangular-formity of the operculum was a synapomorphy which indicated a gymnotid-siluroid link. However, while the opercular series of catfish are highly modified [see e.g. Alexander, 1965; Mahajan, 1966] a triangular operculum is not unique to the gymnotids and catfish. The operculum is triangular in Acanthopsis choirophthalmus and, less markedly, in several Cobitini, and in Vaillantella [fig.xxxv].

An anterodorsolateral digitiform process of the operculum providing for the insertion of the m. dilator operculi is almost invariably well-developed in cobitoids, and Ramaswami [1953] suggested this process might be characteristic of the Cobitidae. However, I have observed the presence of the process within all the ostariophysean outgroups I have examined, and interpret it as a plesiomorphic ostariophysean character; a conclusion endorsed by the observation of Howes [1980] that the process is well-developed in Opsariichthys. In the cyprinoid Gyrinocheilus aymonieri, in which the respiratory mechanism is peculiar, the opercular process is absent. Its absence in this species is considered by Hora [1923] and Ramaswami [1952:1] to support the status of the Gyrinocheilidae as a valid family. I note that the opercular process is scarcely raised in both the cobitid Botia macracantha and the cyprinid Barilius bendelisis, in both of which the lateral hyomandibular flange [p.146-7, and fig. xxxvii] provides attachment for the m. dilator operculi. It appears that the opercular process has been lost several times.
times independently within the Ostariophysi.

The nature of the subopercular-opercular-interopercular articulation, from which the operculum is usually excluded, varies in cobitoids, between a loose buttress and a rather tight ball-and-socket joint. In the Noemacheilini the suboperculum is a falciform plate and the interoperculum is relatively long. The interoperculum extends anterior to the preoperculum which itself extends anterior to the symplectic. In some flat-headed noemacheilines an ascending process is produced on the dorsal border of the interoperculum posteriorly; the interopercular-retroarticular ligament is short and strong, and thus there is substantial rigid ventral support for the suspensorium.

By contrast, in the Cobitini the anterior limit of the interoperculum is posterior to that of the preoperculum [although only slightly so in Misgurnus]. The symplectic extends further forward than the preoperculum and the interopercular-retroarticular ligament is long. In the Botini the symplectic, preoperculum, and interoperculum end above each other in the same vertical plane as they do also in the noemacheilid Vaillantella.

In the peculiar noemacheilid, Ellopostoma, the symplectic extends anterior to the preoperculum and interoperculum, reflecting the posterior-ventral displacement of the mouth in this species. In Ellopostoma the opercular bones are comparatively short and deep, approaching the condition of these bones in the kneriid Parakneria, and the gymnotids Gymnotus and especially Hypopygus amongst the outgroup species examined.
The form of the cobitoid preoperculum corresponds to that of the suspensorium as a whole; it is variably falci-form and only occasionally contains the preopercular sensory canal. More usually in cobitoids the preopercular canal passes in the skin lateral to the preoperculum [p.253].

**LOWER JAW** [fig. xxxvii [a-h]]

The lower jaw of the cobitoid fishes is, as in the cyprinids, invariably edentulous.

In the noemacheilids the lower jaw articulates on each side through a slightly twisted saddle joint formed between a wide toggle-shaped articular head on the quadrate and a socket on the posterior of the angulo-articular unit. The coronomeckelian (= sesamoid angular) is present as a small flat triangular ossification on the medial face of the dorsal process of the anguloarticular unit, and serves as an insertion for the tendinous insertion of the A3 [see p.32 ]. No coronomeckelian is found in the specimen of *Oronectes platycephalus* examined and the bone is slightly enlarged and displaced in *Lefua* [fig. xxxviiiib] so that its upper half extends over the anguloarticular border. In the noemacheilid lower jaw the Meckel's cartilage is of variable length, extending between a small osseous buttress on the anguloarticular, and a similar buttress on the dentary anteriorly. The retroarticular is invariably present as a more-or-less rhomboidal wedge of bone, synchondrotically united to the posteroventral part of the anguloarticular.

The dentary has a well-defined and vertical rectangular coronoid process. In *Noemacheilus nigromaculatus* and N.
yarkandensis, the coronoid process slopes distinctly obliquely anterodorsally. The dentary bars curve anteromedially in the horizontal plane towards each other. The rami are flattened and become trough-like in the most flat-headed noemacheilid species.

The lower jaw of Vaillantella [fig. xxxviiid] is of the usual noemacheilid type. The lower jaw of Ellopostoma [fig.xxxviiic] has half the coronomeckelian protruding above the dorsal border of the reduced, almost square anguloarticular. The coronoid process is raised half anteriorly on the dentary and thus, in general proportions, the lower jaw of Ellopostoma more closely resembles the cobitine than noemacheiline type, although the dentary bar is wide and flat as it is also in many noemacheilines.

In the Cobitini the lower jaw is narrow, but otherwise resembles that of a typical Noemacheilus. However, in Lepidocephalus annandali, L. guntea and L. caudofurcatus [fig. xxxviii f and g] and, with less definition, in L. thermalis there is a prong of bone issuing from the anguloarticular, dorsolateral to the quadrate articulation. There are no muscles attaching to this structure. This development appears to be a synapomorphy uniting species of the genus Lepidocephalus [fig.xCII].

In Cobitini the anguloarticular unit is elongated and tapering with its ascending process minimally defined. Ramaswami (1953) records that in "Acanthophthalmus and Cobitis the dentary and angular are practically the same size", and that the coronomeckelian is absent. In all the cobitines I examined the coronomeckelian is apparently
present only in *Lepidocephalus guntea* and *L. caudofurcatus* (fig. xxxviiif). In these species it appears as a peculiar floating sesamoidal ossification of the A2 division of the adductor mandibulae. Nelson (1973) stated that the coronomeckelian was very variable in its degree of development throughout the Ostariophysi, but the disappearance of the coronomeckelian can be identified as a characteristic condition for Cobitini.

A peculiar looseness of the articulation of the anguloarticular with the dentary on the Cobitini was noted by Ramaswami (1953) and is emphasised here. The nature of this articulation appears to allow dorso-ventral level movement about a peg and socket joint.

The coronoid process originates about half way along the dorsal border of the dentary in the Cobitini, and as in the Noemacheilini, is typically rectangular. This process is unusually low in *Somileptes* and is anvil-shaped in *Acanthopsis*. Each ramus of the dentary is slim and convex laterally in cobitines.

In the Botini the lower jaw is compact, and in *Botia* rather shorter than in the Cobitini. The ascending part of the anguloarticular is produced and this unit shows some tendency to fuse with the dentary - a condition most realised in *B. berdmorei* (fig. xxxviiih). The coronomeckelian and Meckel's cartilage are in their plesiomorphic form.

The coronoid process is raised on the back of the dentary. The rami of the dentary are rather flat with raised sides. The dentary rami are slimmed down in *Botia macracantha*, and in this species and in *B. almorhae* the symphysis is long. In the Botini generally the two halves
of the lower jaw approach each other closely.

It seems that in each of the 3 subfamilies of the Cobitidae recognised traditionally (viz. the Noemacheilini, Botini and Cobitini) a different feeding strategy has been adopted, and this is reflected in the coordinated morphology of the jaws, the m. adductor mandibulae and the barbels. Therefore some of the "characters" apparent from these actually form part of character complexes, and this must be taken in to account when drawing up hypotheses of relationship.

THE UPPER JAW (fig. xxx ix)

Premaxilla

The premaxillae of the Cobitidae are characterised by very long ascending or rostral processes, which are invariably as long as the horizontal limbs, rendering the bone L-shaped. These paired rostral limbs are usually slim and digitiform, and their dorsal tips are bound to the kinethmoid by ligamentous tissue. The horizontal limb excludes all but the most posterior part of the maxilla, which projects posterior to it, from the oral border.

In the Noemacheilini the horizontal limbs of the premaxillae are more robust than the ascending limbs. The two limbs are usually at right-angles to each other, but form a more acute angle in Noemacheilus botia, N. corica and N. fasciatus of those species examined. Ramaswami [1953] contrasted the noemacheiline premaxillae with those of the Botini, stating that in the latter taxon the angle of the bone was produced anteroventrally to form a beak, which did
not feature in the former. I note that in the noemacheilines Orthrias tschaliyssuensis, N. rupecola [fig. xxxixb] and N. nigromaculatus, in contrast to e.g. N. corica, N. strauchi [fig. xxxixa] and Oronectes platycephalus which show the most typical form of the noemacheiline premaxillae, the anterior angle is produced into a beak, and accompanying this, as in the Botini, the ventral profile of the horizontal limb is concave. Very strong development of this beak-like condition of the premaxillae in Noemacheilus potanini led Nicholls [1925a] to state that in this species the pre-maxillae were "fused into a rounded point above" the mouth, and he suggested that the species represented a monotypic genus Homatala. The premaxillae of specimens of N. potanini examined by me are not fused together, and I do not consider Homatala a valid genus.

Alexander [1968] discussed the development of beak-like jaws in some cyprinids which feed by scraping. It appears that the production of a somewhat beak-like premaxilla in some Noemacheilus and in Botini is a similarly derived condition.

Of the other noemacheilids, in Vaillantella [fig.xxxixc], the premaxillae resemble those of typical noemacheilines, but in Ellopostoma [fig. xxxixd] these bones are modified following the obliquely anteroventrally planed rostrum of this species, leaving the horizontal limb considerably shorter than the ascending limb. In Glaniopsis the premaxillae are of the typical noemacheilin type. However, I do not consider that the similarity of the upper jaws of Glaniopsis and Noemacheilus demonstrates relationship between
these, because the condition is not unique to them.

In the homalopterines and gastromyzonines the proportions of the premaxillae are variable. According to Ramaswami (1948) the ascending processes of *Balitora brucei* are long, as in *Noemacheilus*, but those of *Homaloptera zollingeri* are shorter, "as typical of Cyprinidae", and the ascending processes are long in *Protomyzon* and shorter in *Vanmanenia*. I note the ascending processes are effectively as long as the horizontal limb in *Homaloptera orthagoniata* (fig. xLiiid). I further note that they are long and sculpted in *Gastromyzon borneensis*, in which they lie immediately posterior to the modified, bumper-like lachrymal. In *Gastromyzon borneensis* the medial ends of the horizontal limbs of the premaxilla are expanded sagittally to form a symphysis, and the ascending limbs arise slightly lateral to this. Each ascending process bears a small lateral shelf mid-dorsally, which articulates over the dorsum of the expanded rostral process of the maxilla. This modification increases the stability of the upper jaw of this species (see fig. xLiiic).

In the Cobitini both the horizontal and the ascending limbs of the premaxilla are slim and flat, except in *Niwaella* where the horizontal limb is robust (fig. xxxixe). Nalbant (1963), in proposing *Niwaella* as a new genus, commented on the sucker-like nature of the whole mouth which is unusual amongst Cobitini. The nature of the premaxilla of *Niwaella* emphasises this peculiarity. The premaxillae of the cobitine *Acanthopsis choirorhynchus* are also unusual in that the horizontal limb has a deeply concave ventral profile and forms an angle of 80° with the ascending limb, resulting in
slight beak production (fig. xxxixf).

In the Botini the premaxillary limbs are of equal length, and the horizontal limb is expanded to some extent. Production of the anterior part of the premaxilla to resemble a beak is usually marked. There is an extreme peculiarity in the nature of the premaxilla of Botia hymenophysa, B. berdmorei and B. beauforti in that there is a large oval fenestra between the ascending processes (fig. xxxixg). Ramaswami (1953) described this feature as "a semicircular arch of the premaxillae formed in front, to support the tuft of maxillary barbels". He illustrated B. hymenophysa, but he did not make it clear that the premaxillary fenestra is present only in the 3 botine species above, which constitute the Hymenophysa species group of the Hymenophysa subgenus of Botia, delineated by Taki (1972) on the basis of this character. I interpret the premaxillary feature as a synapomorphy indicating that the 3 species in which it develops are a natural group.

Amongst ostariophysean outgroups the development of the ascending processes of the premaxillae is very variable. In Catostomus, as observed by Weisel (1960) in Catostomus macrocheilus, the small premaxillae are "L"-shaped; it is confirmed by my observation on the premaxilla of C. catostomus that the ascending processes are as long as the horizontal and that the bone very much resembles that of a typical Noemacheilus. In catostomids, as in cobitoids, the ascending processes of the premaxillae rest against the rostral processes of the maxillae, and the horizontal ramus of the premaxilla does not contact the maxilla. Weisel
pointed out that, as a result of this, on protrusion the premaxilla is carried some distance forward from the lower jaw.

By comparison with the condition in catostomids and cobitoids, the ascending processes of the premaxillae are short in the cyprinids Barilius and in Aulopyge and in the gobionine species examined. This appears to be more typical of the cyprinids in which, as shown by Alexander (1966), upper jaw protrusibility is primarily increased by introduction of the kinethmoid lever, to which the tips of the ascending premaxillary pedicels are rather tightly and intimately bound. In the cyprinids in which the mouth is ventral, the ethmoid is curved ventrally, and the ascending processes of the premaxillae are not particularly elongated.

It may further be noted that in Gyrinocheilus the premaxillae are expanded and plate-like and the ascending process is much longer than the horizontal to produce an overall form of the bone not unlike that seen in Ellopostoma (fig. xxxixh and d). This contrasts with the situation in the sand-burrowing hill-stream cyprinoid, Psilorhynchus, in which the premaxillae are robust but the ascending limb is short, and its tip is laterally displaced from the kinethmoid (Ramaswami, 1952.2).

Matthes (1963) concluded that marked development of the ascending premaxillary pedicles, or processes allies strong protrusability to high rigidity in the jaws of cyprinids. He noted that they are long in predaceous forms. However, the processes are small in some, for example, the carnivorous Macrocheilus, and it is clear that the pattern
Matthes described is not invariable. Howes (1981) pointed out that within the cyprinids the ascending processes of the premaxillae are seldom as long as the horizontal limbs of those bones.

Alexander (1966) concluded that cyprinid premaxillary protrusion was of principal value in allowing closure of the mouth while maximum buccal-cavity volume was maintained. From the outgroup study it emerges that the ascending premaxillary process is elongate in some non-cobitoid ostariophysean taxa with ventral mouths - namely, Catostomus, and Gyrinocheilus. The feature seems to increase the potential volume of the buccal cavity. It is accompanied by a decrease in anterior protrusibility of the jaws, but ventral protrusibility is promoted (as noted by Weisel, 1960) by the lack of intimacy of articulation between the maxillae and the horizontal limb of the premaxilla when this is the case, as it is in Catostomus and the cobitoids. I conclude that long ascending premaxillary limbs in Ostariophysi are a derived, but not necessarily unique condition.

Maxilla

Fig. xxxix illustrates the variability of the shape of this bone within the cobitoid group. The plane lateral face of the plesiomorph cyprinid maxilla is rectangular, with a mid-dorsal ascending process of which the anterior border is convex and the posterior concave (Howes, 1981). By comparison to this, a general notable feature of the cobitoid maxilla is a low ascending process apparently correlated with the presence of the lachrymal ossification lying dorsal to this bone.
In no cobitoid does the body of the maxilla have a foramen. The significance of maxillary foramination in cyprinids was discussed by Howes [1980, 1981] who indicated the foramen as an apomorphy serving to transmit the division of Cr VII innervating the anterior barbel. By contrast to the situation in the division of the cyprinids in which the maxilla is foraminate, the thick nerve trunk passing to the anterior barbels of the cobitoids courses dorsal to the maxilla; it passes over a more-or-less well-defined concavity lateral to the preethmoid facet of the maxilla. From this it seems logical to conclude that despite superficial resemblance in the position of the anterior barbels of some cyprinids and cobitoids, the cobitoids actually share a more recent common ancestry with the group of cyprinids in which the maxillary foramen has not been derived than with those cyprinids in which the foramen is present.

Ramaswami [1953] described it as typical of Cobitidae that the maxilla has 4 processes; one "ventral, or rostral" one "anterior premaxillary", one posterior for articulation with the preethmoid, and one anteroventrally, for the insertion of A1. These 4 maxillary processes are shown in fig. xxxix, and discussed in turn below.

Each rostral process provides attachment for a ligament which passes to the kinethmoid thus providing a pivot about which the bone can act as a rocking lever, generating typical cyprinid jaw protrusibility [Alexander, 1966]. The rostral process on the cobitid maxilla is rather long and digitiform. It is stout and strong in the Noemacheilini and Botini, but more refined in the Cobitini, except notably in Niwaella in
which, as described [p.158], the upper jaw is unusually robust, and in Acanthopsis choirocrynchus in which the snout is extremely elongated. I note that the process is very slightly forked in Glaniopsis and in the Homalopteridae, where it provides additional lateral tenure for the kinethmoid in these very wide snouted forms.

The anterior, or premaxillary, process of the maxilla of the Noemacheilini takes the form of a small rubbin, ridge, or flange which is vertically disposed, and which provides attachment for the palatomaxillary ligament. In the Cobitini that ligament is rather fine, and the anterior part of the maxilla is produced forward as a plate in correlation with elongation of the ethmoid region of this group [see fig. xxxix]. The palatomaxillary ligament may attach to the ventral edge of this process, or as described in the myology section [p. 43], be displaced dorsally.

In Botia the anterior process of the maxilla is characteristically well-produced. It constitutes the anterolateral parts of a cradle formed around the kinethmoid and the ascending tips of the premaxilla. This cradle is not well formed in Leptobotia. It clearly constitutes part of the character complex associated with the anteriorly organised oral function of Botia.

The posterior process of the maxilla as indicated by Ramaswami [1953], is a variably raised posterodorsal peduncle against which the preethmoid, and premaxilla when this is present, articulate. In the Noemacheilini it is usually solid, low and wide, providing for the articulation of the of the preethmoid and, lateral to it, the prepalatine. In
the Botini the process is considerably more produced, and constitutes the posterolateral wall of the premaxillary cradle.

The A1 or anteroventral horn-like process of the maxilla indicated by Ramaswami (1953) is present in all cobitoids. It is more strongly developed in flat-headed forms in which the horizontal bulk of the A1 muscle is increased [p.34-5].

The condition of the maxilla in the non-noemacheilin noemacheilids shows some peculiarities as follows:— The maxilla of Ellopostoma is effectively square [fig.xxxixd] and this condition is not approximated elsewhere in the cobitoid group. It is noted particularly that despite sharing extraordinary truncation of the horizontal limb of the premaxilla with Ellopostoma, the maxilla of Gyrinocheilus [fig. xxxixh] does not at all resemble that bone in Ellopostoma.

In Homaloptera orthagoniata the anterior process of the maxilla is extremely produced into a curved vertical plate. This plate extends to reinforce the snout and protect the premaxillae anterolaterally. Each maxilla does not meet its fellow in the anterior mid-line. In Gastromyzon borneensis primary protraction for the snout is provided by the lachrymal bumper, and the anterior process of the maxilla is a stout peduncle abutting this. The rostral process is produced as a robust horizontal shelf of bone which supports both the premaxillae and the kinethmoid medially [fig. xLiiiic].

Some further peculiarities developing in association
with the maxilla of cobitoids may also be noted. Ramaswami (1953) described an additional "large lateral" process of the maxilla of *Somileptes pongota*; I record a raised, two-eared dorsolateral flange on the bone in this fish, which provides insertion for the A1v. The A1d inserts on the anteroventral maxillary horn, and is crossed by the independent tendon of A1v. It is noteworthy that on neither *Acanthophthalmus semicinctus*, or the Gobioidae, in which a similar crossed tendon arrangement is also found (see p.54-5), is such a process raised.

The anterior lateral part of the maxilla of *Acanthopsis choirohynchus* (fig. xxxixf) is raised into 4 or 5 blunt nipples. One of these attaches the palatomaxillary ligament, while the others, together with the anterior maxillary plate support the long tendon dv. It is notable that in *Somileptes* and *Acanthopsis* the body of the maxilla is similar and rectangular in shape. Similarities in the jaw morphology of these 2 cobitine species are further discussed on page 337.

**THE KINETHMOID**

The derivation of the kinethmoid, or rostral bone, is not established. Goodrich [1909] considered it to have arisen by fragmentation from the anterior of the ethmoid. Regan [1911] stated its presence as derived and characteristic of the Cypriniformes in which he included four families, the Cyprinidae, Homalopteridae, Catostomidae and Cobitidae. Howes [1981] pointed out that the kinethmoid was frequently bifurcated and that it was likely there was a phylogenetic ossification into a single unit, of two premaxillary-ethmoid
ligaments, i.e. it may be that the bone arose as a sesamoid in this ligament system in which it is invariably found.

In its plesiomorphic condition the kinethmoid is rod-shaped (Howes, 1981). In the cobitoids the bone is very variable in shape (see fig. xL) in correlation with the very variable proportions of the ethmoid region in these fish. However, a general feature in cobitoids is the anterior displacement of the kinethmoid from its relation to the ethmoid tip, which is never forked or cupped and to which attaches the long ligament passing obliquely anteriorly to the kinethmoid base. The distance by which the kinethmoid is displaced from the ethmoid in cobitoids is reduced by frequent elongation of the ethmoid tip anteriorly in many noemacheilines; this phenomenon is also marked in *Catostomus*. The displacement of the kinethmoid from the ethmoid is greatest in the long-snouted cobitines, in which the kinethmoid appears to have lost all relation to the ethmoid block. However, it is emphasised in all cobitoids the kinethmoid retains immediate association with the tips of the ascending processes of the premaxilla.

In the Noemacheilini the kinethmoid is stout, and expanded dorsally where it forms a cup of variable depth to which the premaxillary tips are bound by ligamentous connective tissue (fig. xL a-c). In all the species examined by me, except *N. nigromaculatus* (fig.xLd) the kinethmoid has paired lateral expansions attaching the ligaments passing to the rostral process of the maxilla of each side. These lateral processes are indicated as a derived but not unique feature of the bone (Howes, 1981).
Of the other noemacheilids the kinethmoid of *Vaillantella* is a slim rod, with a slightly expanded dorsum and a lateral process on each side. That of *Ellopostoma* is a simple rod. The kinethmoid of *Glaniopsis* is elaborate [see fig. xLe], while that of *Homeoptera orthogoniata* is a stout cylinder. In *Gastromyzon borneensis* the kinethmoid bone is extremely enlarged to provide central support for the ethmoid region, and is surrounded by the ascending premaxillary processes anteriorly, the maxilla dorso- and ventrolaterally, and the ethmoid posteriorly [fig. xLiiic].

In the Cobitini the kinethmoid usually assumes the form of a small sagittal plate with a slightly expanded dorsum supporting the premaxillary tips [fig. xLf and g]. Tiny lateral expansions for the ligaments described above are observed in *Acanthopsis choirocrhynchus* [fig. xLh] and *Acanthophthalmus semicinctus*.

In the Botini the dorsal expansion of the kinethmoid [see fig. xL i and j] is marked. Not only does this provide accommodation for the premaxillary processes, but it also provides attachment for dense ligamentous tissue lying over the dorsum of the rostrum, in which the additional sesamoid preethmoid ossifications [p. 170] lie when these are present. This system constitutes the posterodorsal wall of the premaxillary cradle.

**PREETHMOID OSSIFICATIONS**

The preethmoid ossifications are of considerable interest in the cyprinoids and their phylogenetic derivations and homology has been a source of much discussion. The pre-
Ethmoid ossifications of Cobitidae are of particular interest because the bones are very variably represented in this family.

Patterson (1975) described the preethmoids as paired endoskeletal ossifications present in esoids and many cyprinoids, in which they are found lying directly over paired dorso-lateral processes of the vomer. The ossifications articulate with the palatine laterally and the maxilla anteriorly. Patterson considered that the cyprinoid preethmoid was a neomorphic ossification associated with the development of protrusibility and characteristic of that group.

Alexander (1966) suggested that the preethmoid arises as ossification of the anterolateral processes of the mesethmoid cartilage. Observation of the ontogeny of Barbus (Howes, 1981) corroborated this.

De la Hoz & Chardon (1975) considered that a phylogenetic developmental state of the preethmoid was illustrated by the gymnotid Sternopygus macurus, in which the ventral part of the supraethmoid extends as two pansaggital flanges fusing in with the hypoethmoid, forming a partial dorsal hypoethmoid, as features in Notropus and other osteoglossomorphs. It is this structure (see fig. xLia) that they considered to be the homologue of the cyprinid preethmoid.

The plesiomorphic form of the cyprinoid preethmoid is concluded to be a single lateral ossification of ethmoid cartilage, distally articulating with the maxilla and the palatine (Howes, 1980) and proximally, at least in all cyprinids except the abramines, accommodated in a fossa
formed of the mesethmoid and vomer (Howes, 1981).

The preethmoid may ossify in more than one part, and the naming of the separate ossicles, or cartilage blocks thus produced has not been established, neither has their homology. The review below is to clarify the terminology which will be used here.

In many cyprinids the preethmoid extends anteriorly, and this elongate bar may ossify in two parts, or, as frequently is the case, the anterior portion may remain unossified as a distinct cartilage, although in the cobitoids, Gobiinae, and catostomids the anterior portion is particularly well represented as a bony rod. Ramaswami (1952:3) proposed that this anterior element as he observed it in homalopterids and cobitids was actually homologous with the plesiomorphic cyprinid preethmoid despite, as he stated, that "at first sight the posterior appears topographically comparable with that of cyprinids". Thus Ramaswami labelled the anterior preethmoid PE1, and called the posterior a "second preethmoid" or PE2, suggesting that this PE2 was a new apophysis of the ethmoid. Howes (1981) emphasised that the anterior of the two ossifications in question actually appears to be the original element, and I follow the authors above in calling this PE1, and the posterior PE2.

Ramaswami (1955a) assessed the preethmoid region of the Gobiinae and reversed the terminology he proposed in 1952:3 and 4. He concluded from studies on a number of cyprinids that the anterior preethmoid element articulating with the maxilla was of secondary derivation, and should therefore be called the PE2. This nomenclature is not
followed here.

PE1 as here identified is synonymous with the sub-maxillary of Sagemahl (1891), Regan (1911), Starks (1926), Gregory (1933), PE2 Ramaswami (1955a) and possibly the submaxillary meniscus as described by Alexander (1966) in *Leuciscus*.

PE2 as here identified is synonymous with the septo-maxillary of Sagemahl (1891) and Regan (1911) the preethmoid of Starks (1926) the anterior process of the ethmoid of Ramaswami (1948) and PE1 of Ramaswami (1955a).

In addition to the preethmoid ossifications identified above, a separate bony rod between the palatine posteriorly and the maxilla anteriorly may be present in some cyprinoids. This element was called the "lateral rostral" by Ramaswami (1948) or the prepalatine Ramaswami (1952:3), and is called prepalatine here.

The peculiar round sesamoid bone, present in *Botia* and sometimes in *Noemacheilus*, which develops in ligamentous tissue over the rostrum, and lies dorsolateral to the kinethmoid bone was described by Ramaswami (1953) and simply called "sesamoid bone". I use the same name.

The ossifications developed in the preethmoid region are particularly variable in the noemacheilids. This variability is tabulated in fig. xlii. In the Noemacheilini one preethmoid rod and dorsolaterally and in parallel to this a separate prepalatine are invariably present.

It is interesting to note that an aliziran transparency of *N. fasciatus* shows clearly that there are two separate cones of ossification in the PE1 in this species.
In noemacheilines the PE2 is sometimes developed. When present it is usually a wedge of bone firmly articulating with the mesethmoid and the vomer (fig. xLiiia). Ramaswami (1953) also commented on the occasional presence of the PE2 ossification in the noemacheiline skull, and I note that he described it as present in _N. botia_. It is absent from specimens of _N. botia_ dissected by me, and therefore it must be concluded that there is probably intraspecific variation in the presence of this ossification in _Noemacheilus_.

The sesamoid bone is occasionally present in _Noemacheilini_ and it is noted that in the species examined, the PE2 is absent when the sesamoid features: it is also absent from some species where there is no sesamoid.

Of the non-noemacheilin noemacheilids, in _Vaillantella_ the preethmoid ossifications are represented by a single PE1, and a prepalatine rod (fig. xxxiii). In _Ellopostoma_ PE1 and PE2 are present but in contrast with the condition in the noemacheilines, there is no prepalatine (fig. xxviii). In _Glaniopsis hanitschi_ PE1, PE2 and a prepalatine are present. Ramaswami (1952:4) described 2 prepalatines in _Glaniopsis_ lying parallel to each other which he considered were derived by splitting of the original rod. I find only a single ossification in the specimen of _Glaniopsis_ examined by me. In _Homaloptera orthagoniata_ PE1 and a prepalatine are present (fig. xLiiid). Ramaswami (1952:3) described a PE2 bone in many of the homalopterines examined by him. In _Gastromyzon borneensis_ I observe PE1 and PE2, but no prepalatine (fig. xLiiic). Ramaswami (1948) noted that of all the gastromyzonines examined by him, only in _Crossostoma_
was the prepalatine present.

In the Cobitini the preethmoid is single and invariable in form. It is a Y-shaped bone with the fork posteriorly disposed. One of the two posterior heads articulates with both the ethmoid and the vomer, the other head which is dorsolateral to the former, articulates with the palatine. Anteriorly the preethmoid articulates with the posterior process of the maxilla (see fig. xii).

In the Botini a rod-shaped PE1, and separate prepalatine are invariably present; PE2 is absent. The sesamoid bone is present in all the Botini examined, except *Leptobotia fasciata*.

The pattern of ossification in the preethmoid region has been used to suggest the interrelationships of cobitoids, especially with regard to the Gobiinae and Catostomidae because, as in most Cobitidae, there are two pairs of preethmoids in these two families.

The conclusion reached by Ramaswami (1956a) was that the elongate and sometimes ossified anterior preethmoid (PE1 here) of the Gobiinae resembled that of *Catostomus*, and that this provided evidence of relationship between these two groups. Ramaswami agreed with the proposal of Nicholls (1943) that the gudgeons were "supercessory to the catostomids in China". However, Ramaswami did not consider that the similarities between the preethmoid ossifications of the gudgeons and cobitids suggested relationship between these two groups. He described the presence of a prepalatine in *Gobiobotia*, but emphasised that this was a parallelism of, and not equivalent to the prepalatine of Cobitidae. I
illustrate a small ossification in the palatovomerine junction in the gobioine Abbottina [fig. xLiiif].

Weisel (1960) described three pairs of cartilages in the preethmoid region of Catostomus macrocheilus. A prepalatine and two preethmoids are also present in C. catostomus [fig.xLiiig]. Weisel pointed out that in Carpiodes the anterior preethmoid and prepalatine were short bony rods, as in the cobitoids. He concluded that the various preethmoid developments conferred increased mobility on the ethmoid region, and that their similar appearance in catostomids and cobitids did not indicate relationship between these 2 groups.

The extent of variability in the preethmoid region in cyprinids has already been outlined. It is also noted there is a clear prepalatine chondrification in the peculiar cyprinoid Gyrinocheilus [fig. xLiiih].

There are paired developments in the preethmoid region of Hypopygus lepturus, and generally in gymnotids (de la Hoz & Chardon, 1975). The homology of the two hiliform "submaxillary" (Chardon & de la Hoz, 1974) elements present is obscure (as is that of all the bones of the ethmoid region of these fish [see fig.xLib]). The authors above commented that elements apparently in the same position as their "submaxillaries" featured in all cypriniids, but they did not comment on the possible significance of this. Fink & Fink (1981) pointed out that in the gonorynchiform Chanos, many Characiformes (as defined by them), and some other teleosts (Patterson, 1975) a cartilage, probably homologous with the preethmoid is found between the palatine,
maxillary, and ethmoid bones, and Fink & Fink (1981) implied the level of universality at which they considered the preethmoid ossification to be plesiomorphic, by suggesting that the absence of this ossification in Siluriformes (as defined by them) could be used as a synapomorphy to unite this group.

My conclusion is that the presence of a preethmoid is plesiomorphic and that the potential for this to appear as two ossifications has been realised more than once, within the cyprinoids. Thus neither the presence of PE1 or PE2 should be used to define the inter- or intrarelationships of cobitoid fishes.

Ramaswami (1953) proposed that the presence of a prepalatine is specifically characteristic of the Cobitidae. I conclude that the prepalatine is plesiomorphic amongst cobitoids and interpret its absence from Ellopostoma and Gasteromyzon as the result of, not necessarily unique, secondary loss. The prepalatine is not formed as a separate ossification in the Cobitini. I consider the presence of a chondrified prepalatine in Catostomus and Gyrinocheilus indicates that this ossification is apomorphic at a greater level of universality than amongst the cobitoids, and that the potential for its separate development is probably realised in various wide-snouted ostariophyseans employing high ethmoid mobility.

The disposition of the preethmoids has also been used to define the intrarelationships of the Cobitidae. Ramaswami (1953) interpreted the preethmoid arrangements of the Botini and Noemachilini as derived from the single long
preethmoid observed by him in the cobitines Cobitis, Acanthophthalmus, Misgurnus and Somileptes. He suggested that, if the single preethmoid of the Cobitini split horizontally, the dorsal part extending between the palatine and the maxilla, would form a prepalatine and the ventral part would be in the position of a preethmoid. Ramaswami considered that the ethmoid arrangement of the Homalopteridae was like that of the Noemacheilini and Botini and he concluded that the Homalopteridae, and the Cobitidae "having taken their origin from a cyprinoid ancestor have evolved on parallel lines". Ramaswami's hypothesis suggests that the Cobitini are more primitive than the other loaches, which I do not consider them to be. It seems to me that the cobitine preethmoid bone can as readily be interpreted as derived by elongation from the plesiomorph preethmoid condition (Patterson, 1975; Howes, 1980). Alternatively the cobitine preethmoid can be interpreted as secondarily derived from a multiple preethmoid arrangement, by fusion of separate elements into a single rod.

An interesting, possible predisposition towards the cobitine preethmoid condition emerges in some Noemacheilini, where an intimate articulation between the PE1, and prepalatine may be formed. In Noemacheilus yarkandensis and Oronectes platycephalus each preethmoid bone has a small flange ventrally, increasing the articular area between the PE1 and PE2. In N. botia, N. corica, N. rupecola and N. montanus the prepalatine has a small dorsal flange, which wraps over the preethmoid. In N. denisonii a small condyle is produced on PE1 and this is embraced by ventral flanging
from the prepalatine. In *N. strauchi* a small condylar process towards the preethmoid, is produced on the prepalatine (see fig. xLiiib). This study has not explored the possibility of exploiting these devices as α-level phylogenetic tools.

The sesamoid bone of most Botini and some Noemacheilini is interpreted as a derived cobitid feature. I do not consider its distribution allows elucidation of the phylogeny of the Botini because of the lability of sesamoid ossifications generally and because of lack of any indication of the homology of this particular bone.

**THE PALATINE** (fig. xLiv)

The palatine lies between the upper jaw and the suspensorium. In cobitoids this bone frequently articulates with both the ethmoid and the vomer medially. Occasionally it also articulates with the lachrymal, or the lateral ethmoid laterally.

In the Noemacheilini the palatine is a more-or-less shaft-like bone. Anteriorly it articulates with the prepalatine ossicle, which itself articulates anteriorly with the maxilla. The palatine has a short anteromedial process which provides an attachment for the palato-ethmoid ligament. This process is unusually long in *Lefua* and *Oronectes*. Anterolaterally the palatine may be produced into a process attaching the palatomaxillary ligament. This process is emphasised in *Orthrias* and *N. barbatulus*. In all Noemacheilini the palatine articulates with the base of the ethmovomerine block medially. Posteriorly the palatine forms a strong
condyle which articulates with the entopterygoid. In no noemacheilines does the palatine meet the lachrymal laterally. In *Vaillantella* the palatine is long and disposed as above. In *Ellopostoma* the palatine gains little medial support from the ethmoid. The palatine-ethmoid articulation is a ball-and-socket joint formed between the palatine anteromedially and the cartilage PE2 vomerine head. In *Ellopostoma* there is no prepalatine bone, and the anterior end of the palatine tapers [fig. xxviii].

In the homalopterids the palatine is usually short. It has a well-defined anteromedial ethmoid process, and always articulates with the ethmovomerine block medially. In most of the gastromyzonines the palatine articulates with the lachrymal bumper laterally [fig. xLiiic], although it fails to do so in *Crossostoma* (Rameswami, 1952:4) and also in *Glaniopsis*. Of the homalopterines, *H. amphisquamata* and *H. rupecola* are unusual in that the palatine does not show a lachrymal facet.

In *Cobitini* [fig. xLiva and b] the palatine invariably articulates anteriorly with the shorter, posterodorsal limb of the "Y"-shaped preethmoid. The palatine is produced to a prong of bone anterodorsally, over this articulation and the palatomaxillary ligament attaches to this process. There is no anteromedial ethmoid process of the palatine in *Cobitini*. The bone forms the socket portion of a ball-and-socket type of articulation formed with the ethmovomerine block medially.

The palatine of *Cobitini* never articulates with the lachrymal laterally, although the palatine and the lachrymal
act together as levers in the erection of the suborbital spine (Chranilov, 1928, see p.193). The palatine, entopterygoid and lateral ethmoid bones are characteristically closely related to each other in Cobitini, and this articulation is also operative in mobilising the spine (p.193).

In most Cobitini the palatine has a triangular flange posterolaterally. The most anterior fibres of the m. adductor arcus palatini insert onto this flange (Takahasi, 1925; Gosline, 1975). In Acanthopsis and Somileptes [fig. xLii b] the muscle inserts onto an elongate rough ridge raised along the ventrolateral palatine. Typically in cypriniforms the adductor arcus palatini inserts onto the pterygoid series (Winterbottom, 1974). This is further discussed on p.337.

In the Botini the palatine abuts the prepalatine anteriorly. It is produced to neither lateral nor medial processes. Medially the palatine articulates with the ethmovomerine base. Posteriorly it articulates with the entopterygoid.

Although in Leptobotia [fig.xLii c] there is a small digitiform process on the palatine, lateral to the articulation of this bone with the entopterygoid, unlike in the Cobitini, no muscle fibres are observed to insert onto the palatine of the Botini. This process, as described in Leptobotia, appears to stabilise the palatoentopterygoid articulation. In Botia [fig.xLii d] the anterior of the lateral ethmoid spine is more laterally positioned than it is in Leptobotia, and I consider the posterior process of
the palatine has been secondarily lost from *Botia*. It appears that the palatine is less immediately involved with spine erection in the Botini than in the Cobitini (see p.196-7) and the more immediate relationship of the spine to the posterior part of the lachrymal in *Botia* than *Leptobotia* is noted.

An articulation between the palatine and the lachrymal develops in some hill-stream Ostariophysi other than the Cobitidae. For example, it occurs in *Gyrinocheilus* and is also evident in *Psilorhynchus* although not in *Parapsilorhynchus* (Ramaswami, 1952.2). However, lachrymal-palatine apposition does not occur in the Cyprinidae, and is not a feature of Catostomidae.

In the catfish *Glyptothorax* there is a pivot joint between the lateral ethmoid, and bar-shaped palatine, and this joint generates the "teeter-totter" mechanism of catfish barbel erection described by Gosline (1975). Some development of this articulation, accompanied by the insertion of *m. adductor arcus palatini* directly onto the posterior of the palatine is typical of catfish.

Roberts (1973) considered palatine mobility as a shared, derived feature of cypriniforms and siluroids. Fink & Fink (1981) considered that palatine mobility was non-homologous in these two groups because, uniquely in catfish, the mobility is achieved via the direct insertion of the *m. adductor arcus palatini* onto the bone. However, a similarly direct muscle insertion onto the palatine also occurs in the cobitine Cobitidae, and this cannot therefore be interpreted as a condition unique to catfish and unknown in cypriniforms.
For this reason Roberts' (1973) hypothesis is not refuted. Moreover, it may be the case that the unossified oval plate representing the palatine of Gymnotidae is also mobile (see p. 251).

My conclusion on the systematic significance of palatine anatomy in cobitoids is that I interpret the relationship of the posterior end of the palatine, the m. adductor arcus palatini, the anterior lateral ethmoid condyle and the lachrymal as a character complex uniting the Cobitini, and I consider elongation of the palatine flange on which the adductor inserts which is shared by Somileptes and Acanthopsis as a derived condition in these 2 species.

I interpret the posterolateral palatine horn seen in the botine genus Leptobotia as homologous with the flange palatine of the Cobitini, and that this indicates Leptobotia is more closely related to the Cobitini than is Botia. The absence of this feature from Botia is proposed as a secondary loss, accompanying lateral displacement of the proximal suborbital spine, and reorganisation of the spine erection mechanism in this genus (see p. 147 and 201).

I also consider the morphology of the palatine-entopterygoid articulation to be significant in cobitoid evolution. This is discussed on p. 144-7.

ETHMOID BLOCK [SUPRAETHMOID, MESETHMOID AND VOMER]

The ethmoid block is discussed as a unit here because Ramaswami (1953) considered it a definitive characteristic of the Cobitidae that in this family the prevomer was fused
to the ethmoid ventrally, and formed a composite bone, which he called the ethmoprevomer. Ramaswami stated that this condition was unique amongst the Cyprinoidei. I note that in all cobitoid fishes the "ethmoprevomer" constitutes a discrete functional unit, but do not agree with Ramaswami as in many of the Cobitidae, while the prevomer is firmly attached with the ethmoid base, I find it separable from, and not strictly fused to it. I do not consider it possible to differentiate between this type of articulation and that of the prevomer to the ethmoid in e.g. Gobioinae, which is also firm.

In this discussion the dorsal, anterior, posterodorsal, mesial and posteroventral portions of the ethmoid, and then the vomer are considered in turn.

The dorsal portion of the ethmoid block is extremely variable in the cobitoids. It is frequently very narrow. In the Noemacheilini the dorsal portion of the ethmoid is present at its widest in *Noemacheilus nigromaculatus* (fig. xLva) and *Oropectes platycephalus*. However, it is usually represented as a tiny pair of alae (see fig. xLvb), which partially roof the nasal capsule. These wings are interpreted as being derived from the dorsal mesethmoid, and not from the supraethmoid, as they are frequently cartilagenous peripherally. Thus it seems that the supraethmoid is absent from the Noemacheilini, except perhaps posteriorly, where a portion of it may contribute to the interdigitating suture made by the ethmoid block with the frontals.

In all cobitoids with the exception of *Ellopostoma* (fig. xxviii) the anterior part of the ethmoid is more or
less produced as a rostral process. This process is occasionally just forked at its tip and provides attachment for the oblique ligament which passes to the kinethmoid. This as already discussed (see p.166), is anterior, and distant from the ethmoid. In Ellopostoma the kinethmoid ligament attaches posterovertrally to the tip of the anterior ethmoid plate.

*Vaillantella* has a plate-like ethmoid which is as reduced as the ethmoid of the cobitines. In *Ellopostoma* the dorsal part of the ethmoid is unique and bizarre (see p.96). In this species, what appears to be part of the supraethmoid flanked by mesethmoid extensions, has rotated anteroventrally and lies coronally, forming the fan-shaped anterior rostral wall (fig.xxviii).

In *Gianiopsis* the dorsal aspect of the ethmoid is narrow and shield-shaped. In both the homalopterines and the gastromyzonines the dorsal aspect of the ethmoid is wider and the supraethmoid is obviously present (see Ramaswami, 1952:3 and 4).

In the Cobitini the ethmoid is so narrow that it appears effectively linear in dorsal view (fig. xlvc). It occasionally has tiny alae, and sometimes forms a minute fork anteriorly.

In the Botini the dorsal portion of the ethmoid is also narrow, although it is never as narrow as it is in cobitines. In *B. macracantha* the ethmoid is comparatively wide in dorsal view (fig. xlvd).

It is not easy to evaluate the phylogenetic significance of the generally reduced condition of the dorsal portion of
the cobitoid ethmoid block. Ramaswami (1953) recorded the narrow ethmoid of the Noemacheilini and he concluded that this showed that homalopterid-noemacheiline similarities were the result of convergence, and not phylogeny, because as he stated "if the noemacheilines have given rise to the homalopterids it is difficult to explain how the slender supraethmoid part of the ethmoid of the former could have become so broad as it is in the Cyprinidae". Howes (1981) suggested that in its plesiomorphic condition the supraethmoid of cyprinids is broad. Fink & Fink (1981) emphasised that a broad supraethmoid was plesiomorphic throughout the Ostariophysi, and these authors interpreted the narrow supraethmoid of the Siluriformes (as defined by them) as synapomorphic for this group.

In light of the reduced condition of the supraethmoid portion in cobitoids, I find this conclusion of Fink & Fink difficult to accept.

Evidently considerable narrowing of the ethmoid has occurred many times within the Ostariophysi. In the case of the Cobitidae it appears that the supraethmoid is more or less completely unossified. Lenglet (1974) states that in the Kneriidae "the supraethmoid as a single mid-line dorsal element is lost". This is confirmed by my observation of Parakneria witti, and in this species the ethmoid block appears very like that of many Noemacheilini, and especially, superficially, like that of Ellopostoma in dorsal view. In the case of Ellopostoma, it is impossible, without resource to ontogeny, to ascertain whether it is actually the supraethmoid which forms the peculiar anterior rostral wall, or
whether this part is mesethmoidal in origin. However, it is interesting to note for comparison that the supraethmoid is tilted vertically in the cyprinids *Semiplotus* and *Scaphiodomichthys* in response to ventral feeding (Howes, 1981) and that Alexander (1965) recorded the same adaptive feature in the catfish *Synodontis*.

The anteriorly produced condition of the ethmoid recorded in cobitoids is not unique amongst Ostariophysi. Fink & Fink (1981) suggested that some rostral production of the anterior part of the rostrum was plesiomorphic for Otophysans. De la Hoz & Chardon (1975) and Daget (1964) commented that such a process was characteristic of the Ostariophysi. Howes (1981) suggested that in the plesiomorphic cyprinid condition the anteroventral ethmoid is slightly produced to form a broad rostral process which is frequently notched anteriorly.

Howes (1981) noted that an extensively rostrally produced ethmoid occurred in many bottom feeding Otophysans. It appears that the marked anterior production of the ethmoid of cobitoids can be similarly correlated with feeding habit. However, in cyprinids the tip of the ethmoid invariably has a notch to accommodate the kinethmoid, while in cobitoids the kinethmoid is distant from the anterior tip of the ethmoid and the kinethmoid notch of the ethmoid is absent.

The nature of the posterior articulations of the ethmoid block is peculiarly variable within the Cobitidae. Regan (1911) divided the Cobitidae into two groups because he observed that in the Noemacheilini the mesethmoid was firmly
united dorsally with the frontals, while in the Cobitidini, [embracing the Botini and Cobitini] the mesethmoid-frontal articulation was moveable. In fact mobility at this articulation is limited in the Botini [see p. 186-9].

Berg [1940] divided the Cobitidae into the three major subfamilies currently recognised, because he observed that in the Noemacheilini the mesethmoid and prevomer were fixed, and the mobile lateral ethmoid spine was absent, and that this contrasted with the condition in the Botini where the mobile suborbital spine was present, but the ethmoid block was immobile, and in the Cobitini, where the mesethmoid, prevomer and lateral ethmoid were all moveable. Fang [1935a] also recorded the distinctive ethmoid mobility of this group, and he stated that "the moveable articulation of supraethmoid in Cobitinae might be suggested as a specialisation to adopt the digging habit of this group of fishes, rather than considering it as a primitive character".

My observations show that in the Noemacheilini the ethmofrontal articulation is frequently a deeply interdigitating suture which clearly prohibits movement between the two bones. However when the ethmoid is narrow posteriorly this suture is reduced, and in more narrow-headed species such as Noemacheilus fasciatus and N. botia the mesethmoid is forked posteriorly and each prong makes a very short suture with the frontal of each side.

In the Noemacheilini the sagittal mesethmoid is a robust plate separating the two nasal capsules except where it is evacuated posteriorly, and its border is concave. Ventrally it makes a firm articulation with the orbitosphenoids.
In the Cobitini the posterior end of the plate-like ethmoid lodges in a notch between the frontals in which it is free to rotate. However, this movement is only possible because the posteroventral part of the ethmoid, which articulates with the orbitosphenoid, is produced to a hemicircular horizontal shelf which rests on, and can rotate over an approximately congruent shelf on the anteroventrum of the orbitosphenoid (fig. xLvi). This arrangement confers both dorsoventral support, and the potential for horizontal movement on the cobitine ethmoid block.

In the Botini the posteroventral portion of the ethmoid is fixed where it approaches the orbitosphenoid as it is also in the noemacheilids and all outgroups examined; the ethmoid mobility of the Cobitini is characteristic of the group.

Clearly the ethmoid block can only be mobile if the vomer is not articulated in such a way as to not prevent this movement, and within the cobitoids characters of the ethmoid and vomer are in complex together. In all cobitoids the vomer assumes a more or less "T"-shape, as the posterior process of that bone is narrow and may be extremely elongate. This vomer morphology is in contrast with that described as plesiomorphic amongst cyprinids where the bone is short and broad with a short posterior process (Howes, 1981).

In the Noemacheilini the head of the T-shaped vomer may, as noted by Ramaswami (1953), be fused to the ventrum of the ethmoid block. The long slim posterior of the bone is invariably held in a groove formed on the ventrum of the anterior parasphenoid shaft. I suggest that firm
articulation of the vomer with both the ethmoid and parasphenoid in Noemacheilini is a prerequisite for reduction of the width of the dorsal portion of the ethmoid in this group.

In Vaillantella the T-shaped vomer has an unusually long slender posterior process held in the parasphenoid groove [fig.xxxiii].

In Ellopostoma the vomer is approximately leaf-shaped [fig.xxviii]. It has a rather short posterior process, and makes a comparatively loose articulation with the ethmoid, while in Glaniopsis, the homalopterines and gastromyzonines the form of the vomer varies, between T- and leaf-shaped and the posterior process is never extremely produced.

In the Cobitini the head of the T-shaped vomer is, as in the Noemacheilini, attached firmly to the ethmoid ventrum, but the posterior process of the vomer in the Cobitini is a comparatively short digitiform prong which lies ventral to, and free from, the parasphenoid shaft. Thus the vomer can accompany the ethmoid in rotation in the horizontal plane, and this comprises part of the character complex allowing cobitine ethmoid mobility [fig.XLvi].

In the Botini the vomer is not always entirely fused to the ethmoid ventrum and the posterior process of the vomer, which may be very long, is held tightly in a groove in the anterior parasphenoid shaft.

A mechanism for the evolution of the variable cobitoid ethmoid is proposed below. In the noemacheilids the potential to reduce the dorsal area of the ethmoid is increased by fixation of the vomer to the ethmoid, and to
the parasphenoid ventrally. This condition is most fully realised in *Vaillantella* in which the mesethmoid is planar and firmly fixed ventrally to the parasphenoid by the very long posterior process of the vomer. In the Cobitini the vomer is freed from the parasphenoid and thus the ethmovomerine block can move, while acting as a median support for the snout, parallel to the elongate pair of preethmoid rods flanking it. In the Botini the ethmoid is narrow. The ethmoid is fixed both dorsally to the frontals, and ventrally to the parasphenoid via the vomer. It is not possible to ascertain whether these fixations are secondary in the Botini.

Fig. xLvii demonstrates two hypotheses of relationship suggested by ethmovomerine characters of cobitoid fishes.

**LATERAL ETHMOID**

The Botini and Cobitini are both characterised by their possession of a moveable suborbital spine, derived in part at least from the lateral ethmoid bone. The presence of the suborbital spine has been consistently considered as indicating the Botini and Cobitini to be related.

In the literature Fang [1935a] compared the suborbital spine of *Botia*, *Leptobotia*, and Chinese Cobitini and noted the general similarity of the structure in the groups.

Berg [1940] used the name Cobitidinae to embrace the spined loaches, but did not discuss the phyletic relationship of this group to the Noemacheilini. Following Berg in this thesis the Botini and Cobitini are together referred to as the Cobitidini (p. 17).

In his study on cobitid skulls, Ramaswami [1953] stated:
"the lateral ethmoid is built on a common plan in the Botini and Cobitini. In the two subfamilies a number of spine-like processes are noticed and one of them is the suborbital spine which is of great systematic importance. Misgurnus is peculiar in lacking a suborbital spine. In Noemacheilini the bone is smaller, and devoid of a spine like process." However Ramaswami's overall conclusion on cobitid phylogeny was that the Botini were the most primitive, the Noemacheilini more derived and the Cobitini the most derived of the family, and Ramaswami did not discuss the problem of the absence of the spine in the Noemacheilini which is posed by this conclusion.

Nalbant (1963) assessed cobitine and botine inter-relationships, using as part of his assessment the morphology of the suborbital spine. Nalbant followed Ramaswami in concluding that, of the Cobitidae, "the Botini seem most primitive in general organization, the Noemacheilini retain some botine characters, and the Cobitini appear as the most evolved of the whole family." However, in his "phylogenetical scheme" [fig. xxv] Nalbant placed the Noemacheilini at the base of the phyletic tree, and the Cobitini and Botini adjacent to each other, so that his exact interpretation is unclear.

Nalbant & Banarescu (1977) discussed the phylectic position of Vaillantella within the Cobitidae, and adopted a more cladistic view of the significance of the suborbital spine. They commented that the Botini and Cobitini were usually considered more closely related to each other than to the Noemacheilini, with mobility of the lateral ethmoid
as their shared specialisation. Nalbant & Banarescu pointed out that Vaillantella shared more characters with the Botini than with the Noemacheilini, but stated that in this issue "the presence or absence of the suborbital spine may be more phyletically significant". Their phyletic assessment in this paper is illustrated [fig.xixc] and this shows that actually Nalbant & Banarescu concluded that the absence of the spine from Vaillantella was less phyletically significant than some overall morphological similarities between Vaillantella and the Botini.

This brief literature survey should make it clear that the problem is that, historically, the suborbital spine has not been considered as a character sensu Hennig (1966). If the spine is considered as a character it must either definitively indicate the Botini and Cobitini to be a monophyletic assemblage, more closely related to each other than, and derived over the Noemacheilini, or it must be shown that the spine is non-homologous in the two groups, or secondary loss of the spine from the Noemacheilini must be proposed.

Resolution of the problem of the suborbital spine is made more difficult because the precise homology of the structure has not been established. From its position the spine appears to have been derived from part of the ethmoid complex. However, the ethmoid complex is formed of three bones, namely the parethmoid, lateral ethmoid, and prefrontal, and the extent to which the suborbital spine can be attributed to modifications of each of these bones is not agreed upon.
Lilljeborg (1891) interpreted the suborbital spine as being derived from the lateral ethmoid exclusively. Sagemahl (1891) defined it as an antorbital apophysis of the prefrontal, and Chranilov (1927) shared this opinion. Takahasi (1925) considered the spine was a unique ossification, which he called the preorbital.

Monod & Le Danois (1966) discussed the homology of the spine and their main conclusion was that the structure was "unlikely to include part of a much modified infraorbital, as there is never any connection between the spine and the infraorbital series". Without embryological substantiation Monod & Le Danois then presented the hypothesis that the spine is an entirely new formation, because they considered its histological structure differed from that of other bones, consisting of a dense matrix enclosing a cavity. Monod & Le Danois described the formative substance of the spine as not unlike dentine, and similar to the tissue found on the spines of the moon-fish, Monodactylus argenteus. Monod & Le Danois proposed that the articular base of the suborbital spine of the Cobitidini was derived from the orbitosphenoid because the spine articulates with that bone basally. These authors' observations may cast some light on the possible origin of the cobitidinid spine, but the issue of homology of the structure in cobitines, with regard to botinines remains unclear.

There is considerable difference between the morphology and the operative mechanism of the spine in the Botini and in the Cobitini, and no condition intermediate to the two types is known. Some fossil suborbital spines are
known from the Saisson Nor Lake (Lebedev, 1959) but these spines are typically cobitine, and show only that a species of loach very like *Cobitis taenia* existed in the Mid-Miocene era. Thus there is little evidence to refute or endorse a hypothesis proposing diphyletic origin of the suborbital spine. The problem is compounded by the fact that there is no obvious incipient condition of the spine evident in the Noemacheilini, or any non-cobitid ostariophysean, nor do any possible morphological conditions predisposing to the formation of the spine appear to have been considered.

In the section following the anatomy of the suborbital spine in the Cobitini and in the Botini is considered first. The condition of the lateral ethmoid of noemacheilids and representatives of various ostariophysean outgroups is discussed subsequently.

The typical cobitine spine is illustrated [fig. xl viiiia] and within the group there is little variation from this type. The lateral nipple on to which the A1LE inserts may be low; it is absent in the species of *Misgurnus* from which this muscle is also absent. The anterior process of the spine is usually low and rectangular and approaches the posterodorsal part of the palatine. In *Somileptes* and *Acanthophthalmus muraeniformis* the anterolateral part of the anterior process is somewhat elongated, and in *Niwaella* [fig. xl viiib] this elongation is such that the anterior part of the spine appears bifurcate. In all cobitines the anteromedial condyle of the spine lodges in a socket formed on the orbitosphenoid in which it can rotate. The ascending process of the spine is invariably a well-produced
vertical digitiform prong which is accommodated in a hemicylindrical socket formed by lateral rolling of the anterior edge of the orbitosphenoid. Medially the spine has a distinctively scarped edge which attaches a ligament, passing to the parasphenoid and limiting abduction of the spine. Distally, both a main and a more lateral spinous process, or thorn are present.

Chranilov (1928) proposed that the cobitine spine was erected via palatine leverage. He suggested the process of spine abduction to be initiated by contraction of the m. adductor arcus palatini, pulling the proximal end of the palatine, and so the anterior process of the spine, medially, and thus levering the distal part of the spine laterally into the erect position. Chranilov recognised adduction of the spine to be brought about by contraction of the A1LE. muscle described on p. 40.

Chranilov (1928) suggested that the spine in Cobitis has no primarily offensive function. He pointed out that species of the genus Cobitis frequent sandy or gravelly bottoms of freshwater streams, and that they frequently bury and wriggle through restricted space. During these activities the suborbital spines are necessarily depressed. However, Chranilov observed that, if Cobitis, or Lepidocephalus was held in the hand, the spine of the side of the head against the hand was erected and pressed into the skin, and that the fish then pulled or flipped its body over the anchor thus provided. Chranilov further observed that if Cobitis was placed in a tunnel of appropriately limited width, it pressed both suborbital
spines against the walls of the tunnel and became almost impossible to pull out from behind because of the action of the ligament between the spine and the braincase.

Chranilove suggested the spine-braincase ligament was a remnant from the *m. adductor arcus palatini* [with the main body of the muscle having migrated anteriorly, see p.39]. He proposed that the ligament is long enough to allow erection of the spine to the width of the "normal habitat hide". Chranilov gave the results of an experiment substantiating his hypothesis, carried out with groups of *Cobitis* in which the right, or left spine had been removed. These turned proportionally more often to the left and right respectively at the end of a Y-maze, in comparison with a control group of intact specimens.

In support of this hypothesis I note that when the spine is fully erect the tips of the lateral and main thorns align parallel to the long axis of the body, and are thus best disposed to provide lateral grip.

Uniquely amongst the Cobitini the genus *Misgurnus* has an extremely reduced suborbital spine [fig. xlviii]. This reduction has frequently been commented upon, but its state has not been satisfactorily assessed. Fang [1935a] described the lateral ethmoid as actually "unmodified" in the *Misgurnus*. Ramaswami [1953] noted the lack of a functional spine in the genus, and indicated that the condition was primitive. He proposed that *Misgurnus* [with *Cobitis* and *Somileptes*] occupied a "lower and separate phylogenetic position in the Cobitini". Nalbant [1963] described the spine of *Misgurnus* as non-functional. Nalbant
considered that the angle of 80-90° between the main and lateral thorns of the typical cobitine spine contrasted systematically with the angle of 50-78° between the two thorns of the spine of the Botini, and that the size of this angle of 70-72° in Misgurnus showed that Misgurnus occupies a phylogenetic position between the Botini and the Cobitini. Nalbant regarded Misgurnus as the most primitive genus of the Cobitini on the basis of this character.

I do not consider the angle between the thorns of the spines of Cobitidinae can be used in this way to define relationship. I suggest the differences in the proportions of the spines of cobitidinids actually reflect the differences in the habitats of the spined loaches and in the function of the spine. I interpret the spine in Misgurnus to be vestigial and not primitive, because of the presence of an A1LE muscle in M. fossilis [see p.41-2].

The suborbital spine of a typical representative of the Botini is illustrated (fig. xLixa). My observations on its anatomy essentially agree with those of Fang (1935a) and Nalbant (1963). The ascending process of the spine is stout and is angled posteriodorsally. The medial orbitosphenoid process has the form of a series of rugose projections, which articulate with a broad articular surface on the orbitosphenoid (fig. xLixb). The anterior process of the spine is bifid. The medial division of this process is related ventrally to the palato-entopterygoid articulation. The lateral division lies immediately posterior to the oval lachrymal when this bone is present.
The lateral division of the anterior process provides the insertion for the A1LE ventrally. The lateral thorn-like process of the suborbital spine is absent in some species of *Leptobotia* including *L. elongata* [fig.xlix]. Hora (1922d) suggested that the genus *Leptobotia* should include only species in which the spine is not bifid, and that bifurcation is characteristic of *Botia*. This division is not recognised currently (see p.72-3, p.340).

No spine-braincase ligament is present in the Botini. Nalbant (1963) proposed that erection of the botine spine is achieved via "a direct abductor muscle inserting on the anteromedial process", which acts to lever the distal spine laterally. The A1LE as described here (p.48) is the direct adductor of the botine spine. Nalbant emphasised that this mechanism contrasts with that by which the cobitine spine is operated, because both a direct abductor and adductor muscle feature in Botini. I note the base of the suborbital spine in Botini is very firmly held into the orbitosphenoid socket by dense fibroelastic tissue, but cannot detect a distinct abductor muscle in this tissue.

Monod & Le Danois (1965) proposed a mechanism operating the spine of *Botia macracantha*, which according to them involved the action of a large number of muscular and ligamentous slips in the ethmoid region, each of which they named.

Monod & Le Danois implicated the palatine bone as the central lever of the mechanism. They suggested that spine erection was initiated by erection of the maxillo-
mandibulary barbels which acted on the maxilla. Monod & Le Danois suggested that following this, tension was
developed sequentially in m. preorbitalis interne, the
palatine, the pterygoids, the ascending premaxillary
processes, the ethmoid bones, the ethmopalatine ligament,
and finally a spinopalatine ligament, and that the spine
was erected via tensing of the spinopalatine ligament.
The authors above also suggested that the action of the
spinopalatine ligament might be supplemented by contraction
of a small direct abductor muscle.

My conclusion is that the palatine is involved as a
lever in producing erection of the suborbital spine in
Botini (as it is also apparently in Cobitini); my dis-
sections of Botia macracantha have not revealed the many
small slips of muscle described by Monad & Le Danois (1966)
and I do not consider that it is possible to determine
details of the possible function of these muscle slips
from morbid anatomy.

My observations on living specimens of Botia lead me
to agree with the generally held opinion that the sub-
orbital spine of the Botini serves a primarily defensive-
-offensive purpose. Sagemahl (1891) tentatively proposed
that the spine in B. macracantha might be associated with
a venom apparatus, but added that despite special attention
he had been unable to find any anatomical structure
identifiable as such, and no such structure has been
recorded since.

I consider that the essentially similar osteology,
the presence of an A1LE division. and the involvement of
the palatine in the operation of the spine in both the Botini and Cobitini, support homology of the structure in the two groups and this hypothesis of homology [rather than non-homology] clearly influences subsequent discussion on cobitidinid spine morphology.

With this in mind, the lateral ethmoid anatomy of representatives of various non-cobitidinid ostariophysan taxa was investigated in this study in order to look for features which might allow the more plesiomorph form or function of the cobitidinid suborbital spine to be assessed.

In the Noemacheilini (which constitute a non-cobitidinid cobitid outgroup), the lateral ethmoid forms the anterior wall of the orbital cavity. The lateral ethmoid has a small horizontal base plate which articulates with the ventral part of the ethmoid, the parasphenoid and the orbitosphenoid. The base plate never contacts its fellow of the opposite side. The vertical plate of the lateral ethmoid is concave posteriorly. It is occasionally perforated for the superficial ophthalmic nerve. Medially it meets the anterior ledge of the orbitosphenoid. Anteolaterally the lateral ethmoid is produced into a longer or shorter lachrymal process; this process lies medial to the lachrymal bone.

There is a sexual dimorphism in the male of some Indian Noemacheilus species (Hora, 1922c). These species have a hornified tuberculate lachrymal pad [see fig.1a] into which there is a small osseous extension from the lateral ethmoid. In e.g. *N. botia* this feature takes the
external form of a gristly cone of tissue which is attached to the distal lateral ethmoid and supported by a slightly hypertrophied lachrymal process of that bone in the male (see fig. Lb). The female of the species does not develop this modification (fig.Lc). This lateral ethmoid modification of e.g. *N. botia* cannot be said actually to predispose the formation of the cobitidinid suborbital spine, but it does demonstrate an interesting lability of the lateral ethmoid area in cobitid fishes.

Of the other noemacheilids, in *Vaillantella* the lateral ethmoid bone is small; its basal part lies in a distinct shallow cup formed on the orbitosphenoid ventrally (p.116). The lachrymal process of the lateral ethmoid is very long, but is only lightly ossified.

In *Ellopontoma* the lateral ethmoid is very large. The lachrymal process is short and stout. The bone also has an additional anterior flange (see p.98).

In the homalopterines the lateral ethmoid is always solidly formed. The lachrymal process of the bone is frequently massive. It articulates with the large lachrymal bone laterally (see Ramaswami, 1952:3).

In the gastromyzonines (see Ramaswami, 1952:4) and also in *Glaniopsis* the lateral ethmoid appears tripodal in dorsal view; the lachrymal process of the lateral ethmoid is produced along the lachrymal bumper anteriorly, and there is also a curved posterolateral process of the bone, which lies medial to the ossifications formed round the infraorbital canal.

From the non-noemacheilid ostariophysean outgroup
representatives it can be seen that the development of a lachrymal process of the lateral ethmoid occurs frequently amongst ostariophysii. However, a posterolateral elongation of the lateral ethmoid does not usually develop.

Within the Ostariophysii there is some variation in the extent of the development of the basal portion of the lateral ethmoid. Commonly, although not invariably, in Ostariophysii the left and right lateral ethmoid bones articulate synchondrotrically with each other on the ventral mid-line. The pair of bones always fail to make this articulation in cobitoids, and it would appear to be a prerequisite for the pair to fail to meet if they are to develop mobility.

The lateral ethmoid of Psilorhynchus is of especial interest because the structure of the adductor mandibulae suggests that Psilorhynchus might have affinity with the spined loaches (see p.79-80). The lateral ethmoid of Psilorhynchus (fig. Li) has a short lachrymal process which abuts the lachrymal posteriorly. It also has a peculiarly "c" shaped medial portion, the ascending part of which articulates with a shallow vertical gutter formed on the anterior orbitosphenoid. The lateral ethmoid of Psilorhynchus articulates with the second infraorbital bone distally.

It is evident that no obvious precondition of the cobitidinid spine has been found. However, I suggest two alternative hypotheses which may elucidate the possible phylogenetic development of this enigmatic structure.

On the one hand it can be proposed that the large gastromyzonine type of lateral ethmoid shows a predisposition
to allow development of the cobitidinid spine because the lateral ethmoid in the gastromyzonines has distally both anterior and posterior extensions as noted by Ramaswami (1952:4), and the posterior extension is in the position of the main spine thorn of the cobitidinids. The expanded lateral ethmoid of gastromyzonines provides not only protection for the ethmoid region in these torrent dwelling animals but also an appropriate shovel for burrowing. If it is assumed that the cobitidinid suborbital spine is derived from a lateral ethmoid condition resembling that of Gastromyzon, it can be hypothesised that the primary function of a lateral ethmoid development in the position of the suborbital spine is locomotor (as in the Cobitini) and not offensive (as in the Botini).

An alternative hypothesis is offered by the lateral ethmoid of Psilorhynchus. A suborbital spine-like structure could be derived by fusion of the distal portion of the lateral ethmoid with the non-canal bearing part of the infraorbital with which it articulates in Psilorhynchus (p.100), and production of this infraorbital portion to the spine. It is interesting to note that the high altitude Psilorhynchus exploits a similar habitat to Gastromyzon. Psilorhynchid adaptation to this habit is discussed by Hora (1952a). The possibility of Psilorhynchus being the sister group of the Cobitini is further discussed on p.79-80, p.207 and p.307-8.

However, the important problem of the derivation of the mobility of the cobitidinid suborbital spine remains unresolved. Of all the non-cobitidinid species examined
by me the form of the orbitosphenoid bone in *Vaillantella*
displays the most likely precondition for allowing this
[see p.204], but no other feature of the lateral ethmoid
morphology of this species appears to predispose subor-
bital spine formation.

I conclude from this discussion of lateral ethmoid ana-
tomy that:
- The Botini and Cobitini are more closely related to each
other than either is to the Noemacheilini. The Botini and
Cobitini share as their specialisation the possession of a
suborbital spine.
- The different morphology of the suborbital spine in Botini
and Cobitini suggests that these two groups diverged from
each other early in their evolutionary history.
- The form, operative mechanism and function of the botine
type of suborbital spine appears to be more highly derived
than of the cobitine spine.
- There is no evidence from lateral ethmoid anatomy
unequivocably to refute the hypothesis proposed on p.79-80,
that *Psilorhynchus* is the primitive sister group of the
Cobitini.

**BRAINCASE**

Braincase anatomy is very variable in the cobitoids,
in correlation with the very variable shape of the head
in the group. In the noemacheilids except *Vaillantella*
the head is flattened, wide, and rounded anteriorly. In
the Cobitini the head is flask-shaped, and is very narrow
anteriorly. In the Botini the shape of the head is not
unlike that of *Barbus*, or *Aulepyge*, which are both bottom feeding cyprinids.

In this section braincase elements are considered as a sphenoid series (orbitosphenoid, and pterosphenoid) otic series (sphenotic, prootic and pterotic) and occipital series (epioccipital, basioccipital, exoccipital and supraoccipital). The parasphenoid is then discussed separately. Morphological features consequent to the construction of the braincase are also considered in separate subsections and these features include the trigemino-facial chamber and the temporal depressions and openings.

**SPHENOID SERIES**

**Orbitosphenoid**

Ramaswami (1953) considered that the family Cobitidae was characterised by an orbitosphenoid peculiarity. He stated, "In the Cobitidae the orbitosphenoids have united together in a single bone, a unique feature noticed nowhere else amongst the cyprinoids. Moreover it projects anteriorly on each side of the ethmoprevomer and peculiarly in the Botini the lateral ethmoid gains articulation with a special facet of the orbitosphenoid. The occurrence of a united orbitosphenoid appears to be as distinguishing a characteristic of the Cobitidae as that of the united ethmoprevomer".

Ramaswami (1957) stated that his observations on various cyprinids had lead him to conclude that a united orbitosphenoid was not so exclusively cobitid as he had
indicated in the 1953 paper. It is not actually clear what Ramaswami meant by "a united orbitosphenoid". Typically in ostariophyseans the orbitosphenoid is a single "U" shaped bone with a deeper or shallow interorbital septal part contacting the parasphenoid ventrally, and the orbitosphenoid in cobitoids rarely differs from this condition.

In the flat-headed noemacheilids the septal part of the orbitosphenoid bone is minimal, if formed at all. In Oronectes platycephalus (fig. Lilia) and Lefua nikkonis there is a particular and peculiar orbitosphenoid condition. In these species each "limb" of the orbitosphenoid is completely separated from its fellow by the expanded parasphenoid shaft. Thus the orbitosphenoid is present as a pair of oval plates between the eyes in these species.

In all noemacheilids except Ellopostoma the orbitosphenoid articulates synchondrotically with the pterosphenoid posteriorly with the optic foramen formed between these bones. In Ellopostoma the pterosphenoid is in a unique position (see p.99 , fig. xxixb) and does not contact the orbitosphenoid.

The ventral surface of the orbitosphenoid of Vaillantella is unusual. It has an hour-glass profile and on its anterior portion bears a pair of particularly well-developed flat sockets in which lie the small basal plates of the lateral ethmoid (fig.xxxiii). This can be compared to the condition of the anteroventral orbitosphenoid in the Cobitidini.

In the Cobitini the orbitosphenoid is extraordinarily reduced. It is limited to the anterior end of the orbito-
temporal region, where it supports the anterior end of the frontal bones dorsally. There is a large interorbital vacuity posterior to the orbitosphenoid, and the eyes are thus separated by membrane (fig. XLvi).

The cobitine orbitosphenoid is further modified as shown in fig. LII. The anterior vertical edge of the bone on each side curves laterally and forms a hemicylindrical socket in which lies the ascending process of the suborbital spine. Ventrally the orbitosphenoid forms a round socket for the basal condyle of the suborbital spine. The orbitosphenoid is flattened ventrally between these round sockets.

The cobitine orbitosphenoid contributes to a moveable anterior articulation which it makes with the ethmoid and vomer, already discussed (p. 186).

In the Botini the orbitosphenoid invariably extends posteriorly to meet the pterosphenoid. As in the Noemacheilini, the orbitosphenoid usually contributes to the optic foramen. Unusually, in Botia almorhæ, B. sidthimunki and B. macracantha, the optic foramen is slightly posteriorly displaced and is enclosed between the pterosphenoids and parasphenoid only.

The form of the orbitosphenoid socket for the suborbital spine of Botini is shown in fig. XLIX. Anteroventrally the orbitosphenoid tends to develop into a platform between these two sockets; this platform is apparently the "special facet" of the orbitosphenoid which was recorded in Botia by Ramaswami (1953). The derivation of the orbitosphenoid platform is not clear. In some cyprinids a lateral ridge of the orbitosphenoid occasionally develops to support the
superficial ophthalmic vessels and nerves (Howes, 1980), but the platform of *Botia* does not appear to have been formed by ventral carriage of a ridge such as this. An apophyseal braincase platform formed from the prootic and parasphenoid is described in *Raimus* (Howes, 1980), but again this does not appear to be equivalent to the structure in *Botia*, which is therefore interpreted as a *de novo* modification associated with the particular form of suborbital spine in this taxon.

The orbitosphenoid platform is fully developed in all species of *Botia* examined (fig.Lii.c) but comparatively undeveloped in *Leptobotia* (fig.Lii.d). I interpret the full development of this platform to be a synapomorphy uniting the species of *Botia*. I note the lesser development of the orbitosphenoid platform in *Leptobotia*. The platform *per se* is absent from the Cobitini although there is a distinct horizontal ventral part of the orbitosphenoid between the lateral ethmoid sockets on that bone, and I consider the full development of the orbitosphenoid platform substantiates the position of the Botini as the derived members of the Cobitidini.

In the representatives of the ostariophysean outgroups examined, the orbitosphenoid always contacts the pterosphenoid and this is recognised as the plesiomorphic condition of the bone. The reduced state of the orbitosphenoid bone in Cobitini is thus interpreted as derived, and is associated with the production of a flask-shaped skull.

Although no orbitosphenoid platform of the form described as characteristic for Botini is found in any
ostariophysean taxa outside this group, the ventral surface of the orbitosphenoid of _Psilorhynchus_ is flattened, and slightly horizontally expanded anteroventrally [fig.Liie].

A note is added on the peculiar "double" condition of the orbitosphenoids recorded in the noemacheilines _Oronectes_ and _Lefua_. In the gymnotids examined the orbitosphenoid assumes the same double plate configuration and this peculiar condition, which is not recorded in any other wide-headed ostariophysean must be interpreted as a rare ostariophysean apomorphy.

**Pterosphenoid and anterior trigeminofacial foramen**

The various relations and proportions of the pterosphenoid [fig.Liii] demonstrate the variability of the cobitoid braincase.

In the noemacheilids the most usual form of the pterosphenoid is rectangular. Each pterosphenoid is longer than it is wide and contributes the posterior portion of the orbital cavity. In all noemacheilids except _Ellopostoma_ the pterosphenoid meets the orbitosphenoid anteriorly. The pterosphenoid articulates with the frontals dorsally and with the sphenotic posterolaterally. Neither the pterosphenoid nor the sphenotic is deeply excavated ventrally; the dilatator fossa is usually scarcely produced in cobitoids (see Howes, 1981). In the Noemacheilini the anterior part of the socket for the sphenotic hyomandibular head extends onto the pterosphenoid.

Posteromedially the pterosphenoid articulates with the
parasphenoid; it does not meet its fellow in the midline and the pterosphenoids and the parasphenoid contribute to the borders of the optic foramen.

In almost all noemacheilids the pterosphenoid meets the prootic laterally (fig.Liii). Each pterosphenoid contributes substantially to the border of the anterior trigeminofacial foramen. The significance of the construction of the anterior trigeminofacial foramen of cobitoid fishes is discussed on p.210-13.

The pterosphenoid of noemacheilids shows little variation. In Vaillantella the pterosphenoid is elongated in proportion with the elongated skull of this species [fig.xxxiii]. In Ellopostoma the pterosphenoid is unusual. The bone lies coronally across the posterior orbital wall [see fig. xxixb]. Unlike that of a typical noemacheilid the pterosphenoid of Ellopostoma does not articulate with the orbitosphenoid anteriorly and does meet its fellow ventromedially.

In the Cobitini the pterosphenoid is a very short triangular bone lying in the posterolateral part of the wall of the orbital cavity, and contributing the lateral borders of the optic foramen. The pterosphenoid articulates with the frontal, sphenotic, parasphenoid and prootic, and never articulates with the orbitosphenoid, being separated from that bone by the interorbital vacuity described on p.204.5.

In many genera of Cobitini the pterosphenoid contributes to the border of the anterior trigeminofacial foramen. However the position of the pterosphenoid in the Cobitini
is very variable. In the cobitine genera *Lepidocephalus*, *Sabanejewia*, *Acanthopsis* and *Somileptes* the pterosphenoid makes no contribution to the border of the anterior trigeminofacial foramen. In these species the pterosphenoid is displaced anteriorly and excluded from contributing to the border of the anterior trigeminofacial foramen by the ascending process of the parasphenoid (see fig.Liii). This condition is most fully realised in *Acanthopsis* and *Somileptes*. In *Acanthophthalmus* the pterosphenoid is also excluded from contributing to the boundary of the anterior trigeminofacial foramen by the ascending process of the parasphenoid but in this case the pterosphenoid is displaced posterodorsally and lies in the lateral brain case wall (fig.Liilid).

The extraordinary variability of the pterosphenoid region of the cobitine skull led Ramaswami (1953) to conclude that the Cobitini must be a polyphyletic assemblage. On the basis of a variety of other characteristics both Ramaswami (1953) and Nalbarit (1983) concluded that an *Acanthopsis-Acanthophthalmus* group constituted the most derived unitary lineage of the Cobitini. My observations on the pterosphenoid bones of *Acanthopsis* and *Acanthophthalmus* suggest that while both these genera are highly derived members of the Cobitini, they are not more closely related to each other than to anything else.

I suggest that one lineage of Cobitini is represented by *Lepidocephalus*, *Acanthopsis*, *Somileptes* and *Sabanejewia* and that on the basis of pterosphenoid morphology *Acanthopsis* and *Somileptes* are the most highly derived
members of this lineage. The disposition of the pterosphenoid bones of _Acanthophthalmus_ suggests that this taxon represents a separately derived lineage of the Cobitini [see p.337 fig.xCii].

However, in all Cobitini [see figs Liiid,e and f] the pterosphenoid is in a reduced state and fails to meet the orbitosphenoid anteriorly. In the noemacheilids, the Botini [fig.Liii g] and in Ostariophysi generally the pterosphenoid is not reduced in this way. I consider this reduced state of the pterosphenoid itself characterises the Cobitini as a derived monophyletic assemblage [see p.336, fig.xCii].

The disposition of the pterosphenoid bone clearly affects the construction of the anterior trigeminofacial foramen and this is discussed below. Within the Ostariophysi there are considerable differences in the construction of this foramen, and the cobitoids are also variable in this portion of their anatomy, and before considering the significance of this variation it is important to establish the plesiomorphic ostariophysian condition of the anterior trigeminofacial region. Principles of development of teleostean trigeminofacial morphology are discussed by Taverne [1971].

Howes [1981] showed that _Hypopthalmichthys_ is unique amongst the cyprinids in having a pterosphenoid contribution to the border of the anterior trigeminofacial foramen. Howes reported on the connection between the pterosphenoid, prootic and parasphenoid bones and he identified a sequential series of development in this
region which emerges in all these groups of cyprinids which are identifiably monophyletic. Howes showed that the plesiomorphic condition in cyprinids is for the pterosphenoid to fail to meet the parasphenoid and that the derived condition in cyprinids is for extensive lateral contact between the pterosphenoid and parasphenoid bones to be made. Howes showed that the derived cyprinid condition is achieved by elongation of the pterosphenoid and a lengthening of the parasphenoid wing.

The morphology of the anterior trigeminofacial region of cobitoids contrasts distinctly with that of the cyprinids [see Ramaswami, 1952:3 and 4; 1953:1955]. In the homalopterines and gastromyzonines, and in Glaniopsis and Ellopostoma, the anterior trigeminofacial foramen is entirely between the pterosphenoid and prootic. This is also the case in the noemacheiline Lefua [fig. Liva].

In most Noemacheilini the ascending process of the parasphenoid extends across the parasphenoid and forms the anterior border of the anterior trigeminofacial foramen.

Unusually in Vaillantella and also in Noemacheilus nigromaculatus the parasphenoid does not develop an ascending process; in these species the parasphenoid contributes the medial portion of the border of the anterior trigeminofacial foramen [see fig. xxxiii].

In Oronectes [fig.Livb] the ascending process of the parasphenoid articulates with the pterosphenoid both anterior and posterior to the anterior trigeminofacial foramen and the prootic is excluded from contributing to the border of that foramen.
In the Cobitini the parasphenoid ascending process is long. The anterior trigemino-facial foramen is usually present between the prootic and the parasphenoid with the pterosphenoid making a short contribution to its lateral border. In the case of the Cobitini exclusion of the pterosphenoid from the border of the anterior trigemino-facial foramen is correlated with extreme development of the parasphenoid wing and appears to be a derived condition (see fig.Livc,d and e).

In the Botini the ascending process of the parasphenoid is short. The anterior trigemino-facial foramen is usually pterosphenoidal-prootic with the parasphenoid contributing a portion of its medial border (fig.Livf).

I conclude that the construction of the anterior trigemino-facial foramen in the cobitoids Vaillantella, Noemacheilus nigromaculatus, Ellopostoma, the homalopterines, gastromyzonines and Glaniopsis and the noemacheilines Lefua and Oronectes suggests that these taxa are more or less variously separate from the derived noemacheiline lineage.

Comparison of the morphology of the anterior trigemino-facial foramen of Catostomus (Weisel, 1960) and Psilorhynchus (Ramaswami 1952:2) suggested that the presence of a pterosphenoid contribution and the absence of a parasphenoid contribution to the border of the foramen are plesiomorphic amongst flat-headed Ostariophys, and amongst cobitoids. Thus it can be concluded that there is a general contrast between the cyprinids, and these flat-headed ostariophyseans, in the relationship of the
pterosphenoid to the anterior trigeminofacial foramen. It can further be concluded that elongation of the ascending process of the parasphenoid and contribution from that bone to the border of the anterior trigeminofacial foramen can then, amongst cobitoids, be interpreted as a derived but not unique development shared by the noemacheiline and the cobitine Cobitidae, which is not realised in the Botini in which the braincase is not subject to the extreme modifications of other Cobitidae.

OTIC SERIES

Sphenotic

In the Noemacheilini the sphenotic is an oval bone positioned in the posterodorsolateral part of the wall of the orbital cavity. The sphenotic articulates with the frontal, parietal, pterotic, pterosphenoid and the prootic. The relation of the sphenotic to the epioccipital variable and these two bones may be excluded from contacting each other by a temporal opening [p.210-4], or by the apex of the pterotic. Sphenotic-epioccipital articulation is usually not achieved in the more narrow headed of the Noemacheilini. In all Noemacheilini the sphenotic has an anterolateral heel-like process. The bone is not deeply excavated ventrally as the dilatator fossa is minimally defined in all cobitoid fishes [see p.207]. The sphenotic receives a part of the anterior hyomandibular head in a socket produced on it ventrally.

Of the other noemacheilids in Glaniopsis and homolopterids, the sphenotic always articulates with the
epioccipital. In these taxa the sphenotic has a postero-
dorsolateral process. In *Ellopostoma* each sphenotic is
in the same position as it is in the Noemacheilini but
does not approach the epioccipital. The sphenotic of
*Ellopostoma* is extended laterally in the coronal plane,
posterior to the large eye. In *Vaillantella* the sphenotic
is long. Uniquely amongst noemacheilids the bone has no
lateral process. The sphenotic is separated from the
epioccipital by the anterolateral supraoccipital limb and
by the apex of the pterotic.

In the Cobitini the sphenotic is more or less displaced
from the postorbital margin by the pterosphenoid and by the
descending frontal process extending towards the ascending
parasphenoid process. In Cobitini the sphenotic never
articulates with the epioccipital. In *Acanthopsis* and
*Somileptes*, a small digitiform anterodorsolateral process
of the sphenotic is present. A tiny buttress of bone in
this position is also present in *Lepidocephalus guntea*,
and *L. caudofurcatus*. The sphenotic is smooth in other
Cobitini.

In the Botini the sphenotic is positioned essentially
as it is in the Noemacheilini. It has no anterodorsol-
lateral process, except in *Botia macracantha* and *B. almorhae*,
in which a small anterodorsolateral process is seen. In
Botini the sphenotic usually does not meet the epioccipital
but it does so in *B. macracantha*, and *Leptobotia elongata*.

Comparison of the sphenotic of cobitoids with that
of other Ostariophysi demonstrates that the position of the
bone in the Cobitini is a peculiar derived condition which
can be interpreted in correlation with the positioning of the pterosphenoid in Cobitini [see p.208].

The absence of articulation between the sphenotic and epioccipital bones appears to be a derived cobitid condition which is correlated with the tendency for a temporal opening to develop in the skull [see p.220-4].

The presence of an anterodorsolateral process of the sphenotic dorsal to the dilatator fossa is plesiomorphic amongst Ostariophysi. However the extent of development of the process in this position in Ellopostoma is apomorphic.

**Prootic, and subtemporal fossa**

Howes [1981] showed that, in its plesiomorphic condition, the cyprinid prootic is an almost square bone with a short lateral commissure. The prootic is essentially of this form in all the cobitoids.

In Noemacheilini each prootic is usually slightly wider than long. In the midline the prootics surround a very shallow posterior myodome. The posterior border of the prootic is occasionally invaded by a conical extension of the anterior saccular recess, as is present in the characin *Brycon* [Weitzman, 1962]. The anterior border of the prootic contributes to the anterior trigeminofacial foramen [see p.211-3]. The posterior trigeminofacial foramen is single and is enclosed within the anterolateral part of the body of the bone, as it is in all members of the cobitoid group. In the Noemacheilini the ventral surface of the prootic is convex. The subtemporal fossa is effectively not defined. At most this fossa is produced as a ventrally concave dimple over the prootic-exoccipital-pterotic junction.
The form of the prootic of other noemacheilids resembles that of the Noemacheilini except that there is some variation in the extent of the development of the sub-temporal fossa. The fossa is absent from Vaillantella, Glaniopsis and from all gastromyzorilines except Protomyzon (Ramaswami, 1952:4). In Ellopostoma the subtemporal fossa is comparatively well-developed and the fossa is deep in all homalopterines (Ramaswami, 1952:3).

In the Cobitini the prootic is usually slightly longer than wide. The posterior myodome is shallow as it is in Noemacheilini. The contribution of the prootic to the border of the anterior trigemino facial foramen in Cobitini is described on p.212. In Cobitini the subtemporal fossa is not defined.

In the Botini the prootic is longer than it is wide in Leptobotia and approximately square in Botia. The posterior myodome is shallow. The subtemporal fossa is absent, except as a slight depression seen in B. macracantha.

The extent of the development of a subtemporal fossa is variable amongst Ostariophysi and this is discussed below in light of the variable representation of the fossa in cobitoids.

Howes (1981) stated that the most frequently occurring subtemporal fossa morphology in Cyprinidae is one which is deep and circular or oval. Howes pointed out that as the fossa is the site of origin of m. levator posterior which inserts onto the pharyngeal bone, its size and development is correlated with that of the muscle, and that subtemporal fossa depth covers a wide range throughout the family.
Amongst cyprinoids I note that the subtemporal fossa is quite deep in *Psilorhynchus*. A shallow subtemporal fossa is present in *Gyrinocheilus*, which is noteworthy in light of the absence of pharyngeal jaw apparatus development in *Gyrinocheilus*. A similar apparent paradox was recorded by Ramaswami (1952:4) for the reverse situation. Ramaswami noted that in the gastromyzonines the hypobranchial apparatus is well-developed and stated that the feeble development of the subtemporal fossa in these animals is thus difficult to explain.

Amongst other ostariophysi the subtemporal fossa is absent from catfish and gymnotids. It is very shallow in the Catostomidae. Weise (1960) indicated this shallowness as a specialised feature in the catostomids which he suggested was correlated with the enlargement of the post-temporal fossa in this group, and with the peculiar basioccipital and pharyngeal modifications of the catostomids. I interpret the loss of the subtemporal fossa in the cobitoids as also derived, and suggest that it is correlated with the production of a handle-like process on the pharyngeal bone (see p.328).

Ramaswami (1952:4) suggested that the shallow subtemporal fossa of *Glaniopsis* should be interpreted as a distinctly noemacheiline feature of this species. He concluded that reduction of the subtemporal fossa demonstrated affinity between the Noemacheilini and gastromyzonines, while the more extensive development of the fossa in the homalopterines suggested that this group had a more typically cyprinid ancestor than did the gastromyzonines.
I conclude that the presence of a subtemporal fossa is plesiomorphic to cobitoids, and that because the fossa has apparently been lost more than once in the Ostariophysi its presence or absence in members of the cobitoid group must be used with caution as an indicator of phylogeny. The fossa is considered further on p.331-6.

**Pterotic**

The pterotic in the *Noemacheilini* is present as a wedge-like bone in the posterolateral part of the braincase. It has a triangular dorsal profile. The pterotic articulates with the sphenotic, parietal and epioccipital and with the prootic and exoccipital. It is not deeply excavated ventrally, as the subtemporal fossa is minimally defined. Dorsally the pterotic may contribute to formation of a supratemporal fossa [p.2104]. The pterotic of the *Noemacheilini* does not have a posterior process and the dorsal surface of the bone is smooth.

Of the other *noemacheilids* in *Vaillantella* the pterotic is like that of a typical *Noemacheilus*, but it has a small hook-like posterior process. In *Ellopostoma* the pterotic has a small posterior process. In *Glaniopsis* and the homalopterines and gastromyzonines the pterotic is expanded laterally. It does not have a posterior process.

The typical cobitine pterotic differs little from that of a typical *Noemacheilus* except that with the expansion of the supraoccipital in Cobitini, the pterotic is slightly displaced ventrally. The dorsal surface of the bone is slightly raised around the articulation of the posttemporal.
Ventrally the pterotic has a small, blunt process which meets the ventral part of the posttemporal. In *Somileptes* and *Acanthopsis* there are two blunt digitiform processes on the ventrolateral portion of the pterotic which abut the descending posttemporal [fig. Lv].

In the Botini the pterotic resembles that of a typical *Noemacheilus*. In *Botia almorhae* the bone is unusually elongated along the lateral part of the braincase. The pterotic makes a contribution to the formation of the temporal opening when this is present (see p.212). There is a shallow facet on its surface for the articulation of the posttemporal.

I have not recorded the presence of the opisthotic bone in any cobitoid, and this condition is unusual amongst Ostariophysi. However, it must be noted that the opisthotic is also absent from some cyprinids (Howes, 1978).

**OCCIPITAL SERIES**

*Epioccipital and temporal openings*

The epioccipital in the Noemacheilini is an oval or round bone present in the posterolaterodorsal part of the braincase. It articulates with the pterotic, supraoccipital and exoccipital, and variably [see p.213-5] with the sphenotic. Dorsally it usually forms a very shallow cup supporting the dorsal articulation of the pectoral girdle. It occasionally has low crests providing for the insertion of epaxial muscle fibres.

When a temporal opening is present in Noemacheilini, it develops as a shallow hollow over the junction of the
epioccipital, pterotic and sphenotic bones [fig.Lvia]. This junction is partially covered by the parietal and by the adjacent bones of the dermal skull roof. The temporal opening of Noemacheilini is occasionally rendered patent by separation of the spines of the epioccipital, pterotic and sphenotic bones from their junction.

Of the other noemacheilids the epioccipital bone of Vaillantella and of the homaopterines and gastromyzonines resembles that of a typical Noemacheilus. In Ellopostoma the epioccipital has a hemicircular horizontal shelf-like process on its dorsal surface with which the posttemporal articulates [fig.Lxiia]. A temporal opening does not develop in these taxa.

In the Cobitini the epioccipital varies more than in the noemacheilids. The posterior part of the skull in cobitinines is rounded, the dorsal plates of the exoccipital extend into the dorsal view and the epioccipital is restricted by these parts of the exoccipital and by the expanded supraoccipital. The epioccipital appears to be wedged between the bones surrounding it and is typically cylindrical in shape. Ramaswami [1953] considered it peculiar derived and characteristic of a derived group of the Cobitini that the epioccipital was absent in Acanthophthalmus, Acanthopsis and Lepidocephalichthys [Lepidocephalus]. Nalbant [1963] also considered that loss of this character indicated a natural, derived lineage of the Cobitini. My observations on Acanthophthalmus, Acanthopsis [fig.Lv] and Lepidocephalus suggest that the epioccipital is present in each of these genera, but it is
more or less completely fused to the pterotic, with the small posttemporal lying very firmly attached over the suture. The epioccipital has not been (as was suggested by Ramaswami [1953]) united into the exoccipital. In *Lepidocephalus* the fusion of the epioccipital with the pterotic is incomplete. In *L. annandali* and *L. thermalis* this "fusion" consists only of the loss of articular cartilage between the pterotic and epioccipital. The articular cartilage has also been lost from the same suture in the *Cobitis taenia balcanica* examined.

There is a very unusual condition in the epioccipital part of the braincase of the cobitine species *Lepidocephalus guntea*, *L. caudofurcatus* and *L. thermalis* (fig. Lvib) and also in *Somileptes gongota*. In these the conical epioccipital makes a substantial contribution to the dorsolateral border of the lateral occipital foramen because of a discontinuity in the circumference of exoccipital bone which usually surrounds the foramen. It is notable that this condition does not develop in *Lepidocephalus annandali*. This is discussed further on p. 338.

There is effectively no development of a temporal opening in the Cobitini. Sagemahl [1891] considered that in the Cobitidae a "Temporalhole" was a feature of the Botini and Noemacheilini only. Ramaswami [1953] emphasised the specific complete absence of a temporal opening in *Lepidocephalus*, *Acanthophthalmus*, *Somileptes* and *Misgurnus* and thus implied that he considered a temporal opening to be developed to some extent in the other Cobitini. I do not consider this to be the case.
In Botini the epioccipital is an oval bone in the posterolateral part of the braincase. In Botia almorhas the epioccipital has a spinous posterior process which articulates with the posttemporal medially. In Leptobotia also elongata the epioccipital has a rather well-defined bony crest which is continued onto the parietal (fig.Lviiia), to which epaxial muscle fibres attach.

In all the Botini the temporal opening is clearly developed (fig.Lviiia and b).

Study of the epioccipital bone of representatives of ostariophysean outgroups suggests which of the peculiarities associated with the epioccipital portion of the skull of cobitoids have characteristic value.

Nalbant (1963) suggested that "reduction" of the epioccipital bone was characteristic of the cobitine cobitids. However, it is not easy to define this character. Fusion of the epioccipital with the pterotic bone as noted in some Cobitini has apparently occurred more than once within the Ostariophysi. Mahajan (1966) described the epioccipital of the siluroid Sisor as "indistinguishably" fused to the pterotic. Sisor is highly adapted for a torrential environment. However fusion of the epioccipital with the pterotic in the Cobitini cannot be interpreted as a similarly adaptive response as the Cobitini inhabit slow waters. The cobitine taxa in which the epioccipital and pterotic tend to become fused [Acanthopsis, Acanthophthalmus and Lepidecephalus] are mud and sand burrowing forms and the adaptation could be associated with this habitat. If so because it is adaptive, this fusion should not be inter-
interpreted as an indicator of immediate phyletic relationship between those taxa in which it occurs.

The significance of the various forms of temporal perforation in Ostariophysan phylogenetics was reviewed by Wu Xianen et al., [1981]. These authors proposed that the "plesiomorph and progenitor" form of the perforation is present in the characins. In characins there is an aperture in the temporal part of the skull, and this aperture is crossed, or bridged by the epioccipital which divides an anterior parietal-epioccipital portion of the aperture from a posterior pterotic-epiotic portion. Wu Xianen et al. considered that there have been two directions of ostario-physean evolution from the characin condition of the temporal aperture. One direction is taken by the Catostomidae, Gyrinocheilidae and Cobitidae. In these the aperture (which is named in the three families the supra-temporal fossa, the lateral temporal fossa and the temporal opening respectively) is according to Wu Xianen et al., homologous with the anterior part of the characoid perforation. By contrast in the Homalopteridae (embracing the gastromyzonines), where there is no temporal perforation, and in the cyprinids (where the temporal aperture is called the posttemporal fossa) Wu Xianen et al. suggested that this development took place by conservation of the posterior part of the characoid type of temporal perforation. In the light of the variable state of temporal perforation in the Cobitidae, I conclude that the presence or absence of a temporal aperture per se cannot be considered a reliable indicator of relationship. However
if the loss of temporal perforation from the Homalopteridae is interpreted as derived from the first rather than the second of the two patterns of Ostariophysean temporal perforation suggested by Wu Xianen et al. then it may be that the Catostomidae, Gyrinocheilidae and Cobitidae and Homalopteridae can together be separated from the Cyprinidae on the basis of their temporal opening morphology.

It is interesting that the Cobitidae, Gyrinocheilidae and Catostomidae should be broadly grouped together by this character. The possibility of relationship between these taxa is further investigated on p. 343-5.

**Supraoccipital**

In the Noemacheilini the supraoccipital is a shield-shaped bone and convex dorsally. It is excluded from the border of the foramen magnum as it is in all cobitoids examined. The anterior limbs of the supraoccipital articulate with the sphenotic. Between the anterior limbs the anterior border of the supraoccipital is concave and forms the posterior border of the cranial fontanelle, except in *Noemacheilus nigromaculatus* in which the fontanelle is peculiarly enclosed between the frontal and parietal bones only (p. 246). The dorsal surface of the supraoccipital is smooth in Noemacheilini. The transverse temporal sensory canal is almost invariably enclosed in the anterior part of the supraoccipital (see p. 246).

Of the other noemacheilids, in *Vaillantella* the supraoccipital is shield-shaped. However the transverse temporal sensory canal passes through the skin superficial
to the supraoccipital, and in *Vaillantella* the cranial fontanelle is absent. In *Ellopostoma* the supraoccipital has a low "V"-shaped crest (see p. 101). The supraoccipital, with the exoccipital, forms a facet into which the anterior part of the SN2 element associated with the Weberian apparatus articulates (see p. 101-2). This facet, formed in *Ellopostoma*, is not found in any other cobitoid.

The supraoccipital of the homalopterines and gastromyzonines is like that of the Noemachaulini except that it frequently has some cresting on its dorsal surface (see Ramaswami, 1952:3 and 4).

In the Cobitini the supraoccipital is enlarged but retains its shield-shape. The supraoccipital forms a strong domed roof over the robust rounded posterior part of the braincase of Cobitini. The anterior limbs of the supraoccipital are long, and the cranial fontanelle, when present (which is not invariably the case see p.245-6) extends into an invagination between these limbs. The supraoccipital is most enlarged in *Acanthopsis*, and only in this taxon of the Cobitini does it contain the transverse temporal canal. This otherwise passes through the skin superficial to the bone. There is a supraoccipital crest developed in *Lepidocephalus annandali* and *L. guntea*. The crest is U-shaped and lies posterior to the fontanelle margin, and its presence precipitates slight sinking of the fontanelle. In *L. thermalis*, *L. guntea* and *L. caudofurcatus* and in *Somileptes* the supraoccipital contributes to the lateral border of the unusually formed lateral occipital foramen (see p.221 and fig. Lvib). In *Somileptes* the cranial fontanelle is
distinctly sunk into an oval hollow in the skull. The sides of the hollow are raised by both the supraoccipital and the frontal bones. Posterior to this the supraoccipital of *Somileptes* is raised into two U-shaped crests.

In the Botini the supraoccipital is shield-shaped. It contributes to the border of the fontanelle, and encloses the transverse temporal canal, except in *Leptobotia elongata* in which the fontanelle is absent and the canal passes through the skin. The dorsal surface of the supraoccipital of Botini is domed and smooth.

As a shield shaped supraoccipital is plesiomorphic amongst Ostariophysi, and the bone frequently develops crests [Howes, 1981], the general proportions of this bone in cobitoids are not of characteristic value. The enlargement of the supraoccipital of Cobotini can be interpreted as a derived feature of this group.

The autapomorphic supraoccipital-exoccipital facet formed in *Ellopostoma* is discussed on page 101-2. However it is noted here that articulation between the cranium and the antero-dorsal elements of the vertebral column is not per se unique to *Ellopostoma*. This articulation occurs in many groups of Ostariophysi [see p.372].

**The Exoccipital and the Lateral Occipital Fenestra**

Each exoccipital has a dorsal plate contributing to the posterior skull wall, and a ventral, more or less horizontal plate flanking the basioccipital. The dorsal portion of the exoccipital is considered first. This dorsal part contributes to the border of the foramen magnum, and usually encloses the aperture known as the lateral occipital
foramen (or fenestra as it is better called, as nothing apparently passes through it).

In all Noemacheilini the exoccipitals surround the whole foramen magnum, and this, as indicated by Ramaswami (1952:2) is also the typical cyprinid condition.

In Noemacheilini the lateral occipital fenestra is invariably present, although it may be reduced to a tiny circular aperture as it is in *N. rupecola*. In the Noemacheilini only a small portion of the dorsal plate of the exoccipital is visible in dorsal view.

Of the other noemacheilids, in *Vaillantella* the lateral occipital fenestra is absent. There is an unusual hemi-circular notch in the edge of the posterodorsal border of the exoccipital of this species.

In *Ellopostoma* the lateral occipital fenestra is also absent. The occiput of *Ellopostoma* is modified and the dorsal plates of the exoccipitals meet the supraoccipital to form the additional occipital facet illustrated in fig. Lviia).

In *Glaniopsis*, the homalopterines and gastromyzonines the lateral occipital fenestra is never developed. The absence of the lateral occipital fenestra in the homalopterines and gastromyzonines is also recorded by Sagemahl (1891) and by Ramaswami (1952:3 and 4). Ramaswami suggested that there is "some phylogenetic significance to the absence of the fenestra so commonly seen in the exoccipitals of catostomids, cyprinids and cobitids", but he does not discuss what the significance might be.

In the Cobitini, and the Botini, the exoccipitals
surround the foramen magnum, and in both of these taxa the lateral occipital fenestra is always present. The fenestra is reduced to a tiny slit in the cobitine Acanthophthalmus muraeniformis, and is, as described previously (p.221) bounded by the epioccipital, the supraoccipital and the exoccipital in some Lepidocephalus species and in Somileptes (p.221).

It is difficult to assess the phylogenetic significance of the absence of the lateral occipital fenestra from some cobitoids because the level of universality at which the fenestra is derived within the Ostariophysi is not established. Howes (1981) described some variation in the size and shape of the lateral occipital fenestra of the Cyprinidae. In that family the fenestra is usually small and oval, and enlarged and reduced states are both interpreted as derived. However, the fenestra is invariably present in cyprinids. The fenestra is also invariably present in the Catostomidae and in the Psilorhychidae.

Ramaswami (1952:1) found that in the Gyrinocheilus species examined by him, the exoccipitals did not enclose a fenestra. Ramaswami described notches "between the supraoccipital and exoccipital" as "reminiscent" of lateral occipital fenestration. In G. aymonieri examined by me the exoccipital is typically cyprinid and encloses a fenestra. I have not been able to examine the same species as Ramaswami.

Loss of the lateral occipital fenestra is apparently very rare in Cypriniformes. If loss of the fenestra from species within the Cypriniformes is interpreted as a derived
condition then it can be hypothesised that the cobitoid taxa in which the loss has occurred, namely *Ellopostoma*, *Vaillantella*, *Glanioptis* and the homalopterines and gastromyzonines form a natural group on the basis of this character [see p.334]. This hypothesis allows definition of a non-noemacheiline noemacheilid group, and thus indirectly also allows definition of the Noemacheilini. The hypothesis is strengthened if it can be shown that the lateral occipital foramen is not absent in *Gyrinocheilus*.

Alternative hypotheses are that the loss of the lateral occipital fenestra is a rare but repeated derived development within the Cypriniformes, or that *Gyrinocheilus* is more immediately related to the non-noemacheiline noemachilids than is any other taxon.

The ventral portion of the exoccipital contributes to the formation of the posterior myodome. In all cobitoids the myodome is extremely shallow. The ventral surface of the exoccipital is perforated to allow the exit of the posterior cranial nerves. Ramaswami (1955) described the typical pattern of foramation of this part in Cyprinidae as for the ninth nerve (Cr IX) to exit anterior to, or with Cr X through the jugular foramen in the exoccipital, and for Cr XI to exit posterior to Cr IX and Cr X through a separate foramen in the exoccipital.

The ventral surface of the exoccipital has 3 perforations in all Noemacheilini examined except *N. corica*, *N. yarkandensis* and *N. nigromaculatus* in which the most anterior foramen is absent. There are also only two foraminae in the ventral exoccipital in *Glanioptis*,
Balitora and Gastromyzon.

In Ellopostoma there is a very derived condition in which there is a single large sinus-like opening in the ventral surface of the exoccipital [see fig.xxixa]. There are two or three ventral occipital perforations in all the Botini, Cobitini and representative Ostariophysean outgroups examined; the peculiarity of Ellopostoma is emphasised.

The ventral plate of the exoccipital may be produced laterally into a small foot-like process which articulates with the posttemporal. This feature is best represented in Cobitini where the foot-like process of the exoccipital approaches a similar process of the pterotic described on page218-9.

The Basioccipital and Pharyngeal Process

The basioccipital varies in shape in correlation with the shape of the posterior part of the braincase. It also forms the so-called "pharyngeal process". In cyprinids the pharyngeal process has in association, a horny pad, which acts as a masticatory surface for the pharyngeal jaws. In no cobitoid examined is such a horny pad present, and the pharyngeal processes of the basioccipital of cobitoid fishes are small, and very variable in shape.

Some attention has been paid to the condition of the pharyngeal processes of cobitoids. Regan (1911) stated that it was characteristic of the Cobitidae that the pharyngeal processes of the basioccipital were very small, sometimes extended below the aorta, never united with each other and never supported a horny masticatory pad. Berg (1940)
pointed out that the Noemacheilini differed from the other Cobitidae in that in these the pharyngeal processes did meet, and did unite below the aorta. Ramaswami (1953) agreed with Berg's description but did not offer any interpretation of the significance of the varying development of the pharyngeal processes of Cobitidae.

In the Noemacheilini I record that the pharyngeal process is annular. It has a short posterior process, and its outline is leaf-shaped (fig.Lixa). The only deviation from this form of the process is seen in *N. botia* where the ventral profile of the process is T-shaped (fig. Lixb). Of the other noemacheilids in *Vaillantella* the pharyngeal processes are produced as a pair of small bony plates, diverging distally (fig. xxxiii). In *Ellopomostoma* the "pharyngeal process" is extraordinarily developed into a horizontal reticular plate of bone which delivers cancellous dorsal extensions, and from which there is a small mid-line posterior projection (see fig.L viiiia). The base of the basioccipital of *Ellopomostoma* also issues peculiar digitiform bony ramifications over its sutures with the prootic and exoccipital bones (fig.xxxix a). In *Glaniopsis* and *Gastromyzon* the pharyngeal process is present as a single small flat posterior tab of bone, while in the homalopterines, as reported by Sagemahl (1891) and Ramaswami (1952:3), the pharyngeal process is effectively absent.

In the Cobitini the pharyngeal process is usually similar to that of *Vaillantella*, i.e. a pair of small diverging plates of bone (fig. Lixc). However, in
Acanthopsis choirorhynchus [fig.Lixd] the internal edge of each plate is thrown into convolutions. In Somileptes gongota [fig.Lixe] the pharyngeal process is annular and the external edge of this is thrown into petal-like projections. The pharyngeal process of Sabanejewia aurata balcanica also forms a ring of bone [fig.Lixf].

In the Botini there is invariably the small bifid type of pharyngeal process, similar to that described as typical for the Cobitini.

Small pharyngeal processes per se are not unique to cobitoid fishes. Howes [1981] described the plesiomorph condition of the cyprinid pharyngeal process, as small and triangular with a compressed posterior process, and the tab-like pharyngeal process of the homalopterines and gastrozonirines are similar to this in form.

Furthermore, the pharyngeal processes of the basi-occipital of many non-cyprinid Ostariophysi are small. In Psilorhynchus the process is of the small-tab-like type. It can also be noted that in Gyrinocheilus there is a pair of small prongs on the basioccipital - despite the lack of formation of any pharyngeal teeth in this taxon. In the gymnotids there is some paired ridging on the ventral surface of the basioccipital, issuing as a pair of tiny processes posteriorly, which would appear to be primarily a zygopo-physeal structure. Superficially these processes very much resemble the "pharyngeal processes" of e.g. the Botini.

I conclude that the cobitoids demonstrate a general trend to markedly reduce the pharyngeal processes. As it
appears the processes become insignificant in mastication, the projections from the posterior of the basioccipital might perhaps be more appropriately referred to as aortic processes.

Reduction of the subtemporal fossa in the cobitoids has already been discussed (see p.218). However, the correlation between reduction of the fossa and reduction of the pharyngeal process is imperfect. In e.g. the homalopterines, the pharyngeal process is minute but the subtemporal fossa is quite deep [see p.217]. Furthermore it is clear from the structure of the pharyngeal jaws in cobitoids that the process of pharyngeal mastication is not in degeneration in this group.

I suggest that within the cobitoid lineage the simple, tab-type of the pharyngeal process is plesiomorphic.

The ring-shape of the pharyngeal process is typical and more or less characteristic, of the Noemacheilini; the ring structure may illustrate a specific pattern of reduction from the tab-type of the pharyngeal process.

The production of paired plates on the ventral surface of the basioccipital as in Botini and most Cobitini cannot be used to suggest proximity of relationship between these two groups because there are similar paired structures on the ventral surface of the basioccipital in many Ostariophysi.

The occurrence of an annular pharyngeal process in a few Cobitini is interesting, as it can be proposed that an annular type of process is plesiomorphic to the Cobitini. The elaborate pharyngeal processes of Acanthopsis and Somileptes are interpreted as synapomorphic for these two taxa [see p.337].
The state of the pharyngeal process of *Ellopostoma* is very peculiar and superficially recalls the extreme modification of the pharyngeal processes which is characteristic of the catostomids, as described and illustrated by Weisel (1960). Comparison of the basioccipital region of *Ellopostoma* with that of a catostomid (fig. Lviii a and b) shows that in both taxa cribiformity has developed accompanying expansion of plate-like bones. A straining habit in both is evident from the state of the pharyngeal dentition. However, the elaborate strutting supporting the pharyngeal process development in *Catostomus* is not present in *Ellopostoma*, and the somewhat similar modifications of the two appears to be an interesting quantitative adaptive parallelism. The comparability of their associated soft anatomy has not been investigated.

**Paraphenoid (Fig.Lx)**

The paraphenoid is a ventral strut supporting the braincase.

In the Noemacheilini the anterior tip of the paraphenoid is enclosed between the base of the mesethmoid and the posterior process of the vomer, and the posterior process of the vomer is held tightly in a groove on the anterodorsal paraphenoid, strengthening this part of the skull. The shaft of the paraphenoid of Noemacheilini is always slightly flattened horizontally (fig.Lxa). The paraphenoid shaft is extraordinarily wide in *Oronectes* and *Lefua* (fig.Lxb), and separates the two plates of the orbitosphenoid in these species (p.204). The paraphenoid
ascending process, or wing as it is more appropriately called here, is short in Noemacheilini. The significance of this has been considered with regard to the construction of the anterior trigeminofacial foramen [p.210-3]. Posteriorly the parasphenoid terminates in a fork underlying the basioccipital, except in _N. barbatulus_, where three of four long bony serrations are present in this position. Of the other noemacheilids, in _Vaillantella_ the parasphenoid is narrow in its anterior and posterior thirds, but has a peculiar long, expanded, middle third between the pterosphenoid bones [p.129, fig.xxxiii]. The parasphenoid is forked posteriorly. In _Ellopostoma_ the parasphenoid is narrow anteriorly. It is expanded in its posterior third, which is approximately rectangular, and which is oddly obliquely truncated terminally [see p.102, fig. xxixa]. Roberts [1972] stated that the parasphenoid of _Ellopostoma_ is sutured to the anterior margin of the supraoccipital - presumably a misprint for basioccipital - and he contrasted this arrangement with that in the Cobitidae where the parasphenoid forms a fork distinctly posterior to the anterior margin of the basioccipital. In fact, in _Ellopostoma_ the bone does extend slightly posterior to the anterior margin of the basioccipital. In _Glaniopsis_ the anterior part of the parasphenoid shaft is considerably expanded. The bone terminates in a fringe of serrations below the basioccipital; a distinct fork is not formed [see Ramaswami, 1952.4]. In the more typical homalopterines and gastromyzonines the anterior part of the parasphenoid is never as expanded as it is in _Glaniopsis_. In these taxa the parasphenoid is
sometimes, but not invariably, forked terminally.

In the Cobitini the anterior parasphenoid tip lies free from the posterior process of the vomer, allowing the mobility of the ethmoid block which is characteristic of the Cobitini [p.194-8, fig. xLvii]. The shaft of the parasphenoid is narrow but flat and strong. The ascending process of the parasphenoid is well-defined [fig.Lxc], and is ridged anteriorly where it provides the origin of the lateral ethmoid limiting ligament. The ascending process of the parasphenoid approaches a descending process from the frontal; these two processes actually meet each other in Somileptes lateral to, and in Acanthophthalmus anterior to, the pterosphenoid. Articulation of the frontal with the parasphenoid is interpreted as a derived, but not per se unique condition, associated with the modification of the skull as an awl in association with the burrowing habit which emerges in the Cobitini. The parasphenoid in the Botini has a narrow shaft (Lxd and e) which forms a sagittal plate. The long posterior vomerine process is very tightly enfolded in a groove in this plate. The ascending process is little defined, and, as also in the Cobitini, the parasphenoid is invariably forked terminally.

It is evident that the proportions of the parasphenoid are very variable in cobitoids, but the variations observed are not unique to that group. For example, Howes (1981) remarked on the extreme broadening of the anterior part of the parasphenoid of the chinese major carps. While the condition of the parasphenoid of the noemacheilines Oronectes and Lefua is much more exaggerated than in these
carps, in some gymnotids the parasphenoid shaft is as wide as in Oronectes and Lefua and it is in both these noemacheilines and these gymnotids that the orbitosphenoid bone is represented as two plates [see p.204].

The parasphenoid of Vaillantella is peculiar in shape [fig. xxxiii]. Superficially it most resembles the parasphenoid of Parakneria which has an expanded, and rhomboidal middle one third. It is evident that the shape of the parasphenoid in Ostariophysi is variable and correlated with the general proportions of the braincase.

The posterior termination of the parasphenoid on the basioccipital is clearly forked in most cobitoids. This part of the parasphenoid is also forked in e.g. Parakneria the gymnotids examined, the catfish Glyptothorax, in Catostomus and usually in cyprinids; clearly the absence of forking as in Ellopostoma, and some of the Homalopteridae is the less usual Ostariophyseen condition and appears to be a derived development associated with flattening and broadening of the braincase.

The significance of foramination in the parasphenoid of Ostariophysi is not easy to assess. The parasphenoid of cobitoids is frequently foraminate and a short discussion of this follows here.

Patterson [1975, pp. 518] illustrated the parasphenoid of Pholidophorous germanicus, with two paired arterial foraminae, the anterior of which passes the efferent pseudobranchial artery and the posterior of which passes the internal carotid artery. Patterson interpreted the presence of the internal carotid foramen in the parasphenoid as the
plesiomorph teleost condition. He commented that the anterior foramen is a less frequent feature. The presence of the internal carotid foramen between the parasphenoid and prootic was interpreted by Patterson as a derived development within the teleosts. Howes [1981] considered that the presence of an internal carotid foramen between the parasphenoid and the prootic was plesiomorphic within the cyprinids and characins. Howes noted in contrast with this, the complete enclosure of the internal carotid foramen in the parasphenoid of siluroids and of Catostomus.

In all noemacheilids there is a single pair of foraminae in the parasphenoid. In the Cobitini there is also always such a single foramen present, as there is also in Leptobotia and Botia almorhae. In the other members of the Botini two paired foraminae feature in the parasphenoid (fig.Lxd and e). It must be concluded that parasphenoidal perforation is widespread in the Ostariophysi, and I do not consider it possible to ascribe absolute polarity to the appearance or disappearance of this feature within cobitoids.

FORMATION OF THE SKULL ROOF

The reduced state of the supraethmoid in cobitoid fishes has been discussed with regard to the ethmoid block in these [p.181-3].

Frontals

The form of the frontal bones is phenomenally variable within the cobitoids (fig.Lxi).

In the Noemachseilini the frontals are typically narrow
and somewhat elongate anteriorly. The frontal forms a short interdigitating suture with the posterior of the ethmoid. The frontals form a straight suture in the mid-line, and are separated from each other posteriorly by the anterior of the [posterior] cranial fontanelle. The lateral frontal edge is deeply concave over the orbit. The frontal sensory canal passes through the brow. The frontals expand considerably posterior to the orbit; their breadth in this part is correlated with the general proportions of the head [fig.Lxia].

Within the Noemacheilini deviation from this pattern of frontal morphology occurs in Oronectes, Lefue and Noemacheilus nigromaculatus. In these species the frontals are broad throughout their length [fig.Lxib]. In N. nigromaculatus the frontal does not have a concave excavation over the orbit. The frontal of N. strauchi is unusually narrow [fig.Lxic].

Of the other noemacheilids the frontal of the homalopterines, gastromyzonines and of Glaniopsis and Ellopostoma is rather short and broad. Its lateral edge is concave over the orbit. In Vaillantella [fig.Lxie] the frontal is long and narrow and triangular. The ethmoid articulates in a simple notch formed between the frontal.

In the Cobitini the frontals always have a deep notch between them between which the plate-like mesethmoid of these species articulates. The mesethmoid can undergo lateral rotation about this articulation [p.186 ]. In Misgurnus [fig.Lxif] the form of the frontal is otherwise of the noemacheilinae type, but in most Cobitini [fig.Lxig]
the frontal is extraordinarily drawn out anteriorly, and
develops a slightly convoluted mid-line suture. The post-
orbital part of the frontal of Cobitini is narrower than
in the Noemacheilini, but it is still distinctly expanded,
and has a deeply concave lateral edge.

In the cobitine Acanthopsis (fig.Lxih) the frontal is
extremely elongated, and the frontals tend to fuse together
on the mid-line. The frontal of Somileptes (fig.Lxi i)
is peculiar in that it is anteriorly rather less, and
posteriorly rather more narrow than in a typical cobitine,
and the frontals entirely fuse together in the mid-line.
This frontal fusion is interpreted as synapomorphic for
Acanthopsis and Somileptes.

In Acanthophthalmus (fig.Lxij) the frontals are tri-
angular in shape. The production of narrow, strong more
or less falciform frontals can be correlated with the
burrowing habit in Cobitini.

In the botine Leptobotia (fig.Lxik) the frontals are
long and narrow. Anteriorly they form a rather crude notch
and make a very narrow interdigitating suture with the
ethmoid. In all species of Botia, but not in Leptobotia,
there is a hemicircular excavation on the anterolateral
edge of each frontal, inside which the tip of the ascending
process of the lateral ethmoid spine can rotate. In overall
shape the frontal of B. sidthimunki, B. almorhae (fig.Lxil)
and B. macracantha is short and broad. Its edge is concave
over the orbit. The shape of the frontal of Botini con-
trasts with that of the noemacheilids and cobitines in that
there is no postorbital expansion of the frontal of Botini.
In *B. berdmorei* (fig. Lxim), *B. hymenophysa* and to a slightly lesser extent in *B. modesta* the frontal is particularly narrow; its shape resembles that of *Leptobotia*. However it is emphasised, there is a lateral ethmoid excavation on the edge of the frontal of all Botia and this excavation is not developed in either *Leptobotia*, or in Cobitini.

The significance of the variable shape of the frontal bone of cobitoid fishes is discussed below in the light of the variability of this bone in other ostariophysean taxa.

Howes (1981) described the plesiomorphic shape of the frontal in cyprinids as short and broad, and earlier (1978) showed that of cyprinids, only derived members of monophyletic lineages displayed elongation of the bone.

Fink and Fink (1981) considered that within the Otophysi, the Gonorynchiformes displayed a derived condition in which the frontals are elongated by extending further posteriorly than is the primitive condition displayed by most Otophysi and other primitive teleosts. In most Otophysi the lateral edge of the frontal forms a concave brow. Only in the gymnotids examined here is the anterior part of the frontal as markedly tapered as in e.g. the Cobitini. An extremely narrow frontal can be interpreted and is generally correlated in both the gymnotids and in the Cobitidae with a reduced supraethmoid.

The variations in the condition of the cobitoid frontal are interpreted as follows. It appears that the plesiomorph form of the frontal in cobitoids is as present in the homalopterines, gastromyzonines, *Lefua*, *Oronectes* and in
Noemacheilus nigromaculatus in all of which the bone is wide. The commonest noemacheilin frontal form appears to be derived by elongation and narrowing of this broad type of frontal.

Ellopostoma has a rather typically noemacheilin frontal form [fig.Lxid].

The frontal of Vaillantella is more elongated than that of any other noemacheilid [fig.Lxie]. On the basis of this development and on the production of an anterior frontal notch it can be hypothesised that Vaillantella is more closely related to the Cobitini than is any other noemacheilid [see p. 334].

Of the Cobitini, Misgurnus has a plesiomorphic cobitid type of frontal. However, the commonest cobitine frontal form appears to have been derived by elongation. Within the Cobitini various very highly derived frontal conditions develop as is shown by Acanthopsis and Somileptes, and by Acanthophthalmus and by Cobitis taenia.

In the Botini it is proposed that Leptobotia shares an elongated frontal form, an anterior frontal notch, and the absence of a lateral ethmoid cup in the frontal with the Cobitini, and that on the basis of this, Leptobotia should be interpreted as the plesiomorphic sister group of Botia. Although the frontal in Leptobotia is longer than in Botia, in this case the hypothesis of "elongation = derived" within the Botini is prohibited on the principle of parsimony, because it requires secondary loss of the lateral ethmoid notch from Leptobotia. I suggest the presence of this notch is a synapomorphy which can be used to
unite the genus *Botia*.

Within *Botia* it appears that elongation of the frontal bone occurs as an apomorphic development. It is noted that the frontals are particularly long and narrow in all the species of *Botia* in which three bellies of *m. rostralis* are present with the notable exception of *B. almorhæ*. On the basis of this it is suggested that the species of *Botia* in which *m. rostralis* is triple may be members of a natural group, to which *B. almorhæ* is the primitive sister species. Alternatively, it can be assumed that both triplication of *m. rostralis*, and frontal elongation have taken place more than once within *Botia*. This is discussed further [p.341, fig.xCiii].

The Parietal

In cobitoids the parietal is invariably present, and deviates little from a typical form [fig.Lxi]. It is almost always a short quadrilateral plate of bone varying slightly in proportion with overall skull shape. Each parietal overlies the sphenotic, the epioccipital and the supra-occipital and is sutured to the frontal anteriorly. The parietales are usually completely separated from each other by the cranial fontanelle, and meet each other only when the fontanelle is absent, and oddly in *Noemacheilus nigromaculatus* where the fontanelle is present, but peculiarly disposed and where the parietales meet in their posterior portions. The transverse occipital sensory canal usually runs through the posterior border of the parietal but in some cobitoids passes through the skin superficial
to the bone [see p.247].

Howes (1981) discussed a condition common in cyprinids, in which the parietals are shortened to 30%-50% of the frontal length. In almost all cobitoids the parietals are proportionally much shorter than the frontals although this can be interpreted as at least as much the result of frontal elongation as of parietal reduction. Extreme parietal reduction occurs in many Otophysi. The parietal is very short in many gonorhynchiforms. The parietal is completely lost from catfish. Tilak (1963) suggested that its loss in these is correlated with frontal dominance and the dorsal placement of the eye in a flattened skull. I suggest that reduction of the parietal bone accompanies a variety of skull developments in Ostariophysi, and conclude that a reduced parietal is plesiomorphic amongst cobitoids.

The Cranial Fontanelle

A cranial fontanelle is present in the skull of almost all cobitoid fishes and it has frequently been suggested in the literature that this feature indicates relationship between the cobitoids and various other Ostariophysi in which a fontanelle also develops. Fink & Fink (1981) noted the occurrence of a cranial fontanelle in Catostomidae, Cobitidae, Homalopteridae, Gyrinocheilus and some cyprinids, primitive characins, gymnotids and siluroids, but not in Gonorhynchiformes. These authors showed that the fontanelle is probably an otophysean feature which has been independently lost in many otophysean lineages. I agree with them and conclude that the presence of the fontanelle does not
elucidate cobitoid interrelationships.

Within the cobitoid group the fontanelle is very rarely absent - it lies between the frontal and parietal bones and excavates the supraoccipital posteriorly.

The fontanelle is present in all Noemacheilini, and usually oval. It is frequently expanded posteriorly in the more depressed forms, to the extent that in Aborichthys it is anchor-shaped, with a wide supraoccipital border. Peculiarly in Noemacheilus nigromaculatus the fontanelle is triangular with its posterior apex enclosed between the parietals, so that the supraoccipital is excluded from its border. In some Noemacheilini there is also a small anterior ethmofrontal fontanelle.

In Glaniopsis the posterior cranial fontanelle expands posteriorly and assumes an anchor shape. The fontanelle is usually but not invariably absent from homalopterines, and is usually, although not invariably, present in gastromyzonines. A large fontanelle is present in the skull of Ellopostoma. The fontanelle is absent from Vaillantella.

A long oval cranial fontanelle is present in all the Cobitini examined here except Acanthophthalmus muraeniformis, from which the fontanelle is absent.

The fontanelle is present in all Botini examined here except Leptobotia elongata. The fontanelle is reported as also absent from Botia superciliaris [Sinibotia] [Fang, 1936]. The loss of the fontanelle from some of the Botini has resulted in speculation on the phylogeny of this lineage.

Fang [1936] considered that Leptobotia elongata was
typical of *Leptobotia* and on the basis of the loss of the cranial fontanelle in this species, he concluded that the genus *Leptobotia* "probably occupied a higher natural position than *Botia* and the others". Fang suggested that *Leptobotia* had evolved in parallel with *Sinibotia* from which the fontanelle was also absent. Taki (1972) emphasised that *Sinibotia* should be recognised as the most derived subgenus of *Botia* on the basis of the same character.

I interpret the absence of the cranial fontanelle within the Cobitoidea as a repeatedly derived condition which cannot be used as an indicator of relationship within the group.

The functional significance, if any, of the frequent formation or retention of the fontanelle in so many ostariophysans of hill-stream habitat remains enigmatic. Sagemahl (1991) concluded that the fontanelle was "insignificant". Ramaswami (1952:1) suggested that the fontanelle may have "some physiological purpose in hill stream and burrowing forms, and other loaches". The fontanelle may help to dissipate pressure stresses through the braincase of bottom living forms. However in the Noemachilini and generally, I note the consistent association of the fontanelle with the part of the supraoccipital margin through which runs the transverse temporal sensory canal, except in *Noemacheilus nigromaculatus*. This species is also peculiar in that it is one of the few noemacheilines in which the posterior part of the cephalic canal system runs over the head in the skin, and not in the skull roof bones (see p.224). I suggest there may be some functional coordination between the fontanelle and the sensory canal system.
Ossifications Associated with the Cephalic Sensory Canal System

The remaining dermal skull roof ossifications of cobitoids including the circumorbital bones have immediate association with the cephalic sensory canal system. The cephalic sensory canal system of cobitoids is distinctive in two general features. Firstly the ossifications carrying the sensory canals - especially the circumorbital bones, reduce and tend to become tube-like. The second feature is that the sensory canals, with or without the tube-like ossifications in their walls, tend to become altogether separated from the skull roof bones and to course through the skin.

It should be pointed out that reduction of the cephalic canal carrying ossifications to tube-like bones is not unique to cobitoids. This development appears to have occurred many times in the Ostariophysi. Howes [1978, 1980] discussed the presence of tubular infraorbitals in several groups of cyprinids. From a study on catfish Alexander [1965] concluded that tubular infraorbitals represent a very general adaptation to a bottom-living habit in Ostariophysi. Tilak [1963] concluded that infraorbital reduction is actually primarily an adaptive response to torrentiality, rather than to the bottom habit, and it seems clear that the development of tubular infraorbitals in Ostariophysi has occurred accompanying more than one other development.

Some dissociation of the sensory canals from the skull is also not unique to cobitoids, but has occurred in several bottom living Ostariophysi. The condition is most fully
realised in the Catostomidae in which the canal system is entirely integumental. The canal system is largely integumental in many noemacheilid and cobitine cobitoids, but in the Botini the canal system lies within the bones of the skull roof.

In general terms, the layout of the cephalic canals of cobitoid fishes is similar to that described by Gosline [1974] as the basic cyprinid type with the canals forming a single interconnected system over the head. However, particularly anteriorly, the sensory canals of cobitoids are arranged distinctly differently from those of a typical cyprinid, and this anterior portion of the sensory canal system is described below.

In all noemacheilines the anteroterminal parts of the frontoparietal and infraorbital canals converge. These two canals both pass into a lightly ossified triangular plate-like bone which lies anterior to, and is usually completely separately from, the lachrymal bone.

In all noemacheilids the lachrymal does not carry a canal. It is usually a long oval or triangular bone lying between the lateral ethmoid posteriorly, the triangular ossification described above anteriorly and the frontoparietal and infraorbital canals above it and below it respectively [see figs iii-vi]. In homalopterines, and especially gastromyzonines the lachrymal is often extraordinarily developed into a bumper-like structure which affords mechanical protection for the anterior part of the skull [see Ramaswami, 1952:3 and 4 and figs.xliiiic and d].

In the cobitines there is frequently no trace of
ossification in the walls of the anterior of the frontoparietal and of the infraorbital canals. However, these two canals can be seen to open towards each other anteriorly. In Acanthopsis this portion of the canal system is enclosed in a triangular plate-like bone resembling that of the noemachelines [fig.xb].

In all Cobitini the lachrymal is present in the same position that it is in Noemachelines. In the Cobitini the lachrymal is a long slim falciform bone which apparently acts as a lever in the operation of the suborbital spine (see Chranilov, 1928, and p.193).

In the Botini the arrangement of the anterior part of the sensory canal system is very similar to that of the Noemachelines (see figs xii and xiii).

It is not possible to interpret the anatomy of the anterior canal system of cobitoids without identifying the ossifications associated with it, and the homology and derivation of the anterior bones associated with the circumorbital bone of teleosts is not very clearly established. Nelson (1969b) discussed some aspects of this problem. It appears most likely that the anterior, triangular, canal-carrying plate of bone described in the noemachelines and in the Botini is an antorbital. Ramaswami (1948) identified it as such in the homalopterines, but referred to what appears to be the same bone in cobitids as a rostral ([1953].

The antorbital described in Amia (Allis, 1898) is canal bearing, as it is also in the indeterminate paraseminotic illustrated by Patterson (1975) where it is clearly shown to contain the anterior termination of both the supra
and infra-orbital canals. Weitzman (1962) described an antorbital in the characin *Brycon meeki* which does not contain a canal, but he pointed out that a short part of the termination of the infraorbital canal does invade a bone in the same position in *Brycon alburnus*. Gosline (1961) concluded that the antorbital of *Amia* is actually compounded of two lateral rostral bones and the antorbital of *Elopes* (Westall, 1937). Gosline suggested that the antorbital is rather widespread amongst lower teleosts, but is apparently incorporated into the lachrymal in higher forms, and then usually reduces or loses its sensory canal. An antorbital ossification is unknown in the Cyprinidae. The retention of the antorbital in many cobitoids seems to be an adaptation of the anterior sensory canal system or primarily bottom living forms.

The lachrymal of cobitoids appears to have lost all immediate association with a sensory canal and this condition is very unusual. Its unusualness is emphasised if this part of the sensory canal system of cobitoids is compared with that of representatives of ostariophysan outgroups. In cyprinids and in the hill-stream taxa *Psilorhynchus* and *Gyrinocheilus* the lachrymal is frequently large but always contains the anterior or lachrymal part of the infraorbital canal. In the catfish *Glyptothorax* the frontoparietal and infraorbital canals are both enclosed in the lachrymal. In *Parakneria* it appears that the lachrymal is extremely reduced and present only as ossification in the wall of the anterior sensory canal [Lenglet, 1974].
In an alizarin preparation of *Catostomus* the canal system cannot be seen because it is integumental in position. However there is a large lachrymal plate in catostomids [see Weisel, 1960], which resembles that of the noemachelines. Some fibres from the A1 division of the *adductor mandibulae* [see p.50] insert onto the lachrymal in *Catostomus*.

In the gymnotids the ethmoid region is very unusual [see fig.2A and b]. However it appears that in this taxon a bony plate identified as the lachrymal provides the insertion for the whole of the A1 division of the *adductor mandibulae* [p.77], and no canal passes through this lachrymal ossification.

In light of the very varied anatomy of the anterior part of the cephalic sensory canal system throughout the teleosts the significance of the lack of immediacy of the association of the lachrymal bone with its canal as in cobitoids is not easy to assess. However, it appears that a strong ossification in the position of the lachrymal, in which sensory canals are not contained, is a feature shared by the cobitoids, gymnotids, and catostomids. It further appears that in each of these taxa the lachrymal serves at least in part a peculiar mechanical function and frequently has fibres from the *adductor mandibulae* inserting onto it. From this it can be put forward as an interesting hypothesis that the cobitoids, catostomids and gymnotids comprise a natural assemblage. The possibility of this is further discussed on p.345-6.

The more posterior part of the cephalic sensory canal
system of cobitoids shows fewer distinctive features than
the anterior portion. In all cobitoids the frontoparietal
canal passes over the olfactory capsule in a lightly
ossified, tubular nasal bone. There is a similar tubular
nasal bone in many ostariophyseans. The frontoparietal
canal passes through the brow of the frontal bone in all
noemacheilids except for Lefua, Noemacheilus yarkandensis
and N. nigromaculatus in which this part of the canal
system is integumental. In Oronectes and Vaillantella
the frontoparietal canal only enters the frontal bone for
a short portion of its length. These 5 species above are
also unusual amongst noemacheilids in that the whole of
the posterior part of the sensory canal system is dissociated
from the skull roof. In the Cobitini the frontoparietal
canal passes through the skin over the frontal bone
while, by contrast, in all Botini the frontoparietal canal
passes through the frontal bone.

The frontoparietal and infraorbital canals join and
pass posteriorly as the temporal canal. In cobitoids, as
in many cyprinids, the junction above is achieved in a
triradiate ossification which is frequently disposed con-
siderably lateral to the sphenotic, and presumably consists
largely of the dermosphenotic. Ramaswami (1957) noted that
the sphenotic part of the temporal canal was detached from
the surface of the bone in all Cyprininae except Esomus,
and also in Gyrinocheilus, Psilorhynchus, the gobioines,
and homalopterids as well as in the cobitids.

The preopercular canal of cobitoids also tends to
become integumentally disposed. In the noemacheilids
there may be traces of supraperiopercular ossification in the wall of the proximal part of the preopercular canal. In these the preopercular canal usually does not enter the preoperculum but passes through the skin lateral to it. It is however contained in the bone in *Noemacheilus botia*, *N. fasciata*, and *Ellopostoma*. In Cobitini all this part of the canal system is invisible in the skin. In the Botini, the supraperiopercular may be present as one, two or three tubular ossicles and in Botini the preopercular invariably enters the preoperculum.

In some cobitoids there are ossifications in the wall of the preopercular sensory canal distal to the preoperculum itself. Mahajan (1966) described a condition in *Sisor* in which the preoperculum fails to meet the angular-quadrate articulation, and so "inferior preopercular" ossifications develop round the gap. Ramaswami (1952:3 and 4; 1953) also described such ossifications in several homalopterines, gastromyzonines and cobitids. I record two or three of these ossicles in *Orthrias*, *Noemacheilus fasciatus* and *N. strauchi*. Distal to these in all cobitoids, are very light ossifications around the dentary sensory canal by the side of the lower jaw.

Posterior to the origin of the preopercular canal there is some variation in the extent to which the sensory canal system is separate from the bones of the skull roof, and in the ossification present in its walls, although there is no variation in the basic layout of this part of the system in cobitoids.

Ramaswami (1952:3) described 3 ossifications across the
temporal region of homalopterines, and emphasised that, because of the intimate relationship these have with the posterior temporal canals, individual dermal elements in this region are not very readily identifiable. Ramaswami (1948) suggested 3 bones he observed should be called "lateral, anterior, and posterior extrascapulars" according to their position, but he concluded in (1952:3) with regard to the cyprinid homologues of these bones that that bone between the supracleithrum and skull was actually the posttemporal, the element medial to this was the supratemporal, and the most lateral was the lateral extrascapula, lying between the temporal and lateral line canals. Ramaswami's (1952:3) nomenclature is followed here.

In the noemacheilids the supratemporal is usually developed as a triradiate tube of bone from which the transverse occipital canal passes through the posterior border of the parietal. The transverse occipital canal then enters the anterior border of the supraoccipital, except in the case of the species listed on p.146 in which this part of the system is in the skin. In Elloiopostoma [fig.Lxxia] the supratemporal is an unusually well-developed rectangular plate of bone and in this species a lateral extrascapula is also better represented than in other noemacheilids.

Of the Cobitini, in Acanthopsis the posterior part of the canal system is free from the skull and its associated bones are reduced to minute traces of ossification in the canal walls. In all other Cobitini this part of the canal system is also free from the skull and the ossification
associated with it is lost.

In the Botini a supratemporal and large posttemporal are present, and the lateral extrascapular ossification is also robust [see fig.Lxiib and c].

In all the noemacheilid and botine fishes, but in no Cobitini, there is some ossification in the wall of the proximal lateral line, taking the form of a series of ossicles resembling chain-linking. Similar ossifications also develop in other Ostariophysi. In many catfish these chain-like ossifications continue to the caudal, while in the gymnotids, and in Gyrinocheilus and some Gobioinae only 2 or 3 such elements in the wall of the lateral line are present, immediately distal to the supracleithrum.

Ossification in the wall of the lateral line appears to be an adaptation associated with the bottom habit.

Note is made of two other superficial dermal ossifications which are occasionally present in the orbital region of cobitoids.

A supraorbital in which no canal is contained is present in all representatives of the Cobitini. It is a falciform ossification lateral to the frontal. A supraorbital is also present in some homalopterines (Ramaswami, 1952:3). It is present in Ellopostoma, but absent from all gastromyzonines (Ramaswami, 1952:4) and all other cobitoids. Fang [1935a] described both a supraorbital and discreet "isodiametric praeorbital" in Misgurnus, considering the latter to indicate the primitive status of the genus. I have been unable to find the ossification in question.

Fink & Fink [1981] considered the absence of a supra-
orbital from gymnotids and siluroids as a derived feature shared by these two groups, because the bone is present in primitive gonorrhynchiforms, cypriniforms and characiforms, and in primitive teleosts generally. I note the absence of a supraorbital from *Catostomus* as well as some cobitoids, and I conclude that while its presence is plesiomorphic amongst Ostariophysi, its occasional distribution, especially within the cobitoids, forbids the use of its absence as a character to indicate ostariophysean interrelationships.

Orbital sclerotic ossifications are present in most cobitoids. Fink & Fink (1981) recorded the widespread distribution of these in primitive teleosts, and considered the absence of sclerotic ossifications from gymnotids, and siluroids as shared derived and characteristic of the two groups. These ossifications are also absent from *Lefua* and *Vaillantella*, and many Cobitini, and thus their loss may be derived, but is not unique with the Ostariophysi.

**Posttemporal**

In noemacheilids the posttemporal is typically a small, flat, boot-shaped bone, articulating with the skull rather loosely over, or close to the pterotic-epioccipital suture (fig.Lxiiia). The posttemporal is particularly small in the noemacheilids of hill-stream habit. The posttemporal is a long slim splint of bone in *Vaillantella*. In *Ellopostoma* (fig. Lxiiia) the posttemporal is a large horizontal rectangular plate, lying on the epioccipital, and is stabilised anteriorly by the large lateral extrascapula.
bone which is present in this species.

In the Cobitini the posttemporal is reduced. It is firmly attached to the skull; apparently it is fused to the skull in *Misgurnus* species (Gosline, 1977). Bacescu [1970] stated that the posttemporal to be absent in *M. fossilis* and *M. errikssonii*. I note that a posttemporal is present in *M. anguillicaudatus*, as a small triangular plate which is very tightly attached to the skull. In *Misgurnus anguillicaudatus* the supracleithrum makes an articulation on the epioccipital in which the posttemporal does not participate. Usually in Cobitini the posttemporal has the form of a small, flat, hiliform plate which is slightly expanded ventrally where it is secured between the exoccipital and the pterotic (fig. Lxiid). In *Acanthopsis* and *Somileptes* additional braincase features associated with the articulation of the posttemporal develop (fig. Lv, p. 219).

In the Botini the posttemporal is a comparatively large, but flat and simple bone which articulates onto the side of the head. In *Leptobotia elongata* and *Botia almorhae* a peculiar elaborate articular surface for the posttemporal derived from the parietal and epioccipital bones is present (p. 212, fig. Lxiic). Usually in Botini the posttemporal articulates on a flat facet on the epioccipital.

I cannot confirm the observation of Bacescu [1970] that in male *Noemacheilus barbatulus* specimens here is sometimes an upper prolongation of the posttemporal which is "reminiscent of the bifurcation of this bone in cyprinids". I find no indication of forking of the posttemporal in any
cobitoid. An unforked posttemporal is the plesiomorphic ostariophysean condition, while the posttemporal of cyprinids is characteristically forked. I suggest the absence of forking of the cobitoid posttemporal emphasises the separateness of the cobitoids and the cyprinids.

THE PECTORAL GIRDLE

Supracleithrum

In the Noemacheilini the supracleithrum is a rather broad, short oval bone. It lies lateral to the upper two-thirds of the ascending limb of the cleithrum. The supracleithrum has an ascending process which lies medial to the saddle articulation formed between the supracleithrum and the posttemporal. The ascending process of the supracleithrum is absent in Lefua, Oronectes and Noemacheilus nigromaculatus [Fig.Lxiiib and c]. In these 3 species it appears that the supracleithrum can achieve a particularly extensive range of movements about its dorsal articulation with the posttemporal, because this dorsal articulation has the form of a ball-and-socket joint.

In the homalopterines and, to an ever greater extent, in the gastromyzonines, the pectoral girdle as a whole is modified to allow the use of the pectoral fins to cling to rocks in torrential streams. In homalopterines and gastromyzonines the supracleithrum is usually a broad robust plate of bone.

In Cobitini the supracleithrum is an elongate strong, slim falciform bone. It is disposed vertically and lies lateral to the upper four-fifths of the ascending cleithrum.
limb. Dorsally the supracleithrum forms a saddle joint with the posttemporal, and this articulation takes place between the blunt ventral process of the pterotic and exoccipital bones described on p.230. The supracleithrum is of this type in all Cobitini except in Somileptes where the bone is a comparatively loosely articulated and oval bone. The supracleithrum is oval in Leptobotia, Botia almorhae and B. macracantha. In most Botia the supracleithrum is strongly falciform in shape. The ascending part of the bone is invariably present.

Postcleithrum

The postcleithrum is absent in most cobitoids. There is however a single postcleithrum present in all representatives of Botini except Leptobotia elongata, in which the postcleithrum is absent. The presence of a postcleithrum in the Botini led Bacescu (1970) to conclude that the Botini were the most primitive of the cobitids, and that in possessing a single post-cleithrum the Botini demonstrated the cyprinid ancestry of the Cobitidae. However, Gosline (1977) showed that there is a tendency for postcleithra to be lost in Ostariophysi where the supracleithrum is strongly falciform in shape. Brousseau (1976) indicated that the three postcleithra formed in the characin Piranha demonstrated the generalised ostariophysean condition, and that reduction in postcleithra was a derived condition, and Fink & Fink (1981) suggested that postcleithral reduction has occurred more than once independently in the Ostariophysi. I am led to conclude that the
presence or absence of a postcleithrum is a poor indicator of phylogeny, and suggest that the presence of a postcleithrum in the Botini can be attributed to the fact that the pectoral girdle in these is generally less derived than in other cobitoids.

Cleithrum

Howes (1980) pointed out that the most variable feature in the construction of the cyprinid pectoral girdle is the relative length of the horizontal, and vertical limbs of the cleithrum. The relative lengths of these parts is also very variable within the cobitoids. The polarity of this variability within the Ostariophysi is however not well established. Broussseau (1976) suggested that a relatively long ascending limb of the cleithrum, as in the characin Piranha represented the generalised ostariophysan condition and that elongation of the horizontal limb (accompanied by obliteration of the coracoid and cleithral oblique laminae, and the coracocleithral foramen) as in e.g. gymnotids, should therefore be interpreted as the derived ostariophysan condition. Bacescu (1970, 1973) maintained that within the cobitids a comparatively long horizontal cleithral limb was the primitive condition. Howes (1980) indicated a short broad ascending cleithral limb in Opsariichthys, and suggested that this represents the generalised cyprinid condition.

In the noemacheilids (see fig.Lxiv) the horizontal cleithral limb is as long as or longer than the vertical or ascending cleithral limb, with this ratio increased in
the more flattened forms. *Ellopostoma* differs from all other noemacheilids as in this species the horizontal limb of the cleithrum appears to be truncated, and is shorter than the vertical limb (Fig. Lxivc).

In all the Cobitini the ascending limb of the cleithrum is invariably considerably longer than the horizontal limb.

In the Botiri with the exception of *Leptobotia elongata*, the ascending limb of the cleithrum is slightly longer than the horizontal limb. In *Leptobotia elongata* the horizontal limb is substantially drawn forward, and elongated.

The proportions of the cleithrum of cobitids led Bacescu (1970) to conclude that the Noemacheilini were the most primitive, and the Cobitini the most derived of the Cobitidae. My own conclusion is that the proportions of the cleithrum of cobitoids vary according to habitat and in accompaniment to the general proportions of the pectoral region, and are not per se reliable indicators of phylogeny.

The extent of derivation of the ostariophysian pectoral girdle is also considered to be shown by the extent of lamina development on its major component bones. The laminae of the cleithra are discussed below, following the terminology of Brousseau (1976).

In Noemacheilini the posterior lamino of the cleithrum is always present, usually as a triangular flange of bone extending from its external angle. In *Noemacheilus montanus* (Fig. Lxiva) and *N. rupecola* the posterior lamina curves medially, and forms a shallow dome ventrally. The lateral lamina of the cleithrum is well-developed in
Noemacheilini especially in the more flattened species. The oblique lamina of the cleithrum, which extends towards the coracoid is variably developed in Noemacheilini. Sometimes it is only present as a ridge on the horizontal limb of the cleithrum, but it is never entirely absent.

The development of the coraco-cleithral foramen clearly affects the development of the oblique lamina of the cleithrum. The coraco-cleithral or anterior foramen is not present in all cobitids. Bacescu (1973) emphasised the absence of an anterior pectoral foramen from many Noemacheilini, and he considered that the presence of the foramen in the noemacheilin subtaxa Acanthocobitis and Schistura "recommend these as separate and generalised noemacheilin forms, with regard to Oronectes, in which the foramen is closed". I note that the anterior pectoral foramen is actually usually closed in Noemacheilini. I record the presence of the foramen only in Aborichthys and Orthrias as well as representatives of the subgeneric taxa Acanthocobitis and Schistura. I follow Brousseau (1976) in interpreting the loss of this foramen as a derived condition of multiple occurrence within Ostariophysi.

The cleithra of other noemacheilids show some features in contrast with those of typical noemacheilines. On the cleithrum of Vaillantella the posterior and lateral laminae are low. Both the oblique lamina and the anterior foramen are present.

In Ellopostoma (fig.Lxivc) both the oblique lamina and the anterior foramen are absent. The lateral and horizontal laminae of the cleithrum are both well-developed. The
horizontal lamina has a notch just below where mesocorocoid articulates with it. A similar notch on the cleithrum was described in the cyprinids Abramis and Xenocypris (Howes, 1981) and in these the notch accommodates the dorsal part of the inferior pharyngeal bone.

In Glaniopsis [fig.Lxivb] the lateral and horizontal laminae of the cleithrum are extensive. Both the oblique lamina and the anterior foramen are present. In Glaniopsis the posterior lamina of the cleithrum forms a facet which articulates with the swimbladder capsule on each side. This articulation between the capsule and shoulder girdle is also made in homalopterines and gastromyzonines. Homalopterid pectoral girdles are frequently extremely highly derived structures and in this I have not had the material available with which to be able to compare satisfactorily osteological development of these with pectoral girdles of other cobitoids. Homalopterid pectoral morphology is discussed by Hora [1922a] and Chang [1945].

In the Cobitini the ascending cleithral limb is falciform and alaminate. The lateral lamina of Cobitini is however not entirely absent as indicated by Bacescu [1973] but is produced as a strong spur or horn from the horizontal cleithral limb. This spur is present in all Cobitini.

In many Cobitini there is also a spur-like process on the medial face of the horizontal limb of the cleithrum [fig.Lxvia]. This process is absent in Misgurnus, Cobitis, Niwaella, Sabanejewia, and per se in Acanthopsis. However, Acanthopsis choiophrynchus [fig.Lxva] shows a peculiar long
separate ossified splint of bone in this position. The derivation of this splint is unknown. It is somewhat similar to a postcleithrum in appearance, but its relations suggest that it is homologous with the medial spur described above, which has developed as a sesamoid ossification of the pectoral adductor muscle. In all Cobitini the oblique lamina of the cleithrum is very reduced. It is usually present as a digitiform process of bone, extending towards the coracoid, more or less excluding the scapula from the posterior border of the anterior foramen. The anterior foramen is invariably present in Cobitini.

In Botini the lateral lamina of the cleithrum is fully developed. In Botini the oblique lamina of the cleithrum and the anterior foramen are also always present. The anterior part of the girdle is rather deep and particularly so in B. almorhae (fig.Lxvb).

It appears that many of the variations observed on the cleithra of cobitoids have occurred many times both within the group, and also within the Ostariophysi and thus cannot be used to indicate phylogeny at this level. Both Rendahl (1933) and Bacescu (1970,1973) used variation of general features of pectoral morphology to indicate possible cobitid phylogeny. Under cladistic analysis the conclusions of these two authors, based on such general characteristics, are not valid.

I suggest that some features of cobitoid cleithral morphology are apomorphic and may be used to indicate relationships within the group. These features are as follows:
The articulation between the cleithrum and the swim bladder capsule in *Glaniopsis* and in homalopterines and gastromyzonines does not develop in the Noemachilini, nor is the articulation known outside the cobitoid group. It is considered as a possible character on p. 333.

The reduction of the lateral lamina to a spur-like process occurs in all cobitines, but not outside this group. This is therefore interpreted as a synapomorphy uniting the Cobitini (p. 336).

The production of the horizontal lamina as a spur-like process occurs in some, but not all Cobitini. I suggest the Cobitini can be divided on the presence or absence of this process (p. 337).

Scapula

In cobitoids the scapula is invariably more or less quadrilateral in shape. It articulates with the cleithrum and coracoid, and surrounds a round foramen which occasionally excavates the posterior edge of the cleithrum. The scapula may have a triangular ascending process posterior to the cleithrum. The scapula is thickened adjacent to the coracoid, and this part contributes more or less half the low mesocoracoid pedestal.

The scapula forms the glenoid socket for the articulation of the dorsal head of the first ray \([R + 1]\). The depth of the glenoid socket clearly is correlated with the range of movement of the leading pectoral fin edge which is possible for a given species. When the glenoid socket is deep, \(R + 1\) makes a ball-and-socket articulation
and a full range of fin movements is possible.

Brousseau (1976) considered that a limited range of movement of the leading pectoral fin edge is a derived ostariophysean condition. Brousseau suggested that the plesiomorphic ostariophysean scapula has a long external scapular margin, and a well-developed "eminentia glenoidalis" i.e. a deep glenoid socket. Bacescu (1973) commented on the presence of a long external scapular margin and a well-developed eminentia glenoidalis in Botini. He considered that these scapular features are usually developed to some degree in Noemacheilini but are always absent in Cobitini, and he concluded that, on the basis of these developments, the Noemacheilini, Botini and Cobitini were indicated as a sequentially derived series. However, I note that the extent of development of eminentia glenoidalis is graded throughout the cobitoids, and is related to the nature of the articulation of R + 1, and to the general body form and swimming mode. This articulation is more or less condylar in Botini, semi-condylar in noemacheilines, and of saddle-type in cobitines, with all intermediate types represented. I follow Brousseau (1976) in interpreting the form of the glenoid cavity as a correlate of fin mobility, and inappropriate for use as a cladistic character in indicating phylogeny.

Coracoid

In its plesiomorph form the coracoid of Ostariophysi is reflected ventrally to form a vertical lamina, and towards the cleithrum to form an oblique lamina (Brousseau,
It contributes to the border of the anterior foramen when this is present \[\text{see p.262}\]. Reduction of the oblique and vertical laminae and, in correlation with this, reduction of the external margin of the coracoid \[\text{as its posterior apposition with the scapula is increased}\] are interpreted as derived conditions for Ostariophysi \[\text{[Brousseau, 1976]}\].

In the Noemacheilini the coracoid is more or less shaft-like. It has a short external margin, and effectively no vertical reflection. Oblique lamination is present only where the coracoid meets the cleithrum across the posterior border of the anterior foramen, when this is present \[\text{see p.262}\]. Anteriorly the coracoid shaft articulates synchondrotically with the cleithrum.

The coracoid of Vaillantella resembles that of a typical Noemacheilus. In Elopostoma there is a well-defined spur of bone projecting from the coracoid ventrally. This spur represents the residue of the vertical lamina. In Glaniopsis a short vertical lamina is also present.

In the Cobitini the coracoid has the form of a bar of bone which is slightly expanded posteriorly. No vertical lamina is produced.

In Botini the coracoid is rather short and robust. It has a strongly defined triangular prong projecting postero-ventrally which represents the vertical lamina. The oblique lamina of the coracoid is clearly defined. The peculiarly deep anterior pectoral fenestra of B. almorhae is enclosed anteriorly by an additional short flange on the coracoid which meets a similar flange of the cleithrum.
It appears that the sort of variations in coracoid morphology shown by the cobitoids have occurred many times within the Ostariophysi (Brousseau, 1976) and these variations cannot be used to indicate cobitoid ingroup phylogeny.

Mesocoracoid

The plesiomorphic form of this bone in Ostariophysi is a broad shaft which has a ventral basal lamina, and a dorsal foot plate, and constitutes an arch across the medial aspect of the pectoral girdle. The proportions of the mesocoracoid vary considerably both within the cobitoids, and within the Ostariophysi generally.

In the Noemacheilini the mesocoracoid is short and strong. Its dorsal foot plate tends to expand obliquely across the dorsomedial aspect of the cleithrum and to pass a descending portion to meet the scapula posteroventrally. In Noemacheilini of non-torrential habitat and in the other noemacheilid species, Vaillantella and Ellopostoma the mesocoracoid is rather poorly developed.

In the Cobitini the mesocoracoid is a slim shaft-like bone. It is Y-shaped, as it makes its dorsal [cleithral] articulation via one limb which descends and articulates with the scapula, and a digitiform extension which ascends across the medial cleithral face.

In Botini the mesocoracoid is of the plesiomorphic type.

Pectoral Fin

In its plesiomorph condition the ostariophysean
pectoral fin articulates with the pectoral girdle via 4 proximal radials and numerous irregular distal radials (Brousseau, 1976). Within the Ostariophysi numerical reduction, and consolidation of these radial elements and a reduction in the full range of fin movement possible has occurred many times, accompanying e.g. a bottom, or digging, or torrential habit, and a variety of specialisations, e.g. the formation of pectoral spines (as in catfish).

In Noemacheilini there are usually 4 proximal radials but a reduction to 3 is recorded in N. barbatulus, N. strauchi and N. stoliczkae. I do not agree with Dacescu (1973) who suggested that a reduction to 3 proximal radials is, amongst Noemacheilini, peculiarly characteristic of the subgenus Acanthocobitis, (which here is represented by N. botia).

In Vaillantella there are 4 proximal radials. There are 3 proximal radials in Ellopostoma, and 4 in Glaniopsis.

When 4 proximal radials are present in noemacheilids generally, typically the lateral 2 of these radial elements articulate with the scapula, and the 3rd and 4th with the coracoid. A derived condition is evident in the noemacheilines Aborichthys, Lefua, Oronectes, Noemacheilus nigromaculatus and N. yarkandensis. In these species the medial 2 proximal radials produce flanges which extend over their neighbours, and articulate exclusively with them rather than with the main pectoral girdle. This arrangement apparently decreases the strength of the articulation of the pectoral fin, but increases the potential for anterior...
and horizontal placement of the fin.

The number of distal radials present in the noemacheilids varies between 8, of which only the most lateral ossify, and none. There is considerable intraspecific variation in the number of distal radials present.

The head of the first dorsal ray \((R + 1)\) in noemacheilids, has a triangular ascending process, a semi-condylar glenoid articular head, and an elongate medial glenoid process, a small ventrolateral flange, and a basal medial thickening, which abuts either the first radial ball, or \(D + 2\). The head of \(R + 1\) is illustrated in *N. barbatulus* by Bacescu [1970].

In Noemacheilini there are 10-13 pectoral fin rays of which the ventral series tend to be the more robust.

In the Cobitini the pectoral fin articulates *via* 4 proximal radials only in *Misgurnus*. In all other Cobitini there are 3 proximal radials of which the 2nd and 3rd may fuse. The 1st distal radial is usually large and well-ossified, but the remainder of distal radial series is reduced.

The males of some cobitine taxa display peculiar developments of their pectoral fin osteology which are sometimes accompanied by developments in the pectoral girdle. Descriptions of these developments were given by Ikeda [1936]. The manifestation of this sexual dimorphism has been used to suggest the differentiation of the Cobitini at the \(\phi\)-taxonomic level [see e.g. Banarescu & Nalbant, 1964, 1966, Bianco & Nalbant, 1980] and the potential usefulness of this is discussed below.
Nalbant (1963) pointed out that sexual dimorphism is
evident in the pectoral osteology of Misgurnus, Cobitis and
of Lepidocephalus, but does not occur in Sabanejewia,
Niwaella, Acanthopsis, Somileptes or Acanthophthalmus.
However neither he, nor apparently any other author, has
considered the possibility of elucidating intergeneric
relationships of Cobitini on the basis of their various
pectoral sexually dimorphic characteristics.

In Misgurnus the pectoral sexual feature has the form
of a round plate of bone which develops from the base of
D + 2 ray of the male (fig.Lxvib). This plate is called the
lamina circularis. It extends medially lying over the sub-
sequent D + ray series. Okada (1960) illustrated slightly
different forms of the lamina circularis in Misgurnus
fossilis anguillicaudatus and in M. anguillicaudatus. He
emphasised that the lamina circularis has never been re-
corded in the European representative of Misgurnus, M.
fossilis, but did not comment on the significance of this.

In the genus Cobitis the pectoral sexual feature is
usually referred to as the organ of Canestrini. This is
produced as some sort of tentacular swelling from the base
of D + 2, i.e. in the same position as the lamina circularis
of Misgurnus. Okada (1960) illustrated an alomorphic
series of the organ of Canestrini in Cobitis biwae, and
Cobitis taenia matsuburee. Okada considered two parts of
the organ of Canestrini of Cobitis to be distinct - one
part of which was beak-shaped and apical and the other part
which was round and basal. Okada suggested that these two
parts of the organ are each subject to differential
development in *Cobitis* species, and that its variation could be used as a systematic tool.

Bacescu (1961) proposed a reclassification of the European species of *Cobitis* on the basis of the form of the organs of Canestrini. Bacescu suggested that subgenera *Sabanajewia* and *Acanestriniia* could be distinguished from other *Cobitis* by the absence of sexual dimorphism in these. He suggested that the species of the subgenus *Cobitis* displayed a single organ of Canestrini, while the organ in the subgenus *Bicanestriniia* appeared to be double. Bacescu identified a peculiarly specialised "evacuated" organ of Canestrini as characteristic of a cobitine subgenus *Ibercobitis*. Bacescu further suggested that species and subspecies of these subgenera of *Cobitis* could be differentiated by the various shapes of their distinctive type of organ of Canestrini.

The reliability of basing classification on this sort of sexual development is questionable because the intercategoric variability of such a development may be considerable. Lodi (1979) discussed the variability of the Canestrini organ within the species *Cobitis teenia*, by comparing the organ in the Ct. *puta* and Ct. *bilineata* subspecies recognised by Bacescu (1961). Lodi concluded that there was a significant morphometric difference between the organ of Canestrini in these two subspecies, but that the males in *bilineata* livery in which the organ is the rather larger, also show higher blood androgen levels than the *puta* males. It seems that until the morphological stability of the organ of Canestrini is established, with
regard to the age, growth, ecology and endocrinology of Cobitis, its variability should be treated with caution as an indicator of the \( \alpha \)-level differentiation of the genus.

The form of the pectoral sexual feature of Lepidcephalus is illustrated [fig. Lxvia]. It involves modification of the terminal pectoral fin rays into a scoop-like structure. Comparison of the pectoral osteology of male and female Lepidcephalus specimens show that this scoop is formed by fusion of \( R \cdot 7 \) and 8 and is accompanied by reduction of the radial elements and by fusion of the supportive girdle elements (scapula, coracoid and cleithrum). The scoop-like structure is bound to the pectoral girdle by a very strong ligament.

In addition to the pectoral sexual features described above in Misgurnus, Cobitis and Lepidcephalus, I note a development in the skeleton of the pectoral fin of a male specimen of Acanthophthalmus muraeniformis in which the 2nd and 3rd proximal radials are clearly fused together, the 1st ray fuses into a compound elemental \( R \cdot 1 \), and \( R + 2 \) is slightly remiform. I have found no record of this development in the literature [fig. Lxvie].

In the Cobitini in which the pectoral fin does not show the peculiar modifications described above the 1st and 2nd proximal radials articulate with the scapula, and the 3rd articulates with the 2nd.

There are between 8 and 11 pectoral fin rays in Cobitini of which the ventral \([R-]\) series is the more robust. The head of \( R + 1 \) has the same processes in Cobitini as it does in Noemachetilini.
In all the Botini the pectoral fin articulates via 4 proximal radials. In Leptobotia and B. almorhae the first 2 proximal radials articulate with the scapula, and the 3rd and 4th proximal radials abut the coracoid. In other Botini all 4 proximal radials articulate with the scapula.

The pectoral fin of Botini apparently can make a wider range of movements than the pectoral fin of other cobitoids. In Botini the articulation of D + 1 with the glenoid is a ball-and-socket joint. The head of D + 1 bears similar processes to those described for Noemacheilini. There are up to 16 distal radials developed in Botini, and 12-16 pectoral fin rays.

General trends of development shown in the arrangement of the pectoral fins of cobitoid fishes can be interpreted as correlates of habitat, and compared with similar trends shown on the pectoral girdles of other Ostariophysi [see e.g. Hora, (1930), Chang, (1945), Bhatia (1950) and Mahajan, (1971)]. For instance, an increase in coracoid contribution to the fin articulation is correlated with elongation of the posterior coraco-scapula apposition and promotes horizontal placement of the fins. Typically in the free-living Botia none of the proximal radials articulate with the coracoid, while in many bottom living Noemacheilini the medial proximal radials do articulate with that bone. In this respect the pectoral girdle of Catastomus and of some gobioines very much resembles that of the Noemacheilini.

The sexually dimorphic developments described in the pectoral fins of cobitines appear to be specialisations peculiar to this group. Of these the scoop-like structure
developed in male *Lepidocephalus* appears to be unique to, and to provide definition of this genus *(fig. xCff)*.

Furthermore, I tentatively suggest that the developments on D + 2 of the male *Cobitis* (the organ of Canestrini) and *Misgurnus* (the lamina circularis) indicates that these 2 genera are more closely related to each other than they are to any other Cobitini. However, the apparent absence of a pectoral sexual feature from some species of these taxa needs further study (see p.339).

The pectoral sexual feature described in *Acanthophthalmus muraeniformis* appears to be autapomorphic.

**PELVIC GIRDLE** *(fig. Lxvii)*

In all cobitoids the pelvic girdle consists of a pair of archipterygial plates each of which is usually, but not invariably, bifid anteriorly. The archipterygium is forked in all cyprinids *(Howes, 1980)* but is unforked in characins and kneriids.

The shape of the archipterygia is variable in the cobitoids. *Bacescu* *(1972)* discussed this variability and concluded it was possible to gain an understanding of cobitid phylogeny from pelvic morphology.

*Bacescu* *(1972)* suggested that the noemacheiline pelvis is characterised by development of strong posterior processes, which he called "os coxaux" and which are here called ischial processes. *Bacescu* pointed out a reduction in the formation of a median aperture between the archipterygia, an increased length of apposition of the archipterygia in the mid-line, and increased interdigitation
at the pelvic symphysis. He concluded that these modifications acted together to produce a strong pelvic fin in Noemacheilini which was adapted for "climbing in hill-streams", and that in this feature the Noemacheilini showed convergence with cyprinids and siluroids of similar habit.

I note a wide range of pelvic morphology throughout the noemacheilids. The most common form is as described as typical for *Noemacheilus* by Bacescu (1972), and shown in fig. Lxviia). However, a median pelvic aperture is present in several non-torrential *Noemacheilus* species. The ischial processes are usually well-defined. They are short, broad and usually appose, and are serrated in *Noemacheilus barbatulus*, *N. denisonii*, *N. montanus* and *Oronectes*. The pelvis is unusual in *N. stoliczkae*, *N. strauchi* (fig. Lxviiib) and *N. yarkandensis*. In these species each archipterygium is rectangular and squared anteriorly so that bifurcation is obliterated. The ischial processes are triangular and closely appose and each ischial process is strongly cupped dorsally.

In all Noemacheilini there are 7, 8 or 9 pelvic rays, and there is also invariably a small lateral pelvic spine which was indicated by Gosline (1961) as an occasional plesiomorphic feature in Ostariophysi, which is also present in *Amia*. Between the pelvic fin rays and the archipterygium there are 3 ossified radial elements, the medial of which tends to brace the pelvic fin against the ischial process. Gosline (1961) indicated these 3 radial elements as plesiomorphic in distribution, and frequently subject to reduction
in Ostariophysi.

The pelvis of Ellopostoma resembles that of a typical Noemacheilus. The pelvis of Vaillantella is peculiarly flask-shaped (fig.xxxiva). It is narrow and elongated anteriorly. The ischial processes are triangular, large and cribiform, and have an extensive apposition. The pelvis of Homaloptera orthagoniata (fig. Lxviid) very much resembles that of N. strauchi in that the archipterygium does not fork anteriorly. In this species the ischial processes extend ventrally and are attached to a ventral mid-line raphe of dense subcutaneous connective tissue. The lateral pelvic spine is absent in Homaloptera orthagoniata. In Gastromyzon borneensis (fig.Lxviiej each archipterygium is forked anteriorly. The body of the archipterygium is modified into a hemicircular plate of bone, supporting a fan of 18 pelvic rays on a single large radial element which allows the development of a powerful ventral suctorial force. The pelvis of Glaniopsis differs from that of all other noemacheilids. Overall it has the form of a wide based triangle, and supports 10 rays on two radial elements on each side (fig.Lxviic).

Bacescu (1972) considered that the cobitine pelvis contrasted distinctly with the noemacheiline pelvis being highly adapted to allow "thrusting" movements. He considered the pelvis of Sabanejewia and Cobitis elongata was the most highly derived of any cobitine. In these species the archipterygium is a strong, slim triangular plate of bone with no anterior division. Bacescu commented on the fragility of the pelvis of Misgurnus and Niwaella, and concluded it
was an adaptation for diving in these taxa. I note that generally the cobitine pelvis is narrow. The mid-line aperture is always present. Each archipterygium tends to form a slim triangular bar, so that the anterior fork is compressed and in several species the anterior fork is closed [see fig.Lxviif]. The ischial processes of Cobitini are tiny. There are 6, 7 or 8 pelvic rays and a lateral pelvic spine. There are either 2 or 3 radial elements.

In the Botini the archipterygium is invariably forked anteriorly. The pelvis encloses a small median foramen. The ischial processes are typically long, and these diverge posteriorly. Three radial elements, a lateral pelvic spine and 8 or 9 rays are present [fig.Lxviig]. Bacescu [1972] concluded that the Botini showed the primitive or progenitive form of the cobitid pelvic girdle, from which two derived adaptive directions had been taken, shown by the cobitine and by the noemacheiline pelvis. I conclude that the variations in cobitid pelvic structure are adaptive and should not necessarily be attributed phylogenetic significance.

**MEDIAN FINS**

The position, and number of rays in the median fins has been used exhaustively to group the cobitids, and especially the noemacheilines, at the a-level, an analysis of which is beyond the scope of this thesis. Some general notes are made here on the osteology of the median fins.

**Dorsal fin**

In the dorsal fin skeleton of the Noemacheilini there are robust proximal radials, a complete series of medial
radials and well-ossified paired distal radials. A posterior stay piece, as illustrated by Weitzman (1962) in *Brycon*, invariably features.

The number of anterior unbranched rays in *Noemacheilini* varies between 2 and 4. Gosline (1978) considered the potential value of these unbranched rays as systematic tools in subfamily cyprinoid systematics and pointed out that "available specimens of *Cobitidae* and *Catostomidae* show greater variability between species in the number of such unbranched rays than do the *Cyprinidae* subfamilies". My observations endorse this statement of Gosline.

In no *noemacheiline* does the overall dorsal fin ray count exceed 14.

The dorsal fin of *Vaillantella* is extraordinarily elongated. *Vaillantella flavofasciata* has rays in its dorsal fin (Vaillant, 1902; Nalbant & Banarescu, 1977, p.118-9).

There is some elongation of the dorsal fin of *Ellopostoma* which has rays and is discussed on p.108.

In *Cobitini* the dorsal fin is somewhat reduced. Only 2 or 3 anterior unbranched rays are present. There are no more than a total of 11 ray elements in any cobitine species except *Acanthopsis* in which the ray count is 3/11. In *Cobitini* some medial radials are frequently lost. The posterior stay piece is fragile or absent.

In the *Botini* the dorsal fin articulates via proximal, medial and distal radials as in the *Noemachilini*. There are 3 unbranched rays in *Leptobotia* and 4 in *Botia*. 
Anal Fin

The anal fin of cobitoids is usually supported by 6 proximal radials. There are very unusually, 11 proximal radials in Vaillantella in which the anal fin is peculiarly elongated [p.134].

CAUDAL FIN [fig.

Gosline (1961) emphasised the essential overall similarity of the caudal skeleton of all Ostariophysi, and pointed out that, in light of this skeletal similarity, in cyprinids at least, the caudal ray count was "surprisingly variable". Gosline made a further general observation that the caudal fin was emarginate in all Ostariophysi, except in the cobitids Cobitis and Misgurnus. He pointed out that in these the caudal profile is peculiarly convex, and that the caudal ray count was "low and variable". The account below indicates the extent of variability of the cobitid caudal skeleton in the perspective of the variability of ostariophysean caudal skeletons generally.

In the Noemacheilini the caudal fin is usually more or less deeply forked. However, the caudal fin is convex in profile in Lefua, Oronectes and Aborichthys. In noemacheilids there are most frequently 9/9 principle caudal rays. At variance with this, primary caudal ray counts of 10/10 in Ellopostoma, 9/10 in Noemacheilus barbatulus, 10/9 in Orthrias tschajyssuensis, N. denisonii, N. fasciatus, and Vaillantella, 8/9 in N. corica, Lefua and Oronectes, and 8/8 in N. nigromaculatus are recorded. In the caudal skeleton of noemacheilids a single uroneural is frequently present
in cartilage, but peculiarly in Lefua neither this nor the epiural is developed. In most noemacheilids there are 5 hypurals (fig.Lviiib) but the more expanded condition with 4 upper hypurals articulating with the urostyle, giving a count of 6 in all, is seen in N. fasciatus, N. corica, N. rupecola, Vaillantella and N. denisonii (fig. Lviiia).

There is usually some production of the parhypurapophysis as a flange or hook on the parhypural. The parhypurapophysis is however absent in Vaillantella, Ellopostoma, Lefua, Aborichthys, Noemacheilus corica and N. barbatulus. The development of the parhypurapophysis has been discussed by Ford [1937] and Nursall [1963], Aleev [1963] and Eastman [1980].

In all noemacheilids the parhypural, and the haemal spine of the first preural centrum are not fused to their centra.

The variable profile of the noemacheilid caudal fin is accompanied by a variation in the number of procurent rays. In e.g. Lefua there are 18 dorsal, and 18 ventral procurent rays [18/18], which serve to increase the overall reminformity of the convex caudal fin of this species. There are only 3/3 procurent rays in the caudal skeleton of Vaillantella, to retain the discretion of the caudal from the long dorsal fin. In most noemacheilids there is a slightly longer dorsal, than ventral series of procurent rays. It is typical of noemacheilids that there is also some hypertrophy of the terminal pairs of intermuscular bones flanking the caudal peduncle (see p.315).

In the Cobitini the caudal principle ray count is
consistently 8/8, except in Sabanejewia where a reduction to 7/7 is stated as characteristic of the genus [Vladykov, 1928].

As recorded by Gosline (1961), in Misgurnus especially and in many cobitines, the caudal profile is convex. Accompanying this, there is a general reduction evident in the caudal skeleton. Uroneurals are absent in all Cobitini. There are almost invariably only 5 hypurals developed. Only in Somileptes are 6 hypurals present [fig. Lxviiiic] and in this species the 4 upper hypurals are all fused together. A variety of fusions take place between the lower hypurals of Cobitini. For example, the parhypural, and HU1 and HU2 are combined in Lepidocephalus annandali [fig.Lxviid], and HU1 and 2 are fused at their bases at least in L. thermalis, Cobitis taenia, Acanthopsis, Sabanejewia and Acanthophthalmus semicinctus. Fusion between the upper hypurals is rarer, but is observed in Acanthopsis, and Lepidocephalus guntea. Fusion of HU3, 4 and 5 to the urostyle proximally occurs frequently in Cobitini.

In all Cobitini the parhypural and the haemal spine of the first preural centrum are entirely fused at their bases to the ural centrum and the first preural centrum respectively. This condition contrasts with that in all other cobitoids and ostariophyseans generally and is characteristic of the Cobitini [see p.337].

In Cobitini the parhypurapophysis is raised only in Lepidocephalus annandali, and L. caudofurcatus. The caudal intermuscular flanks are variably ossified. As in the noemacheilines there are usually a few more upper, than
lower procurent rays in the caudal skeleton.

In the Botini the caudal fin is always deeply forked. Principle ray counts of 10/10 in *Leptobotia* and *Botia hymenophysa* and of 10/9 in all other botine species are recorded.

There are 2 uroneurals in *Leptobotia fasciata* (fig. Lxviii). A single uroneural is present in all other botine species except *B. berdmorei* and *B. macracantha* in which the uroneural is absent. There are invariably 6 separate hypurals in Botini. The HU1 fuses to the parhypurapophysis in *B. berdmorei* and *B. almorhae* (fig.Lxviiif). In Botini the base of the parhypural, and that of the haemal spine of the first preural centrum are not fused to their centra. In most Botini the parhypurapophysis is usually slightly raised. It is large in *L. fasciata* and *B. modesta*. In Botini there is very little development of the inter-muscular skeleton in the caudal peduncle.

The plesiomorphic form of the ostariophysean caudal skeleton was discussed by Rosen & Greenwood [1970] and it is evident that a variety of reductions from this condition have taken place repeatedly within the Ostariophysi [see e.g. Nybelin, 1970]. Consequently patterns of caudal anatomy are poor indicators of relationship within the Ostariophysi. Because of this I consider it inappropriate to impose phylogenetic interpretation on the variability of cobitoid caudal morphology. However, I do consider the variability of cobitoid caudal morphology to be itself of interest. This morphological instability was described by Gosline [1961]. It contrasts very distinctly with the stability of
the catostomid caudal skeleton which was discussed by Eastman [1980].

ANTERIOR VERTEBRAE AND WEBERIAN APPARATUS

It is characteristic of cobitoid fishes that the anterior part of the swimbladder, in association with the Weberian apparatus, becomes more or less completely encapsulated by bony extensions from parts of the anterior 4 vertebrae. The various sorts of swimbladder capsule developed in Cobitidae are described on p.288-303.

Swimbladder encapsulation also occurs in many groups of Ostariophysi as well as the Cobitidae and Homalopteridae, e.g. Gobioinae, Psilorhynchidae, Gyrinocheilidae, Siluroidae, Gymnotidae, and Catostomidae.

The functional significance of this encapsulation has been the subject of considerable discussion in the literature. Hora [1922a and b] compared the encapsulation and its accompanying developments, notably the reduction or loss of the posterior portion of the swimbladder, in Noemacheilini and Psilorhynchidae. Hora was led to conclude that encapsulation developed to protect the Weberian apparatus in torrentially adapted forms, and that increasingly robust encapsulation generally reflected increased phylogenetic derivation. Hora particularly noted that the noemacheiline Diplophysa from deep water in central Asia, was aberrant in that both the swimbladder capsule and the posterior free portion of the swimbladder were well-developed. Hora concluded this condition could be interpreted as secondarily derived. He suggested Diplophysa
might demonstrate a possible alternative mechanism for the production of a capsule if the "neolaminate bladder irritated adjacent bones and was thus encapsulated".

Evans [1925] noted the breakdown of body musculature flanking the lateral extent of the capsule of Noemacheilus [see p.291]. He proposed that this skin-capsule contact allowed expansion and movement of air within the capsule and concluded that this air movement, and thus the capsule itself, functioned to "help maintain orientation".

Jones & Marshall [1953] discussed the possible effects of encapsulation on Weberian apparatus function. They pointed out that Weberian apparatus, which is more or less encapsulated, may function not only in the maintenance of hydrostasis but also in detection of predators by amplifying the water vibrations caused by these. They further suggested that encapsulation of the swimbladder might allow a species to become sensitive to atmospheric pressure changes as it is believed to do in some cobitine loaches [e.g. the weather fish, Misgurnus anguillicaudatus].

Jones & Marshall [1953] noted a general correlation between reduction in representation of the free portion of the swimbladder of Ostariophysi, and the bottom habit, but emphasised that this reduction was accompanied by the retention and protection of the connection of the Weberian apparatus with the inner ear. They concluded that by encapsulation, "everything possible seems to have been done" to increase body density to allow the bottom habit, while keeping the accessory auditory channel. This conclusion led them to suggest that benthicity precipitates
preadaptation for torrentiality.

The work of Jones & Marshall was largely followed by Mahajan (1967) who considered the condition of the Weberian apparatus of Sisor, and of catfish generally. Mahajan concluded encapsulation has developed primarily to allow the bottom habit, and has then persisted to transmit sound vibrations to the internal ear, in isolation from sounds of internal origin. Mahajan pointed out that air bladder degeneration is accompanied by reduction in the auditory organ of some catfish, but that in those species this can be interpreted as a secondary simplification, which is possible because very complete encapsulation has resulted in isolation of the Weberian apparatus from both internal and external interference, so that ultimately it is accessible only via lateral skin-capsule openings (see p.309). Alexander (1965) expanded on the involvement of the catfish capsule with sound production in these.

Alexander (1964) compared encapsulation in the botine noemacheiline and cobitine Cobitidae. He also interpreted encapsulation of the swimbladder in Ostariophysi in general terms, primarily as an adaptive development which increases body density and allows the bottom habit. Alexander pointed out that buoyancy can be secondarily restored to a form with an excapsulated swimbladder by the introduction of air into the body in, for example an accessory respiratory system. This particular development appears to have taken place in many cobitids (see Caligarsanu, 1907; Johansen, 1970). Alexander considered it pertinent to an understanding of the functional
significance of encapsulation that it should be noted that
the cobitid swimbladder capsule is largely constructed from
bony plating from V2 and V4 and not by hypertrophy of ossa
suspensoria, as he considered there is no auditory selective
pressure to initiate the process of encapsulation, although
there is mechanical pressure to complete the capsule to
increase the robustness of the structure.

Dixit & Sharma [1971] concluded that encapsulation of
the ostariophysian swimbladder generally must be inter-
preted as primarily in order to reduce body buoyancy, and
they suggested that this is demonstrated by the ontogeny of
the capsule of Noemacheilus rupecola in which the only
[anterior] part of the posterior swimbladder chamber to
retain its cavity is incorporated into, and encapsulated
with, the anterior chamber.

The review above makes it clear that there is to date
no consensus of understanding of the function of the
swimbladder of Ostariophysi. This is aggravated by the
absence of a comprehensive review of the similarity and
difference of osteological construction between the capsules
of the various taxa in which encapsulation develops to
indicate the actual extent of structural homology of these.
Thus the full value of capsule development as a phylo-
genetic tool has not been realised, although as will be
seen numerous suggestions have been made of affinity between
the groups in which it occurs, especially with regard to
their possibly inter—relationship with the Cobitidae,
because encapsulation is historically regarded as so
characteristic of that group. It is not emphasised in the
literature that the capsule has evidently been structurally elaborated a number of times within the Ostariophysi, and that it may or may not serve the same function in its various forms.

In this study a brief summary of the structure of the swimbladder capsules formed in the cobitoid fishes is given. Further details of cobitoid capsule morphology have been discussed by Chrallov (1925, 1927), Berg (1940), Ramaswami (1952:3 and 4, 1953), Nalbant (1963), Alexander (1964), and Nalbant & Banarescu (1977). The component structure of the cobitoid capsules is then compared with that of capsules developed in representatives of other ostariophysan outgroups in order to select which specific features of cobitoid capsule morphology might actually be of value as characters sensu Hennig (1966). A hypothesis of cobitoid intra- and interrelationships is then drawn up [fig. Lxxxii] based on these characters. In conclusion to this section, the hypothesis suggested in fig. Lxxxii is compared with the conclusions of Fink & Fink (1981). These authors offered a cladistic interpretation of the state of the Weberian apparatus of Ostariophysi, but they did not particularly consider the significance of encapsulation.

In Noemacheilini [fig. Lxix] the swimbladder capsule consists of a pair of bony spheres one each side of the mid-line which intercommunicate posteriorly via a bony canal. In all members of the taxon the first vertebra [VI] is a platycoelous disc-like element, to which are fused paired long lateral processes [P1] extending across the anterior two-fourths of the capsule. Baudelot's ligament
inserts on the free distal tips of these processes.

The centra of V2 and V3 are invariably fused into a single biconical amphicoelous element (V2 + 3). The lateral process of the second vertebra (P2), is fused to, and flares laterally from, the anterior of V2 + 3. The P2 expands to form the anterior wall of the capsule. It articulates with a process of the fourth vertebra (P4) at a well-defined suture in the anterior of the roof of each sphere of the capsule. The top of the horizontal portion of P2 (P2H) projects as a small prong from each side of the capsule. It appears that the descending portion of P2 (P2D) fuses with P4D in the capsule floor; there is no suture visible on the capsule floor.

The fourth vertebra (V4) has a long biconical amphicoelous centrum. The P4 is not fused to V4. It issues laterally [as P4H] from a parapophyseal articulation with its centrum. This P4H forms the posterior part of the roof of the capsule and P4 descends distally as a slim strut dividing the anterolateral, from the lateral aperture in the side of the capsule (p.291). The P4D recurves posteriorly and forms the floor of the capsule. It sutures with its fellow in the sagittal mid-line and contributes the floor of the intercommunicating canal between the two halves of the capsule. Posteriorly P4D joins P4H when the capsule is completed posteriorly.

The ossa suspensoria of Noemacheilini are very characteristically disposed. Each os forms anteriorly a synchondrosis with the basal portion of P2D. The ossa curve posteriorly forming the posteromedial portion of the
capsule wall, and meet each other in the anterior wall of the intercommunicating canal. Alexander (1964) suggested that the ossa suspensoria of Noemacheilini have this form because, as the capsule is displaced dorsally in accompaniment to thoracic flattening in this group, the medial part of the capsule, with which the ossa suspensoria are involved, was "prevented from following" because it retained its ventral relation to the aorta and cardinal vein. The observation that in general, throughout the Noemacheilini, increased flattening of the body is correlated with shortening of the intercommunicating canal, endorses Alexander's suggestion.

There is some morphoclinic variation in the overall shape of the noemacheiline capsule which is illustrated by Banarescu & Nalbant (1964) in the Turkish species of the taxon. There is also some variation in the production of horizontal bony shelves round the capsule periphery, anteriorly, laterally above and below the apertures and posteriorly. In Noemacheilus botia the posterior part of this peripheral shelving takes the form of a pair of blunt, posterodorsally angled horns of bone. The extent of cancellation, or cribiformity of the capsule walls also varies. The cribiformity is reduced to increase the robustness of the capsule in torrential forms. The capsule is frequently incomplete posteriorly, especially when the posterior chamber of the swimbladder is presented. In _Noemacheilus nigromaculatus_ and _Lefua_ the capsule is entirely open posteriorly. In these species the vertically descending part of P4 consists only of a slim strut of bone enclosing
the lateral aperture posteriorly.

Two lateral apertures are a very constant, and characteristic feature of the lateral wall of the noemacheiline capsule. The smaller, anterolateral aperture is enclosed between P2H and D anteriorly and by the anterior descending strut of P4 described on p. 280 posteriorly. The larger, oval, lateral aperture is enclosed between the anterior descending strut of P4 anteriorly, and by P4H and D dorsally, ventrally and posteriorly. These apertures are applied laterally to the internal surface of the body flanks. The flank muscle is broken down over the apertures establishing a skin-capsule contact area.

The dorsal elements surrounding the neural canal over V1-4 of Noemacheilini show limited variation in their proportions. The anterior shield-shaped supraneural (SN2) is invariably present. The neural complex is usually large and long. Posterior to the neural complex a single free supraneural sometimes develops between the neural spines of V4 or V5.

The neural arch of 3 (NA3) is well-represented. Its base articulates synchondrotically with the proximal part of P2H and P4H. Transverse production of NA3 is limited. It may form a short horn-shaped process anteriorly, or a narrow horizontal shelf of bone.

The NS4 is flattened, and in Noemacheilini P4 is not fused to V4 laterally. The NA5 is little modified. It has a typical pleural rib which lies free of the capsule, and which articulates with the centrum of V5 at a cuneiform parapophysis which is not invariably fused to its centrum.
Of the Weberian ossicles, the claustra are well-defined as more or less triangular elements articulating below SN2. The scaphium is small. It has a short ascending process attaching the interossicular ligament passing to the intercalarium. The anterior and articular processes of the scaphium are very reduced. In Noemacheilini the intercalarium is invariably a quadralateral sesamoid of the interossicular ligament; the intercalarium has entirely lost its medial limb.

The tripus of Noemacheilini is V- or Y-shaped, as its transformator process if absent or truncated. Alexander (1964) interpreted the abbreviated condition of the noemacheiline tripus as a correlate of the reorganisation of the attachments of the tunica externa to the inside of a bilateral produced swimbladder capsule. The tripus is reduced to some degree in all noemacheilinae species (see Chranilov, 1925, 1927). It is least reduced in N. nigromaculatus of these species examined here. The articular limb of the tripus meets V2 + 3 between P4H, P2 and the osse suspensoria. The angle of the tripus projects into the capsule on each side. The incorporation of the osse suspensoria into the capsule wall has been described on p.289-90. Here it is reiterated that the osse suture together, but do not fuse distally, and especially in their relation to the aortic canal and to P2, are peculiarly derived (see p.310).

The swimbladder capsules formed in non-noemacheilinae noemacheilids can now be compared with the typical noemacheiline capsule.
In *Glaniopsis* (fig. Lxx) the swimbladder capsule present is very much like that of a typical *Noemacheilus* and this similarity was emphasised by Ramaswami (1952:4). Each bony sphere of the capsule is depressed and wide. There is a short wide intercommunicating canal, into which the ossa suspensoria are apparently incorporated in the same way as they are into the noemacheiline capsule. However, in the case of *Glaniopsis* the ossa fuse together distally in the anterior wall of the canal. Unlike in any *Noemacheilus* the capsule of *Glaniopsis* has a well-defined facet anterolaterally which is formed by P2 and with which the cleithrum articulates (p. 263). In *Glaniopsis* both the anterolateral and lateral apertures are present in the lateral wall of the capsule. A small bony prong projecting over the antero-dorsal part of the anterolateral aperture is interpreted as the termination of P2H, although P2 and P4H are fused across the capsule roof.

Of the dorsal elements, the SN2 shield element is short. The NA4 is fused to the posterior edge of the neural complex. There is no free supraneural in *Glaniopsis*.

The Weberian apparatus is reduced in *Glaniopsis* as in Noemacheilini. The tripus is particularly reduced. It is L-shaped with a much longer articular than anterior limb.

In *Gastromyzon borneensis* (fig. Lxxi) the swimbladder capsule is bilaterally produced and extremely short and wide, with a pipe-like intercommunicating canal. In essential composition, the disposition of the ossa suspensoria, the development of both anterolateral and lateral apertures, and the production of P2H in association with the
former aperture, the capsule of *Gastromyzon* resembles that of *Glaniopsis*. A robust cleithral facet is present on the capsule anterodorsolaterally.

The dorsal elements associated with V1-4 are modified in *Gastromyzon* following the extreme flattening of the body in this taxon. It is notable that the SN2 shield is small. The neural complex is large, humped anteriorly, and meets the occiput. The neural complex has a pair of bony alae posteriorly. The NA4 is tightly sutured to the posterior of the neural complex. NA4 is expanded basally, and forms a very long cartilage lined articular socket for P4.

In the bipartite capsule of *Homaloptera orthagoniata* [fig.Lxxii] P1 is shorter and more curved than in a typical *Noemacheilus*. The ossa suspensoria are incorporated in the medial wall of each capsule half, the intercommunicating canal is incompletely ossified and neither the ossa nor P4D actually articulate with their fellows. The capsule of *Homaloptera* differs from that typical of *Noemacheilini* in some other features. The anterolateral and lateral apertures are not separated, so capsule-skin contact is made via a single large oval opening on each side. This aperture is apparently bounded by P2 anteriorly, and is not closed posteriorly. As in *Gastromyzon* a cleithrum articular facet is present on the capsule anterolaterally.

In *Homaloptera* the dorsal elements over V1-4 are very similar to those of a typical noemacheiline. The Weberian chain of *Homaloptera* resembles that of *Gastromyzon*.

A detailed account of the construction of swimbladder encapsulation in *Ellopogostoma* has been given [fig.xxxi,p.109-13].
The salient features of the capsule morphology are reiterated here. As emphasised by Roberts [1972] the capsule of *Ellopostoma* resembles that of the *Noemacheilini* in its general proportions. It is a deep bipartite structure, the two halves of which communicate via a canal into the anterior wall of which the ossa suspensoria are incorporated, as they are in *Noemacheilus*. However, in *Ellopostoma* only a single large lateral aperture develops in each lateral capsule wall. The P2H is produced as a small horn-like process projecting from the anterodorsal border of this aperture. Apart from this process no separating demarcation of P2 and P4 is evident on the capsule.

Of the dorsal elements over V1-4 the SN2 is produced to a strong condyle anteriorly which articulates in the occipital facet described on p. 101. The neural complex is long and low, and there is a single large free supraneural element between NS4 and 5. The NA3 is raised to a convoluted ridge of bone above the Weberian chain. However, it does not have synchondrotic union with the proximal parts of P2 and P4 in the capsule roof, and the Weberian chain of *Ellopostoma* is exposed in lateral view. The basal part of P2 is expanded, and related to the anterior elements of the Weberian apparatus laterally. The Weberian ossicles themselves are similar to those in *Noemacheilini*; the tripus has no transformator process.

The swimbladder capsule of *Vaillantella* (Fig. xxxv, p.135-8) is less complete than that of any other noemacheilid. The salient features of its construction are given below.

The ossa suspensoria achieve a long apposition with
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P2D, and curve to contribute medial walling of the capsule. They meet each other distally, and their line of suture is deeply concave posteriorly. Although it is partial, in lateral view the capsule of Vaillantella has bony strutting demarcing both the anterolateral and lateral apertures as in Noemacheilini, and the component contribution of the bony boundaries of these apertures in Vaillantella is apparently homologous with that in Noemacheilini.

The dorsal elements over V1-4 in Vaillantella are also typically noemacheilid, except that the NA3 is not disposed to shield or enclose the Weberian chain dorsally.

Unusually amongst noemacheilids the Weberian apparatus of Vaillantella is not reduced. The scaphia are large and oval, with well-defined articular condyles. The intercalarium is L-shaped with a fine articular limb, and the tripus develops a long curly transformator process.

In the Cobitini [fig.Lxxiii] the swimbladder capsule is consistently a single, approximately spherical ossification positioned below V4, and bearing a pair of horn-like processes ventrolaterally. The component construction of the cobitine capsule remains an enigma. Block [1916], Chranilov [1925] and Ramaswami [1953] concluded that the capsule was essentially formed by hypertrophy of the osa suspensoria. Alexander [1964] showed that the relations of the tunica externa demonstrated that the distal tips of the osa suspensoria are present as a tab of bone projecting into the roof of the cobitine capsule. He concluded that most of the walls of the capsule are composed of P4, and that the paired bony horns projecting from the capsule wall
represent the tips of the P40. Alexander considered that P2 is excluded from contributing to the formation of the capsule anteriorly, but that P2 is produced as a forked prong of bone which lies adjacent to anterolateral openings in the capsule on each side. There is a long suture formed ventrally on each side where the anterior border of the capsule articulates with the base of the P2 as interpreted by Alexander. Alexander added that the cobitine capsule could be a largely homeoplastic ossification.

There is some ingroup variation in the form of the capsule in Cobitini, but the nature of this variation actually does little to help elucidate the relationships of the Cobitini. Nalbant (1963) contrasted the capsule of Misgurnus (fig. Lxxiiiia) with all other Cobitini because, according to him, in Misgurnus 2 apertures develop on each side of the sphere (to establish skin-capsule contact) while in all other cobitines "... the aperture through which penetrates the tripus is prolonged even to the front part of the bladder". Nalbant considered Misgurnus as primitive amongst cobitines because its capsule shows some mid-line strangulation reminiscent of the bipartition of the capsule of Noemacheilini. Nalbant thus concluded that increased capsule sphericality was a derived condition in Cobitini.

Bacescu (1965) compared the capsules of several species of Cobitis, and determined two sorts, one which was lightly ossified, with loosely reticulated bony walls, found in C. taenia, C. calderoni and Bicanestrinia, and the other sort of capsule which was more robust and found in
Sabanejewia and Acanestrinia. Bacescu stated that he could not explain the osteological differences between these two capsule sorts, but observed that the cobitines from more rapid streams had more robust capsules than still water types. He agreed with Nalbant (1963) in concluding that increased capsule sphericity is a derived condition for Cobitini.

My observations on the anterior 4 vertebrae of Cobitini show that in these the centrum of V1 is always a disc-like element. The P1 attaches Baudelot's ligament, P1 is invariably short and curved, and reflected posteriorly where it apposes P2. The centra of V2 and 3 invariably fuse. The base of P2 is expanded basally and is related to the anterior Weberian chain laterally. P2 extends horizontally and posteriorly, terminating in a fork.

In all Cobitini P4 is fused at its "parapophyseal" articulation with V4. This is a very unusual condition, apparently unique to this taxon (see p.337).

I record production of two apertures on each side of the capsule in all the cobitine genera examined by me except for Somileptes (fig.Lxxiiiic) and Acanthopsis. Therefore I do not agree with Bacescu (1965) that the presence of 2 swimbladder apertures in Misgurnus is unusual amongst Cobitini. The posterior wall of the capsule of Cobitini is also perforated. The aortic canal develops here as a round mid-line aperture, and this is usually flanked by 2 small fenestra which may become confluent with each other dorsal to the aortic canal.

In all Cobitini the swimbladder capsule has the paired
posterolateral horn-like processes described on p.296. These processes appear to be functionally homologous with the shelving described on the periphery of some noemacheiline capsules [p.290] - maintaining the skin of the body flank in diaphragmatic relation to the capsule apertures. However, assessment of the anatomical homology of the horns on the cobitine capsule begs the question of the derivation of this capsule itself.

Two interpretations of cobitine encapsulation may be considered. The first interpretation is that of Alexander [1964]. He proposed that the capsule is entirely derived from parts of V4. Thus the apertures and bony horns above are also entirely constructed by P4, and the "anterolateral aperture" formed in the capsule of many Cobitini is not homologous with the anterolateral aperture formed in many noemacheilids [see p.291].

Alternatively it can be proposed that the ventral part of the capsule in Cobitini incorporates part of P20 and that the capsule horns develop from the tips of P20. The tips of P20 project ventrolaterally from the partial capsule formed in Vaillantella [p.136]. If this interpretation is accepted it can be assumed in Cobitini that the osseous suspensoria meet P2 (as they do in noemacheilids) in the floor of the capsule and that P4H has secondarily forked to flank the capsule apertures. It can be further assumed that P20 has retained its noemacheilinetype relation to the ventral border of the anterolateral aperture. Under this interpretation the anterolateral aperture of Cobitini is homologous with that aperture in Noemacheilini and loss
of this aperture can be proposed as a derived development within the Cobitini.

It is also possible to interpret the cobitine capsule as a de novo homeoplastic structure, in which case it becomes inappropriate to consider transformable features within cobitoid encapsulation. However, it may be noted that in cobitoid fishes theossa suspensoria have singular relations to the aortic canal, and this in itself suggests that cobitoid swimbladders are homologous structures at some level [see p.370].

The dorsal elements of V1-4 in Cobitini include the SN2 shield, and a deep neural complex which may approach the occiput. In Cobitini no free supraneurals are present posterior to the neural complex. The NA3 is large. It forms an extensive lateral shelf of bone which extends dorsal to the Weberian apparatus as the apparatus passes over P2. The P4 is peculiarly, completely fused to V4, and in all Cobitini the paraphophysis of V5 is also fused to V5.

Of the Weberian ossicles in Cobitini the claustrum and scaphium are small. The intercalarium varies between being a cubical, and bar-shaped sesamoid ossification, and never develops a medial limb. The tripus is invariably produced to a short transformator process inside the capsule.

Hypertrophied intramuscular splints of bone become associated with the cobitine capsule. These splints lie posterior to the epicranial sesamoid splints; the most anterior is joined to P2 by a fibrous connective tissue band. The middle and posterior splints have association with the P4, and with subsequent paraphophyses respectively.
It seems that these splints supplement the function of the ventrolateral horns of the capsule in maintaining the skin of the flank as a diaphragm over the lateral apertures. The splints are particularly well-developed in Lepidoccephalus (fig.Lxxiiiib) in which the bony horns on the capsule are also large.

Within the Botini the extent of encapsulation and representation of the free (posterior) swimbladder portion is very variable. Taki [1972] summarised the most generally held view of the phylogenetic significance of this variability, i.e. that Leptobotia is primitive amongst Botini because in this taxon the capsule form is very incomplete and that within Botia, the subgenus Hymenophysa and B. macracantha are more primitive than Botia s.str. and Sinbotia because the capsule is more incomplete in the former than in the latter taxa.

In all the Botini V1 is robust and platycoelous, and frequently has a rather elaborate ventral zygapophyseal articulation with V2. The P1 is never present as the free digitiform limbs so characteristic of the Noemacheilini. In Botini P1 is typically a strong prong of bone lying in close relation to the base of P2.

The V2 and 3 centres are fused in all Botini except Leptobotia elongata (fig.Lxxiv). The P2 is present in both its P2H and P2D parts. In Leptobotia no part of either P2 or P4 is very expanded; P4D extends slightly posterior to P2D. Amongst Botini, in the subgenus Hymenophysa (fig.Lxxv) P2D expands to contribute the anterior part of the encapsulation of the swimbladder. In the subgenus Botia
str. in which capsule development is greater [fig.Lxxvi] P20 recurves posteriorly to meet and fuse with its fellow P20, constructing the capsule floor, to which P4 does not add. The base of P2 makes a long apposition with the osa suspensoria in Botia, but fails to do so in Leptobotia.

In Botini, as in noemacheilids but in contrast with all cobitines, P4 is never fused to V4. P4H forms a quadri-lateral plate across the roof of the anterior swimbladder chamber. It descends anteriorly as a strut of bone, and meets P20 where it may form terminally as a horn-like process. The osa suspensoria develop from the ventrum of V4. The pair appose at a mid-line convoluted suture. They expand basally and appose P2 in Botia as described. The main plates of the osa curve ventral to, and do not wholly enclose, the aortic canal which is thus disposed subcentrally.

The bony strutting formed by P2 and P4 in Botini demarks the borders of anterolateral and lateral apertures in the same position as these apertures in a Noemacheilus capsule. In Botini the lateral aperture is not closed posteriorly. The similarity of the partial encapsulation in Vaillantella and Botini is commented on by Nalbant & Banarescu (1977) and is emphasised here. In Botia almorhae (fig.Lxxvi) and B. geto (Botia s.str.) the anterolateral aperture is obliterated as the anterior edge of P4 fuses with the division of P2 into P2H and D.

There are some very distinctive developments in the dorsal elements associated with V1-4 in Botini. It appears that the group is united by the complete absence of the SN2 shield element [see fig xCiii]. The neural complex is
large and rhomboidal in shape. One or two free supraneurals are present dorsally in association with NA4 and NA5. The NA2 may bear a small lateral horn or shelf, but this is never produced to the extent that it is in the Cobitini [p. 256]. In Botini the parapophyses of V4 and V5 are not fused to their centra.

In the Weberian apparatus of Botini the claustrum and scaphium are not reduced. However, in all Botia species the intercalarium is present only as a longitudinal bar, or cubical sesamoid in the interossicular ligament, i.e. the intercalarium develops no medial process. By contrast, in Leptobotia species the intercalarium is an L-shaped bone with a medial process articulating with the V2 + 3 medially. The tipus is not extremely reduced in any Botini. The body of the bone is robust and triangular with a short medial (articular) limb. The transformator process is quite long, fine, and rather abruptly angled medially.

I do not consider ingroup comparison of cobitoid capsules can yield any valid indication of the phylogeny of this group until outgroup comparisons have rendered possible some assessment of the uniqueness within the Ostariophysi of the various morphological peculiarities of cobitoid capsules which have been described. This follows below, where the condition of the anterior swimbladder in some cyprinids, gobioines, catostomids, gyrinocheilids, psilorhynchids, gymnotids and siluroids is discussed in turn.

Howes [1980] described the typical state of the V1-4 in cyprinids in which there is no capsule formation. Each of the 4 vertebral elements is discreet. The P1 is a short
horizontal limb. The P2 is a horizontal bar of bone. The P4 is never fused to V4 and P4 is not developed into H and O plates. The NA3 is not produced laterally. The ossa suspensoria descend vertically and basally they surround the aortic canal. The Weberian chain is fully developed [see Ramaswami, 1955b].

The anterior chamber of the swimbladder becomes almost completely encapsulated in some species of Gobiinae. This observation led Nicholls (1943) to include the gobioid genus Gobiobotia, in the Cobitidae. However, Ramaswami (1955a) pointed out that "Gobiobotia is not a loach although in appearance, and especially swimbladder encapsulation it seems to resemble one". Ramaswami illustrated the very differently constructed capsules of Gobiobotia and Saurogobio and concluded that of these the latter "more resembles the cobitid or homalopterid type". Banarascu & Nalbant (1965) considered that the rather complete and distinctive capsule developed in Saurogobio might indicate Saurogobio to be somewhat phylogenetically removed from other primitive gobiid genera.

Fig.Lxxvii shows that the capsule in Saurogobio is a transversely elongated bony sphere, which is incomplete both posteriorly and laterally, where a large leaf-shaped aperture is present above a shelf of bone formed by the capsule wall. The capsule is apparently entirely derived of a P4 which can be interpreted as having H and O parts. The P4 does not fuse to V4. There is synchondrotic union between P2 and NA3 which [as in noemacheilids] is made over the exit of the Weberian chain. In Saurogobio the
Weberian elements are well-developed and do not differ from the plesiomorph cyprinid type.

Nicholls (1943) and Ramaswami (1955a) both considered that the form of encapsulation in catostomids and gobioides was sufficiently similar to indicate closer relationship between these two groups than between either of these groups and the Cobitidae. Nelson (1948) discussed various sorts of encapsulation within the Catostomidae, and emphasised particular variation within the group in the fusion of V2 + 3, the height of NS4, and the development of P1.

My observations on *Catostomus catostomus* here show V1 has no P1 [fig. Lxxxviii]. V2 is separate from V3. P2 develops into both a horizontal prong-like process, and a descending plate, which basally surrounds the aortic canal, and is disposed coronally across the anterior swimbladder wall.

In *Catostomus* P4 expands laterally over the partial capsule roof, and descends anteriorly. It recurves posteriorly and meets its fellow to construct flooring of the capsule. The P4 of catostomids has posterolaterally, a substantial oesophageal process and is not fused to V4.

The ossa suspensoria enclose the aortic canal between their distal portions. They have rectangular processes ventrolaterally which appose buttressing on P4D and complete the surround of the transformator part of the tripus on each side, although encapsulation *per se* is entirely deficient posteriorly in catostomids. An extensive skin-capsule contact area is established laterally between P4H, P4D and
P2H. The NA3 has a rectangular lateral shelf of bone the edge of which is thrown into convolutions. In *Catostomus catostomus* the intercalarium is a transversely disposed hiliform element. The other elements of the Weberian apparatus are not extremely reduced.

Smith (1945) suggested that there was relationship between the Cobitidae, Homalopteridae and *Gyrinocheilus* because of the swimbladder degeneration and encapsulation he observed in *Gyrinocheilus* which was also described by Hora (1923), while Ramaswami (1952:2) considered that the form of encapsulation in *Gyrinocheilus* indicated its relationship to catostomids, rather than to the cobitoids.

In *Gyrinocheilus symonieri* (fig.Lxxix) V1 bears limb-like P1. V2 and 3 are fused. P2 is produced as a strong digitiform P2H part, and a "D" part which expands posteroventrally to appose the P4 at a long suture. P4 does not fuse to V4. P4 forms bony strutting contributing to capsule formation posteriorly. Posteroventrolaterally P4 has a long cesophageal process. In *Gyrinocheilus* the osa suspensoria are very peculiar triangular digitiform structures which are considerably separated from each other distally. The lateral skin contact area is supported by P2H ventrally and by P4. Of the dorsal elements associated with V1-4 in *Gyrinocheilus* the neural complex is very low. It has massive alae posteriorly. NA4 is very low and NA5 approaches the neural complex posteriorly. The NA3 forms a horizontal lateral shelf of bone, extending over the Weberian apparatus. In *Gyrinocheilus* the claustrum is large, the scaphium and its processes are reduced and the
intercalarium is a cubical sesamoidal ossification. The tripus is not reduced.

Ramaswami [1952:1] concluded that the development of swimbladder encapsulation in the Psilorhynchidae should be interpreted as "the first step towards modification of the bony capsule seen in noemacheilines Cobitidae, and the Homalopteridae". This view of Ramaswami was reiterated by Alexander [1964], although he did not examine *Psilorhynchus*.

My observations on *Psilorhynchus balitora* show that the capsule is apparently formed by parts of both P2 and P4 which have fused together (fig. Lxxx). V1 is reduced. It has tiny digitiform P1 processes. The centre of V2, 3 and of 4 fuse together. A long, stout horizontal prong of bone issuing from V2 + 3 + 4 laterally can be identified as P2 because of its relation to the Weberian chain. The P2 contributes part of the anterior wall of the capsule. The P4 does not fuse to V4. It approaches NA3 basally and appears to contribute the posterior part of the capsule framework by recurring internally. A round lateral capsule aperture is enclosed between the P2 and P4. In *Psilorhynchus* the osa suspensoria are broad. They suture together in the midline, and curve around a subcentral aortic canal. The dorsal elements associated with V1-4 are short and deep. NA3 does not expand laterally. In the Weberian apparatus both the articular limb of the intercalarium, and the transformator process of the tripus are developed. I conclude that there is no feature in the encapsulation which can be used to support a hypothesis of relationship
between Psilorhynchidae and Cobitidae.

The anterior chamber of the swimbladder becomes encapsulated in several gymnotid eels. The capsule of the gymnotid Rhamphichthys is discussed here because it closely resembles that of a cobitine cobitid, and because this resemblance does not appear to have been reported in the literature. In Rhamphichthys [fig.Lxxxi] V1 has no P1. V2 does not fuse to V3. P2 is produced into P2H and P20 leaf-shaped bony expansions across the anterior wall of the capsule. The P4 is not fused to NA4. P4 contributes most of the spherical capsule. The P40 portion meets its fellow at a mid-line suture, in the capsule floor. In Rhamphichthys the osse suspensoria curve away from each other and pass around a subcentral aortic canal. The capsular portion of P4 curves posteriorly from its origin. It surrounds the transformer part of the tripus. A lateral skin-capsule contact area is surrounded by the lateral limit of P4 and by 2 bony horn-like processes which project dorsally and ventrally from the lateral capsule wall.

Of the dorsal elements associated with V1-4 the SN2 shield is entirely absent in gymnotids. The neural complex is low. It forms a condyle anteriorly which abuts a shallow socket excavated on the supraoccipital. The NA4 is low. The NA3 is pentagonal. Its lateral process is a distinctive strong bony spine directed posteriorly.

In the Weberian apparatus the bipartite tripus which is characteristic of gymnotids is noted. The intercalarium is sesamoidal. The scaphium is not reduced. The claustrum is entirely absent from gymnotids. As in Cobitini.
in gymnotids strong intramuscular splints are associated with P2, and P4 and these splints contribute to the formation of the border of the lateral aperture.

Postcranial encapsulation occurs in many families of catfish and was discussed by Alexander [1965]. Mahajan [1967] stated that its development may (quantitatively) approach that achieved by the cobitids and homalopterids. I have included a brief description of the swimbladder capsule developed in the torrentially adapted Glyptothorax pectinopterus because this shows clearly that several of the morphological characteristics of swimbladder capsules of cobitoid and other ostariophysii must be interpreted as adaptive parallelisms.

In Glyptothorax pectinopterus V1 is a discoidal element without a lateral process. The centre of 2, 3 and 4 fuse together to form a complex centrum which expands bilaterally to form a solid domed sheet of bone extending between the exoccipital and epioccipital anteriorly, and the dorsal fin spine base posteriorly. A ventral view shows curved osseous suspensoria which are separated from each other distally. The dorsal elements associated with V1-4 are fused together and to the dorsum of the bony dome of the capsule. Anteriorly the dorsal elements suture with the supraoccipital spine. Parts of V5 are expanded and contribute to the capsule posteriorly. In the Weberian apparatus the scaphium is reduced and the intercalarium is a sesamoidal nodule of bone. The tripus is T-shaped, with a somewhat truncated transformator process.

The descriptions above of the form of swimbladder
encapsulation in representatives of various non-cobitoid ostariophysean representatives make it clear that there is an elaborately mosaic distribution of developments in the V1-4 of Ostariophysi. The notes below summarise the features of V1-4 in cobitoids which the comparative review has made it possible to suggest may elucidate the relationships of the group.

It seems that the cobitoid group is characterised by peculiarly disposed ossa suspensoria. The characteristic morphology of these is very recognisable in various degrees of development in Noemacheilini and in Botini. The ossa are horseshoe-shaped, sweep around the medial walls of the anterior chamber of the swimbladder, and tend to extend anteriorly to appose the P2. I suggest it should be assumed that the cobitine capsule includes ossa suspensoria of this type, in a highly derived condition [see p.299].

In all cobitoids the ossa suspensoria appose each other below a subcentrally disposed aortic canal. As a subcentral aortic canal also develops in several other ostariophyseans, e.g. the gobiones, Psilorhynchus and siluroids, the development can be construed as part of a general morphological transformation sequence accompanying flattening of the thorax and capsule.

I note the rather typically cyprinid ossa suspensoria in Catostomus [p.305] and the peculiarly separated triangular ossa of Gyrinocheilus and suggest that neither of these taxa can be interpreted as very closely related to the cobitoids (or to each other) on the basis of ossa suspensoria morphology.
Clearly, even if the assumption that the disposition of ossa suspensoria of Cobitini is similar to that in Noemacheilinini and Botini is accepted, the interrelationships of the Cobitini are not clarified by the study of encapsulation. In general appearance the cobitine capsule is far more closely resembled by the capsule of the gymnotid eel Rhamphichthys than by the capsule of any other cobitoid. The cobitine group can be well-defined on a character associated with encapsulation — the complete fusion of the P4 to V4— and this character is useful in that it allows the Cobitini to be defined as a monophyletic assemblage. However, P4 is not found fused to P4 outside the Cobitini and thus the development does not indicate the interrelationships of this group.

*Vaillantella* may demonstrate some of the possible intermediate conditions leading from the typical noemacheilid to the cobitine type of swimbladder encapsulation. These conditions include expansion of the base of P2 and the withdrawal of P2 anteriorly away from the capsule roof. In *Vaillantella* there is, moreover, no synchondrotic union between NA3 and the roof of the capsule. The synchondrotic articulation between P2, NA3 and P4 has a very characteristic appearance in all other noemacheilids except *Ellipostoma* (see p. 170), but does not develop in Cobitini (p. 200).

Fig. Lxxxii shows a hypothesis of cobitoid relationships based on an interpretation of encapsulation characteristics.

Below is a series of comments on Fink & Fink’s [1981] interpretation of the phylogenetic significance of various conditions of V1-4 in Ostariophysi. These comments are
made in the light of my study of cobitoid V1-4 morphology
and are listed in the order that the points were made by
Fink & Fink in the [1981] publication.

Fink & Fink [1981, character 61] proposed that the
loss of SN2 and the consequent presence of only one dorsal
supraneural element is a synapomorphy for their taxon
Characiphysi and differentiates this taxon from the
cypriniforms in which two supraneurals develop [of which
the anterior is SN2]. I record the absence of SN2 from all
species of Botini and I suggest that absence of SN2 must be
interpreted as an unusual but repeatedly derived condition
amongst Ostariophysi and do not agree that the loss of SN2
is specifically definitive of a group Characiphysi.

Fink & Fink [1981, character 12] suggested that it is
characteristic of the Characiphysi that the neural complex
is tilted forward and meets the posterior of the cranium.
I note the development of a peculiarly well-formed
articulation in Ellopostoma and the approximation of the
bones in question in several noemacheilids, and follow
Howes [1978, 1980] in interpreting this development as an
adaptation consolidating the postcranial region.

Fink & Fink [1981, character 70] discussed the
apparently independent loss of the articular process of
the intercalarium in siluroids and gymnotids, so that the
bone is only a node in the interossicular ligament. I add
that is similarly in a sesamoidal condition in all cobitoids
with the notable exceptions of Vaillantella and Leptobotia
[see $p^{138}, fig \times Cii]$. The intercalarium is also only a node in some
catostomids and in Gyrinocheilus and it seems clear that
reduction of the intercalarium has occurred several times in the Ostariophysi.

Fink & Fink (1981, character 71) discussed systematic variation in the form of the transverse process of NA3. They describe this as a long anterodorsally orientated process in characiphysans in contrast to a shallow ventrolaterally orientated shelf of bone in cypriniforms and a deeper ventrolateral shelf in gymnotids. The variation in the form of this process of NA3 in cobitoids demonstrate the extreme lability of this development. I note especially the deep shelf of bone present as a transverse production of NA3 in Cobitini.

Fink & Fink (1981, character 80) pointed out that fusion between V2 and 3 within the Cypriniforms is of mosaic distribution. My observations on the condition of these two centra in cobitoids (p.283) leads me to agree with this and thus to conclude that this character may be of mosaic distribution throughout the Ostariophysi.

Fink & Fink (1981, characters 88 and 89) discussed the peculiar articulation made between P4 and the pectoral girdle in siluroids and suggested this articulation may be characteristic of this taxon. I have discussed the presence of an articulation of P2 with the pectoral girdle in Glaniopsis and the homalopterines and gastromyzonines and suggest that this articulation must be recognised as an adaptation for torrentiality and must consequently be treated with caution as an indicator of phylogeny.

Fink & Fink (1981, character 92) discussed an elongated
anterior horizontal process of the ossa suspensoria as synapomorphic for siluriforms. Anterior extension of the ossa in many cobitoids has been described [p.302]. The way in which the ossa have elongated in these cobitoids and in catfish is similar and should probably be interpreted as correlated with encapsulation and thoracic flattening.

Finally, Fink & Fink (1981) stated that in their taxon Siluriformes, all pleural rib elements project from their centra at an angle close to the horizontal, while in the plesiomorphic ostariophysean condition pleural ribs project ventrolaterally from their centra. This generalisation appears to be invalidated many times by the disposition of especially P4 in flattened Ostariophysi in which a swim-bladder capsule is present.

INTERMUSCULAR OSSIFICATION

A summary of intramuscular skeletal developments is given below. Weitzman (1962) described these in the characid Brycon as comprising a dorsal series the anterior elements of which are forked, and the posterior unforked. There is also a similarly forked more ventral or epipleural series, the anterior 3 or 4 of which are associated with the last pleural ribs.

This plesiomorphic arrangement of the intramuscular skeleton is evident in noemacheilids. The most anterior element of the dorsal series is related to V4. Over the abdominal flanks the intramuscular skeleton forms an interlocking lattice above and below the vertebral axis.
These lattices are stronger in species of torrential habitat. In noemacheilids the most posterior element of both the dorsal and ventral intermuscular series is short and flat and provides stiffening for the caudal peduncle. Eastman (1980) recorded similar intermuscular reinforcement of the caudal peduncle of the catostomid *Xyranchez texancus*, which inhabits fast flowing waters.

In *Vaillantella*, uniquely amongst noemacheilids, the entire intermuscular skeleton is extremely lightly ossified.

In Cobitini the dorsal intermuscular series is continued anteriorly by the development of 3 distinctive epicranial, besan-like bones of which the anterolateral two are associated with the exoccipital and the most medial, with the basioccipital [fig.1vib]. The subsequent intermuscular bones of the dorsal series approach the tips of the P2(H) and P4(H) of the swimbladder capsule, (p.300) the parapophysis of V5 and through posteriorly. The intermuscular bones associated with the swimbladder capsule are flattened and robust, and as described (p.301) seem to reinforce the skin along the skin-capsule contact area. In Cobitini both the dorsal and ventral intermuscular bones fork and form a lattice-structure along the body wall. The posterior intermuscular bones lying over the caudal peduncle are modified in Cobitini as in the noemacheilines.

In the Botini, there are no epicranial intermuscular ossifications. The most anterior element of the dorsal series is associated with P4. A strong reticular lattice is formed over the abdominal flanks and the caudal reinforcements are slightly developed.
BRANCHIAL SKELETON

In the review below the terminology established by Nelson (1969a) is used, and the hyoid arch, gill support, and the inferior pharyngeal bone (modified 5th cerato-branchial) are considered in turn.

In noemacheilids the basal plate of the urohyal is usually produced into paired limbs anteriorly, but these limbs are minimally developed in *Leufa* and *Oronectes*. It is noted that the urohyal of *Ellopostoma* is considerably expanded. The urohyal of *Gastromyzon* is a wide T-shaped bone.

In the Cobitini the urohyal is narrow. It is usually divided anteriorly, but it is not so in *Acanthopsis*, *Niwaella*, or *Cobitis taenia*.

The anterior fork of the urohyal is shallow in all Botini and absent in *B. macracantha*.

The shape of the urohyal in representatives of ostariophysean outgroups examined indicates how the proportions of this bone generally reflect those of the throat. It appears to be an unusual but not unique condition amongst the Ostariophysi that the urohyal should fail to show any anterior forking. I interpret absence of forking as a repeatedly derived condition in cobitoids.

The noemacheiline basihyal is typically T- or Y-shaped. In *Noemacheilus strauchi*, *N. nigromaculatus*, *Orthias* and *Leufa* there is effectively no division of this bone anteriorly. There is no division of the basihyal anteriorly in *Vaillantella*. The basihyal is a "Y" shaped ossification in *Glaniopsis*, *Gastromyzon* and *Homaloptera* and in *Ellopostoma*. 
In Cobitini the basihyal is of variable shape. It is effectively a simple rectangular bar of bone in *Acanthopsis*, and peculiarly reduced to a small lozenge of bone in *Somileptes*. It is most usually slightly expanded anteriorly, but forms a fork anteriorly in *Lepidocephalus annandali*.

The basihyal in Botini is usually a simple bar-shaped bone. It is divided anteriorly in *Botia macracantha* and *B. almorhae*.

Nelson [1969a] described the widely anteriorly forked basihyal of the Homalopteridae as peculiar, and he suggested that its condition is foreshadowed by the more limited forking of the basihyal of *Noemacheilus*, and by the anterior broadening of the bone shown by *Misgurnus*. Nelson concluded from this that the Homalopteridae are probably most closely related to the Cobitidae, especially those of the subfamily *Noemacheilini*, and that there is no support for a polyphyletic origin of homalopterines and gastromyzonines. My observations on the basihyal endorse this conclusion. I interpret a forked basihyal as plesiomorphic in cobitoids.

In cobitoids, between the urhyal, basihyal and hypohyals of each side, "sublingual bones" posterior basihyal [Ramaswami, 1952:3] supplementary basihyal [Weisel, 1960], basihyal [Branson, 1962] frequently feature. The possible origin and phylogenetic significance of these has received some consideration in the literature. Nelson [1969a] pointed out that such a sublingual bone could be a modified basihyal because this bone is anyway invariably present, and that the sublingual could not be a basibranchial because
although he considered that the first basibranchial was absent from cobitoids (p.320), the first basibranchial was present in some catostomids in which a sublingual also developed. Nelson considered the sublingual should be interpreted as a *de novo* ossification of limited distribution.

In the *Noemacheilini* (fig.Lxxxiiia) sublingual ossification is developed as 2 fusiform elements which are dorsal and ventral in position. These ossifications are absent only from *N. nigromaculatus* of all noemacheilin species examined. They are also absent from *Vaillantella*.

In *Ellopostoma* (fig.Lxxxiiib) the sublingual bone is a single robust quadrilateral wedge. It is similarly developed in homalopterines and gastromyzonines (fig.Lxxxiiic).

In the *Cobitini* there are 2 small fusiform sublingual ossifications present in *Lepidocephalus annandali* (fig.Lxxxiiid) and *L. thermalis*, *Sabanejewia*, *Niwasila* and *Misgurnus*. A single plate-like sublingual is present in *Lepidocephalus guntea* (fig.Lxxxiiiia), *Acanthopsis choiro-rhynchus* and *Cobitis taenia*. Sublingual ossification is absent from *Lepidocephalus caudofurcatus*, *Somileptes* and *Acanthophthalmus*.

Of the *Botini*, there is no sublingual ossification in *Leptobotia*, but in all species of *Botia* (fig.Lxxxiv) there are 2 fusiform sublingual bones of the noemacheilin type.

In non-cobitoid ostariophyseans sublingual ossification is recorded in many gobioines (*Saurogobia*, *Abbottina*, *Sarcocheilichthys*, *Pseudogobio* and *Pseudorasbora*) where it is a single bone which is sometimes bicornuate dorsally
[Ramaawami, 1955a]. A single, solid sublingual bone is also present in the Catostomidae [Weisel, 1960]. As sublingual ossification is frequently absent from, and occasionally appears in Ostariophysi other than the cobitoids, it is not possible to define the level of universality at which the sublingual is plesiomorphic. I interpret the loss of the sublingual a repeatedly derived condition in cobitoids.

The hypohyals of cobitoids have no peculiarities.

The ceratohyal of noemacheilids is a simple bar of bone. In Cobitini the ceratohyal is rather longer and slimmer than in noemacheilids, but also simple. The ceratohyal of Botini shows a tendency to undergo extreme shortening. This condition is maximally expressed in *B. macracantha* and *B. almorhæ* [fig. Lxxxivb] in which the ceratohyal is truncated and crumpled in appearance. In other Botini shortening is less severe [fig.Lxxxiva]. The peculiar condition of the ceratohyal in *B. macracantha* and *B. almorhæ* is investigated as a possible synapomorphy on p.341.

In all cobitoids the epihyal is a more or less robust triangular plate which in Botini is as long as or longer than the ceratohyal because the ceratohyal is so short in this taxon. In cobitoids the interhyal is typically a cylinder of bone. However, the interhyal does not ossify in *Glaniopsis* and many homalopterids. The interhyal is also lost in several other ostariophysean taxa. It is absent from siluroids and the gymnotid *Hypopygus*. It is reduced in *Catostomus* and *Gyrinocheilus*.

Three plesiomorphic branchiostegal rays develop in all
In considering the basibranchial skeleton, the basibranchial ossifications are attributed the name or number of the paired arch elements behind them. Nelson [1969a] emphasised that this nomenclature is practiced for convenience only, as the exact composition of basibranchial copula elements is not established.

Nelson discussed two developmental trends manifested in the cobitoid basibranchial skeleton. The first was the "invariable" absence of the B61 recorded by him in cobitoids and catostomids. The second trend was the occasional representation of additional posterior basibranchial elements. Nelson pointed out that in "some cyprinoids - mainly, if not exclusively catostomids, cobitids and Homalopteridae and may be some siluroids, a tooth plate overlying the 4th and 5th basibranchial has transformed to an ossified 4th or 5th basibranchial". It appears that both those developments discussed by Nelson are associated with the provision of posterior support for a wide branchial skeleton.

The basibranchial copula system and the paired hypobranchial elements become derived in various ways within the cobitoids. In Noemacheilini there are 3 or 4 basibranchials. The 4th basibranchial which is present in N. fasciatus, Aborichthys, and many Indian species of Noemacheilus is usually a small, solid and cuboidal element. In Vaillantella only 2 basibranchials are present. In all other noemacheilids there are 3 basibranchials. The anterior of the basibranchials may be considerably transversely
expanded to form a yoke between the hypobranchials. This condition is clearly shown in Homaloptera. It is extremely developed in Ellopostoma [fig.Lxxxva].

Three hypobranchials are present in all noemacheilid species except Aborichthys elongatus in which a reduced 4th hypobranchial also develops. The HB1 is short. It is a distinctive feature of noemacheilids that HB1 makes a more or less loose saddle articulation with the posterior hyohyal. The HB1 develops as distinct anterior process to achieve this articulation in Ellopostoma.

In the cobitine basibranchial chain there are usually 4 elements of which the 4th is frequently unossified. A reduction to 3 basibranchial elements is only recorded in Somileptes [fig.Lxxxvb]. The BB2 is typically T-shaped. It is particularly transversely expanded anteriorly in Lepidocephalus thermalis and Acanthophthalmus muraeniformis [fig. Lxxxvc]. A 4th pair of hypobranchials, developed as a pair of lumbriform cartilages, is common in Cobitini. The tendency to develop 4 pairs of hypobranchials is an occasional ostariophysan condition, of which Nelson (1969a) cited the cobitine Misgurnus as an example. As in noemacheilids an HH-HB articulation is made in all Cobitini. The HB1 is considerably elongated towards the posterior hypohyal in Niwaella. This development is hypertrophied in Somileptes [fig.Lxxxvb] and Acanthopsis, and this is investigated as a synapomorphy for these 2 taxa on p.337.

In Botini 2 basibranchials are ossified and, posterior to these, there are usually 2 more basibranchial elements produced in cartilage only [fig.Lxxxvd]. The HB1 is short.
It invariably achieves an intimate saddle articulation with the hypohyal skeleton. There are 3 pairs of hypobranchials in Botini with a 4th hypobranchial in cartilage seen only in *B. sidithimunki*.

Mayden considers [pers. comm. fig. Lxxxvi] that the Gyrinocheilidae and Catostomidae are related because uniquely in these taxa, only 2 hypobranchials are present. While my observations on *Gyrinocheilus* agree with those of Mayden, I consider that this hypothesis should be treated with caution because it utilises a character of branchial reduction in two taxa in both of which there are extreme peculiarities of pharyngeal feeding from which no satisfactory synapomorphic features have been assembled.

Mayden further suggests that the cobitoids, together with the Gyrinocheilidae, and Catostomidae can be defined as a monophyletic assemblage, because these 3 families share possession of an expanded ostariophysean condition of 4 basibranchial copulae. I consider this hypothesis is weakened by the presence of multiple copulae in various silurids. It is further weakened by the condition of the gonorhynchiform basibranchial chain shown by *e.g. Parakneria*, which includes 4 elements, with BBI having been lost. There are also 4 ossified copulae in *Psilorhynchus*. The presence of 4 basibranchial elements appears to be plesiomorphic at this level.

The articulation made between the HBI and the posterior hypohyal, which is developed to some extent in all cobitoids, was also recorded by Ramaswami [1955a] as a feature of almost all gobioines. I have not observed the articulation in any
other group. I suggest that the development of this articulation in cobitoids and gobioines should be interpreted as a parallelism in these two taxa, which is associated with the development of yoked hypobranchials and the sublingual ossification described (p.317-9). There is also a peculiar basihyal modification in Gyrinocheilus symonieri, in which the hypohyals are extraordinarily elongate and the ceratohyal forms a ball-and-socket joint with the anterior hypohyal only. I interpret this as another highly specialised, different form of hyoid yoking, the development of which corroborates a hypothesis of parallelism in cobitoids and gobioines.

The epibranchial skeleton of cobitoids presents rather a mosaic of characteristics. Four epibranchials develop in all Ostariophysi. Nelson (1969a) pointed out that the 5th epibranchial is only discernible as a cartilage associated with EB4 and that CB5 is supported by the more or less expanded basal portion of EB4. Nelson further pointed out that EB5 should not be considered as incorporated into the dorsal hook-like process which frequently decorates EB4.

In Noemacheilini a dorsal hook on EB4 is observed only in N. fasciatus and N. denisonii. In Oronectes EB3 bears a dorsal process. However the 4 epibranchials of Noemacheilini are usually anunciate. The epibranchials are also anunciate in all other noemacheilids except in Ellopostoma (fig.Lxxxviib) where a large hook on EB3 is present.

In Cobitini (fig.Lxxxviic) the epibranchials are delicate and rarely develop dorsal processes. A small spinous
process on EB4 is present in Misgurnus. A small spinous process on EB3 is noted in Cobitis taenia, Acanthopsis, and Acanthophthalmus semicinctus.

In Botini (fig.Lxxxviid) there is a process on EB4 in all species except B. sidthimunki. There is also a process on EB3 in Leptobotia elongata and B. almorhae.

Numerical decrease in the infrapharyngobranchial skeleton is evident throughout the teleosts and this part of the branchial skeleton of cobitoids is also reduced. Nelson (1969a) stated that the infrapharyngobranchial ossifications may reduce into their own, or into adjacent epibranchials and that this may in itself indicate that infrapharyngobranchials are interarcual rather than arcual structures. It is evident that infrapharyngobranchial reduction processes have taken place many times during teleostan evolution.

In the infrapharyngobranchial skeleton of Noemacheilini there are usually 2 ossified elements in positions 2 and 3. These elements tend to be long and slim, especially the more posterior of the two which extends towards EB4. Peculiarly in Noemacheilus yarkandensis (fig.Lxxxviia) only a single infrapharyngobranchial (1FB), identified as number 3, is present. In N. fasciatus a 3rd 1FB, identified as number 4 is present in cartilage. In all other noemacheilids 2 ossified 1FB's are present.

In Cobitini, as in noemacheilids, most usually 2 1FB elements are present. A 3rd element (1FB4) is seen as a robust chondrification in Acanthopsis and Acanthophthalmus semicinctus. Only a single 1FB[3] is present in
Lepidocephalus annandali and Somileptes (fig.Lxxxviic). In all Botini there are two IFB bones, the posterior of which is subject to considerable elongation. There is additionally a third, partially ossified element, developed in Botia macracantha and B. hymenophysa.

A review of the epibranchial skeleton of representatives of ostariophysian outgroups emphasises how frequently reductions have taken place in this. It is clear that the presence of dorsal processes on EB4 and EB3 are common developments. Similar processes may also develop on EB2 and EB1.

In the light of the suggestion of relationship between the cobitoids, Gyrinocheilidae and Catostomidae made by Mayden, I note that in Catostomus (fig.Lxxxviie) the dorsal processes on EB1-3 are very well developed and may extend to articulate with IFB2, IFB3 and EB4 respectively. In Gyrinocheilus (fig.xxxviif) the dorsal epibranchial processes are also hypertrophied. In Gyrinocheilus EB1, EB2 and EB3 are stout Y-shaped bones and they articulate with each other and with consecutively. This epibranchial chain is yoked dorsally by 3 large IFB ossifications. A similarly derived and reinforced condition of the epibranchial skeleton is not seen amongst Otophysi other than the Gyrinocheilidae and Catostomidae. These observations on the epibranchial skeleton appear to support a hypothesis of relationship between the Gyrinocheilidae and Catostomidae. However, I note the epibranchial skeleton of Parakneria witti where the processes on EB1-3 extend to articulate with processes from bar-shaped IFB2, 3 and 4 elements which
ossify in this taxon. I suggest that this epibranchial condition of *Parasknoria* raises the level of universality at which intimate interlock between adjacent epibranchials can be considered to be apomorphic. I suggest that the peculiar condition of the epibranchial skeleton in *Gyrinocheilus* and *Catostomus* may be a parallel development in these 2 taxa, correlated with the unusual straining feeding mechanisms they employ. Further I emphasise that there is no such supportative skeletal elaboration displayed in *Ellopostoma* in which straining feeding apparently occurs, and this observation weakens a hypothesis of close relationship between Gyrinocheilidae, Catostomidae and cobitoids.

I have not observed reduction of the infrapharyngobranchial skeleton to a single element in ostariophyseans outside the Cobitidae. I interpret this reduction as a repeatedly derived cobitid condition. In most Otophysi there are 2 IFB's ossified with an occasional third element in cartilage.

The condition of the modified 5th ceratobranchial or inferior pharyngeal bone in cobitoids has been the subject of much discussion in the literature on the issue of the primitive form, and systematic significance, of cyprinoid pharyngeal dentition. Central to the problem here is the apparent similarity of the arrangement of the pharyngeal dentition in cobitids and catostomids. It is important to this study that the significance of this similarity should be investigated. In both catostomids and cobitids a single row of numerous pharyngeal teeth is developed, while by
contrast in the cyprinids the pharyngeal teeth may lie in one, two or three rows on the pharyngeal bone. Sagemahl [1891], Boulenger [1904], Berg [1912], Nicholls [1943], Darlington [1957] and Weisel [1960] concluded that a single row of teeth probably represented the primitive cyprinoid condition. In contrast a triple row of pharyngeal teeth was interpreted as probably representing the primitive condition subject to derivation by reduction, by Chu [1935], Vasnecov [1939], Ramaswami [1957], Greenwood et al. [1966] and Nelson 1969a).

Attempts have been made to resolve the dilemma above by ontogenetic study. Weisel [1967] showed that, although larval Catostomus do not develop more than one row of pharyngeal teeth, there is still a distinct dental succession in ontogeny from teeth very like those of both larval cyprinids and larval cobitids, to a mature type of catostomid tooth which type shows some degree of molarisation. Weisel considered that this demonstrated that catostomids are phylogenetically separate from, and at least as specialised as the Cyprinidae. Eastman [1977] emphasised the specialised nature of catostomid dentition.

Nakajima [in press] stated that it can be generally concluded that amongst cyprinoids, a multirowed larval dentition is a recapitulation of a common ancestry shared with cyprinids. However, he pointed out that the minor row of dentition appears late in cyprinid ontogeny and thus a multiple row arrangement cannot be interpreted simply as the primitive condition. Nakajima compared the dental ontogeny of the cobitid Misgurnus with that of the catostomid
Catostomus and observed that in both these the first tooth to ankylose to the inferior pharyngeal bone assumed position 2. He interpreted this as a shared characteristic of Cobitidae and Catostomidae which distinguished them from the cyprinids (fig. LXXXVIII). Nakajima also pointed out that in cyprinoids the tendency of teeth to develop anteriorly or posteriorly on the pharyngeal bone is generally correlated with the extent of development of the subtemporal fossa and of the pharyngeal retractor muscle. He suggested that the tendency for the teeth to develop more posteriorly as in cobitids and catostomids, accompanies the reduction of the subtemporal fossa which is shared by these two groups (p.215-8).

Within the cobitoid group the morphology of the inferior pharyngeal bone varies rather little (see fig.LXXXIX). In the Noemacheilini the shaft of the bone is gently curved. It usually bears 10-15 teeth in a single row, some of which are not ankylosed to the bone basally. Some increase in tooth number is noted in N. yarkandensis (19-24) Oronectes (22024) and N. botia and N. denisonii (16-18). The bone invariably bears a very characteristic digitiform prong-like process issuing laterally from the slightly expanded tooth-bearing part, and this provides the insertion for the pharyngeal retractor muscle.

In Vaillantella the inferior pharyngeal bone is long and slim. It bears 7 teeth on a rather restricted round basal plate. It has a digitiform lateral process. In Ellopostoma there are some 40 teeth in a single row on the pharyngeal bone. The digitiform lateral process is blunt.
In _Glaniopsis_ and _Gastromyzon_ the pharyngeal bone is like the noemacheiline type. In _Homaloptera orthogoniata_ approximately 25 teeth ossify on the pharyngeal bone. The digiform lateral process is particularly long in this species. Unlike in other cobitoids the subtemporal fossa is present in homalopterines [p.217].

The presence of both a subtemporal fossa and a prong-like process on the pharyngeal bone in _Homaloptera_ means that there is not a simple correlation between reduction of this fossa and production of a prong-like process on the pharyngeal bone in cobitoids. However, I suggest that these two characteristics are linked, and that the prong-like process on the pharyngeal bone is developed to provide leverage at the insertion of the pharyngeal retractor, which is absent at the origin of this muscle because the subtemporal fossa is absent. If this is the case then the subtemporal fossa of both _Homaloptera_ and _Ellopostoma_ is apparently secondarily derived. I suggest that the development of the prong on the inferior pharyngeal bone in cobitoids is also correlated with minimisation of basioccipital involvement with mastication in this group [see p.232-3], and with the cranial immobility which results from post cranial capsule formation.

In the Cobitini the inferior pharyngeal bone is slim. It bears 6-10 teeth in _Niwaella_ and _Acanthophthalmus_, but more typically 10-15 teeth. The lateral process is invariably raised as a slim digitiform prong of bone.

In the Botini there are 5-6 teeth in _Leptobotia_, and 5-10 teeth in _Botia_. The digitiform lateral process is
similar to that of other cobitoids.

A detailed discussion of the numerical condition of pharyngeal dentition in cobitoids is beyond the scope of this project. It is generally noted that the number of teeth forming in a row is diet-linked, with an increase in number generally reflecting decrease in size of the usual food particles taken by a species.

The distinctive prong-like lateral process present on the inferior pharyngeal bone is of interest as such a process is not found outside the cobitoid group. In cyprinids the pharyngeal retractor muscle inserts on a flange, crest or ridge of bone on the pharyngeal bone. The muscle inserts similarly in Gobioinae, Psilorhynchus, Catostomus, silurids and gymnotids and in characins [Weitzman, 1962]. Thus I interpret the digitiform production described in cobitoids as characteristic of the group. It must be considered in complex other characters involved with pharyngeal feeding, including the pharyngeal processes and the subtemporal fossa. The prong-like process of the pharyngeal is further investigated as a possible cobitoid character on p.332.
SUMMARY OF CONCLUSIONS
It is proposed that a natural group which can be identified as the Cobitoidae should be recognised, including two subgroups, namely the Noemacheilidini and the Cobitidini. The Cobitoidae can be defined on the development of an anterior adductor mandibulae division (the m. rostralis p.39-60) and apparently also on the presence of a characteristic prong-like process for the insertion of the levator muscle of the inferior pharyngeal bone (p.328).

The Noemacheilidini are indicated as the plesiomorphic sister assemblage of the Cobitoidae as in these the adductor mandibulae is in its least elaborate form. However dissemination of the Noemacheilidini into phyletic lineages is problematic and the interrelationships of its component groups is not substantiated.

Three alternative hypotheses of the possible relationships of the noemacheilid Ellopostoma were made available from myology (fig. xvii). From the form of the process on the inferior pharyngeal bone (p.115) it is concluded that Ellopostoma is a member of the Noemacheilidini despite its peculiar m. rostralis morphology. It is further concluded that:

- lacking lateral occipital fenestration (p.119)
- lacking a prepalatine ossification (p.174)
- developing a subtemporal fossa (p.100)
- the disposition of the barbels (p.91)
- the form of the swimbladder capsule (p.294-5)

Ellopostoma is indicated as more closely related to the homalopterines and gastromyzonines together than to the noemacheilines, showing particularly homalopterine
similarities. Thus I interpret the aberrant m. rostralis form of Ellopostoma as derived not progenitive and the hypothesis in fig.xviib is chosen although xviiia cannot be refuted.

I have not made a full osteological examination of a full range of homalopterines and gastromyzonines but I have accepted the conclusions of Chen [1978, 1980] that these are two naturally distinct groups, which together do comprise a monophyletic assemblage. With this in mind, a hypothesis of relationship for the homalopterines and gastromyzonines within the Noemacheilidini is put forward (fig.xC). This hypothesis is substantiated by combined myological and osteological evidence. I suggest that the Homalopteridae (including Glaniopsis) possess as a specialised feature, the development of a pectoral girdle-swimbladder articulation (p.263), and point out that this specialisation is not shared by Ellopostoma and Vaillantella or the Noemacheilini. However, Ellopostoma does develop:-

- a notch in the cleithrum in which articulates the inferior pharyngeal bone (p.105-6)
- an articulation between the SN2 and the exoccipitals and supraoccipitals (p.111)

and thus appears to show a predisposition to stabilise the post-cranial region.

The relationship of Vaillantella to the Noemacheilidini and to the Cobitidini remains enigmatic.

The evidence derived from myology suggested that Vaillantella is best interpreted as a derived noemacheiline, which on the basis of several characteristics appears to be
more closely related to the Cobitini than any other noemacheilid. These characteristics are:

- The narrow ethmovomerine region (p. 182)
- Swimbladder capsule form (p. 311)
- The production of a small orbitosphenoid platform (p. 204)
- The long narrow frontals (p. 242)
- The absence of tripus truncation (p. 296)

However, the lateral occipital fenestra is absent from *Vaillantella* (p. 128). The absence of this fenestra may be a characteristic condition of non-noemacheiline noemacheilids (p. 219). If this is accepted, then *Vaillantella* must be concluded to occupy the position shown in fig. xCia, and the characteristics it shares with Cobitini must be interpreted as parallelisms. If the hypothesis illustrated in fig. xCib is chosen, reticulation must be invoked to account for the absence of the lateral occipital fenestra from *Vaillantella*, or respecting that the fenestra does not develop in non-cyprinoid Ostariophysi, the absence of the fenestra must be interpreted as plesiomorphic. I cannot choose between fig. xCib which concurs with Nalbant & Banarescu (1977) (fig. xixc) and indicates the *Vaillantellini* as a discrete phyletic group of the Cobitidae, and fig. xCia which suggests that *Vaillantella* occupies a position in relation to the Homalopteridae, parallel to the position occupied by the Cobitini in relation to the Noemacheilini although this second hypothesis is attractive.

I am unable to resolve the trichotomy presented between the Noemacheilini, the Homalopteridae, and the Cobitidini.
Two of the possible alternative solutions to this are shown on xCia and xCib.

On the basis of the morphological characteristics investigated in this study I conclude that almost all the species included in the Noemacheilini are members of a single phyletic lineage. I conclude that the extreme osteological and myological stability I have observed within the Noemacheilini is in itself significant, and I consider that morphological variations within the group can be shown to be adaptive, or of mosaic distribution and therefore cannot be attributed phyletic significance.

I consider that only Oronectes, Lefua and Noemacheilus nigromaculatus are phylogenetically distinct from the other Noemacheilini examined here. Oronectes and Lefua are united together by their peculiar double orbitosphenoid condition [p.204]. Noemacheilus nigromaculatus has a uniquely bordered cranial fontanelle [p.245], lack m. intermandibularis [p.33 ], and lacks sublingual ossification [p.318 ], sharing the last condition only with Vaillantella of all the noemacheilids examined. Oronectes with Lefua and N. nigromaculatus all deviate from the typical noemacheilin form in possessing wide supraethmoid and frontal bones [p.239 ] and in the construction of their anterior trigemino- facial foramen [p.211 ]. The condition of the supraethmoid and frontal bones and of the anterior trigemino-facial foramen of Oronectes, Lefua and N. nigromaculatus can be interpreted as that which is more or less plesiomorphic amongst noemacheilids.

Banarescu & Nalbant (1968) appreciated the historical
recognition of *Oronectes* and of *Lefua* as distinct from other Noemacheilini in proposing the division of the Noemacheilini into 3 genera, namely *Oronectes* (embracing *Lefua*) and *Aborichthys* only. In this paper Banarescu & Nalbant questioned the validity of the genus *Aborichthys* and I, in disagreement with Hora (1925), conclude that *Aborichthys* is a synonym of *Noemacheilus*, as I can find no apomorphy by which to attribute phylogenetic separation to it. However, I consider that *Oronectes*, with *Lefua* and with *N. nigromaculatus*, demands separate phyletic status from other Noemacheilini. I illustrate these 3 species as forming an unresolved trichotomy either [Fig. xCib] as the plesiomorphic sister-group of the main noemacheiline lineage, or [Fig. xCia] as the plesiomorphic sister-group of the non-noemacheilinae noemacheilid assemblage, and thus separate from the Noemacheilini as currently recognised. With the exclusion of the aberrant taxa above it is possible to define the Noemacheilini on the basis of their shared frontal shape (p.238-9), and I emphasise that I consider that the Noemacheilini contains only one natural group namely the genus *Noemacheilus*.

There are several osteological characters and character complexes by which the Cobitini can be defined, but it should be recognised that these characters are autapomorphic to the Cobitini and thus do not elucidate the relationship of this taxon to other cobitoids.

These characters include:

- the mobile ethmoid (p.186)
- extremely reduced orbitosphenoids and pterosphenoids (p.211)
- a lateral cleithral spur (p.263)
- fusion of the parhypural and the haemal spine of the first preural centrum to the ural centrum and the first preural centrum
- fusion of P4 to the fourth vertebra in formation of the swimbladder capsule.

The osteological study carried out here makes it possible to suggest cobitine intrarelationships [fig. xCii]. Two lineages or Cobitini are indicated on the basis of the presence or absence of a spur-like process on the medial aspect of the cleithrum. The lineage in which the spur is present embraces:

**Acanthophthalmus** which is defined as a natural group on the basis of the peculiarly posteriorly displaced pterosphenoid [p.209].

**Acanthopsis** and **Somileptes** which appear to be united together as a natural group on the basis of:

- the anteriorly displaced pterosphenoid [p.209]
- a single lateral swimbladder capsule aperture [p.298]
- the presence of a bony flange on the palatine [p.178]
- the presence of processes on the pterotic which articulate with the pectoral girdle [p.279].
- the form of the pharyngeal processes of the basioccipital [p.232]
- the presence of tubercular processes on the lateral face of the maxilla [p.165].
- elongation of HB1 [p.321]

Furthermore each of these 2 taxa shows a separate specialisation of the preethmoid bone. In **Somileptes** the preethmoid provides insertion for the A1dd division of the
adductor mandibulae (p.43 ) and in Acanthopsis the pre-ethmoid is phenomenally elongated.

There appears to be phylogenetic affinity between Somileptes and Lepidocephalus. This affinity can only be demonstrated cladistically if reticulation is invoked to account for the absence of the derived lateral occipital fenestra condition in Lepidocephalus annandali (p.121). If this is allowed, L. annandali is indicated as an aberrant Lepidocephalus. The position of L. annandali as such is substantiated by the myological hypothesis (p.46, p.70). I suggest that this species may display neotony (Nelson & Platnick, 1981, p.344).

The phylogenetic position of the cobitine Niwaella remains speculative. I consider the tentative suggestion of relationship between it and the genus Acanthopsis proposed from adductor myology (p.71, fig.xx) to have gained little substantiation from osteology. Niwaella shares a condition of some elongation of H81 with Acanthopsis and Somileptes (p.321). However, Niwaella can be distinguished from all other Cobitini by the autapomorphic condition of the upper jaw (p.158) and by features of its adductor mandibulae (p.43).

I suggest tentatively that Niwaella occupies the phylogenetic position shown on fig.xCii.

I can only define a Cobitis-Misgurnus lineage on the shared capacity of the males of its member species to elaborate the pectoral ray 0 + 2 into a sexual feature (p.215). However, this characteristic is not manifest in all members (p.271-2).
The genus *Misgurnus* is united by the degenerate condition of the suborbital spine. I consider *M. fossilis* to be the plesiomorphic sister species of the other members of the genus, because of *Misgurnus* species, only in *M. fossilis* is the A1LE division of the *adductor mandibulae* present \[p. 42\]. However, *M. fossilis* males apparently do not develop a *lamina circularis* feature on the pectoral ray \([0 + 2, (p.271)\]. The absence of this feature must either be assumed to be the result of a secondary loss, or as a derived character uniting the *Misgurnus* species other than *Misgurnus fossilis*.

The relationship between *Cobitis* and *Sabanejewia* is obscured by the same problem, i.e. the absence of development of a pectoral ray 0 + 2 sexually dimorphic feature \([the organ of Canestrini in \(Sabanejewia\) \(p.271\). It can be concluded that *Sabanejewia* occupies a similar phyletic relation to *Cobitis*, that *M. fossilis* does to the other *Misgurnus* species - i.e. *Sabanejewia* is the primitive sister of the *Cobitis - Sabanejewia* assemblage. In this case the organ of Canestrini of 0 + 2 of *Cobitis* can be considered as a separate evolutionary development from the laminar circularis of the 0 + 2 of *Misgurnus*. Alternatively it can be concluded that the 0 + 2 development does unite the lineage, but is separately not manifested in *Sabanejewia* and in *M. fossilis*. I prefer the second of these alternative solutions. I do not consider *Sabanejewia* deserves a separate generic status from *Cobitis*.

The preliminary hypothesis of botine phylogeny based on developments of the anterior *adductor* element \(m.\)
rostralis) and shown in fig. xxiv has been largely substan-
tiated by osteological investigation (fig. xCiii).

Leptobotia is the plesiomorph botine genus, and can be proposed to occupy a phyletic position between the Cobitini, and other Botini. Of this genus L. elongata is aberrent. This species displays a derived condition of the m. rostralis (p.75-6). It also has an unbifid suborbital spine (p. 196 ] which I interpret as a condition derived by simplification. Leptobotia elongata shares some characteristics with species of Botia, including the absence of a cranial fontanelle which also occurs in B. superciliaris and a parietal-epioccipital socket for the posttemporal and single parasphenoid foramen which also occur in B. almorhae (fig. xCiii).

The genus Botia is clearly defined as a monophyletic assembly on the basis of the:-

- complete representation of m. rostralis max
division of the adductor mandibulae (p.76 )
- presence of a frontal notch accommodating the lateral ethmoid (p.140 )
- development of the orbitosphenoid platform (p.205-6)

Within Botia I interpret the species in which there are 2 bellies of m. rostralis as constituting the plesiomorphic sister group of the other Botia (p.76 ). Sinibotia is a member of this group of species (p.76 ).

After osteological analysis I conclude that development of the triple m. rostralis condition has taken place more than once in Botia and thus the triple condition does not necessarily per se unite a natural assemblage of species.
Two apparently distinct lineages of Botia show the triple condition of m. rostralis. There is one lineage in which the 3 bellies show the "ssd" configuration [p. 51]. This lineage can be further defined by the presence of the pre-maxillary aperture [p. 159]. This lineage is the Hymenophysa species group [p. 47]. The other lineage, in which the 3 bellies of rostralis shows the 'add' configuration. This lineage can be further defined by the development of a prong-like process on the entopterygoid bone [p. 147]. This includes the Modesta species group [p. 47] and also apparently includes B. almorhae. Botia almorhae is the type species of Botia, and thus this group is Botia s. str. Within Botia s. str., B. almorhae appears to be separately derived over the other species. B. almorhae shares with B. macracantha an unusually short condition of the ceratohyal [p. 319] and two distinctive characteristics with Leptobotia elongata [fig. xCIII]. However, none of these above conditions is actually unique to Botia almorhae.

The phylogenetic position of B. macracantha remains enigmatic. It shares the crumpled ceratohyal condition with B. almorhae. However, B. macracantha is unique amongst Botia, in the single condition of its m. rostralis. Therefore, either the shared crumpled ceratohyal condition must be rejected and interpreted as a parallelism between B. macracantha and B. almorhae or the 'add' triple rostralis, and entopterygoid prong of B. almorhae must both be assumed to have been lost from B. macracantha. This latter alternative is prohibited by parsimony. A third solution to this problem would be to invoke reticulation, and allow
that *B. macracantha* is more closely related to *B. almorhae* than to any other *Botia*. A similar assessment must be made of the features shared between *B. almorhae* and *L. elongata*. I have illustrated non-reticular solutions to both these problems in fig. xCiii. I can define four discrete lineages of *Botia*, *Botia s. str.*, *Hymenophysa*, the *B. geto*, *B. robusta*, *B. superciliaris* group, and *B. macracantha*.

**Summary of Outgroup Indications**

While the cobitoid group can be defined clearly on characters of the *adductor mandibulae*, the relationship between the group and any other Ostariophysean is not indicated by myological characteristics. The comparative osteological review on p.141 - p.330 shows that most of the osteological features that have been considered in the literature to show relationship between the cobitoids and various other ostariophysean taxa, actually have a mosaic distribution through the Ostariophysi. The significance of other osteological features is obscured by parallel development to which can easily be attributed functional and adaptive significance. Under strict cladistic criticism these characteristics are invalidated as indicators of relationship, and I find I am unable to offer any positive conclusion on the cobitoid interrelationship problem.

Analysis has shown that the 'cyprinid' features of cobitoids, i.e. the presence of a *kinethmoid*, *preethmoids*, and of lateral occipital fenestrae are actually plesiomorphic at a greater level of universality than can render
them indicators of immediate relationship between the cobitoids and the cyprinids. The cobitoids differ distinctly from typical cyprinids in the morphology of the trigeminofacial chamber (p.212-3), on the development of their basioccipital masticatory apparatus (p.230), on the development of the Weberian apparatus (p.310) and on barbel developments (p.86-7). Furthermore the cobitoids do not display the forked posttemporal bone which is typical of the cyprinids (p.258).

None of the features common to the Gobiinae and cobitoids which have been discussed in the literature, e.g. the elaborations of preethmoid ossification (p.167-176) the presence of a cranial fontanelle (p.244), and of sublingual bones (p.318-9) actually constitute synapomorphies. Comparative swimbladder capsule morphology serves to emphasise the separateness of these two groups (p.304-5).

Gyrinocheilus was shown to be very peculiar in the form of its adductor mandibulae and upper and lower jaws, and in association with these developments the failure of pharyngeal dentition in this taxa. Gyrinocheilus has a forked posttemporal bone, which seems to indicate it has a common ancestry with the cyprinids. However, in some branchial features, Gyrinocheilus resembles at least superficially, both Catostomus, and the cobitoids (p.312) and Gyrinocheilus also shares the presence of oesophageal processes on the swimbladder encapsulation with Catostomus (p.305-6). I am not led to conclude that either of these developments are necessarily strictly synapomorphic for these 2 taxa. I note that the lachrymal bone of Gyrinocheilus encloses a canal
in distinct contrast to the condition observed in *Catostomus*, and in the cobitoids, and consider it is unlikely that there is any immediate phyletic relationship between the Gyrinocheilidae and the cobitoids.

The phyletic position of the Psilorhynchidae in relation to other cyprirnoid taxa remains unclear. The hypothesis proposing psilorhynchid-cobitid relationship made available from myology (p.79-80) can be tested with, and is not refuted by, preethmoid (p.168-74), lateral ethmoid, (p.200-2) and orbitosphenoid morphology. However, from the form of the swimbladder capsule, and from the presence of a canal carrying lachrymal I consider it unlikely that there is any immediate relationship between the Psilorhynchidae and the cobitoids.

There are many general morphological resemblances between the catostomidae and the cobitoids. Furthermore, these two taxa share similarities of preethmoid (p.172-3) and of branchial anatomy (p.322), a reduced condition of the subtemporal fossa (p.217), and a cephalic canal system which is separated from the bones of the skull roof (p.247-8) but it has been shown in the discussion that none of these characteristics can actually be used to define relationship. The catostomids also resemble the cobitoids in developing a substantial lachrymal plate which excludes the lachrymal canal (p.257), and an intermandibularis muscle which is like that of cobitoids (p.80-80). However, while the posttemporal is unforked and hiliform (p.258), the disposition of the ossa suspensoria in Catostomidae is typically cyprinid (p.310). The relationships of the
Catastomidae remain in question.

I consider the general similarities between the gymnotids and cobitine cobitids to be at one level interesting examples of morphological parallelism between anguilliform species. However these similarities seem also strongly to suggest a concentration of shared ancestry within the Ostariophysi which, even when the 'morphological gap' criterion is abandoned, provokes the problem of assessing the intrarelationships of the group.

There are also some rather specific similarities between some gymnotids and cobitids. For instance, I observe the loss of SN2 in the Charachphysi [Fink & Fink, 1981] and in Botia [p.302]. Furthermore the lachrymal bone does not enclose a sensory canal in gymnotids and this condition is shared with catostomids and cobitoids [p.250]. Establishing the level at which this lachrymal condition might be a valid synapomorphy is made more difficult, and the hypothesis of relationship it might indicate is weakened by the lability of the morphology of the ethmoid flank region, and the apparent multiple occurrence of very reduced anterior sensory canal bearing ossifications throughout the Ostariophysi [see p.247]. However, the presence of the canal excluding condition of the lachrymal bone and the close association of the m. adductor mandibulae with that bone [p.251] occurs in gymnotids, cobitoids and catostomids and is unusual amongst Ostariophysi. It is interesting to explore the possibility that the gymnotids, cobitoids and catostomids might be more closely related to each other than they have previously
been thought to be.

The relationships of the gymnotids are probably more poorly understood than those of any other ostariophysean group. Fink & Fink (1981) propose affinity between the gymnotids and the siluroids, but most of the synapomorphies these authors identify can be discharged as reductional. My observations of siluroid morphology here have provided valuable functional outgroup data on extreme adaptation for torentiality but have not substantiated the hypothesis of the authors above.

A gymnotid-cobitoid-catostomid assemblage, if a natural group, is of interest because it displays a transpacific distribution with representatives in North and South America, and in Eurasia. There are possibilities for tectonic scenarios that might account for transpacific groups in a broad sense, but at this stage of understanding of zoogeography, when traditional concepts of distribution and centres of origin are being challenged by vicariance theories (see Patterson, 1981) it does seem that ostariophysean interrelationships are better worked out independently of geography. Congruence between geographic and biological patterns can only actually be tested using cladograms with awareness of the at least chronological discreteness of the two and attempts at general correlations become rather meaningless. With this emphasised a general present day distribution superimposition for each of the cobitoid phylogenies which have been proposed in this thesis is assembled here [fig.xCiv] for comparison with some of the traditional concepts on the zoogeography.
of the group, indicated in the literature cited.

Hora (1953) discussed the 'Satpura hypothesis', which he proposed to interpret the Malayan element in India fauna, especially in Assam. Hora concluded that a major element in the Indian freshwater fish fauna, including the cobitid loaches issues from a centre of origin in South West China, or the Yunnan. Hora suggested that the high Indian fish fauna including the homalopterid element arrived in India from Indochina, from where they migrated fully evolved when the Garro Rajmahal gap was opened. Hora (1952b) offered an interpretation for the dual distribution of gastromyzonines which are present both in Borneo and on mainland China. Hora (1953) investigated the Yunnan fauna. In this paper he emphasised that the Yunnan area had been, in geological terms, recently raised, and that because of this uplift process the area has acted as a generative centre for South-east Asia. Hora discussed features of contrast presented between representatives of may ostariophysean taxa of the North and South Himalayan faces. Hora & Silas' (1955) particular conclusions on the Noemacheilini are in agreement with my own observations. These authors stated that even though the Asian noemacheiline loaches of high altitude have been classified in many genera and species, their systematic position is very difficult, as they all look alike, and their diagnostic features are not well defined! Hora & Silas concluded that morphological characters are stable in the group either "because evolution has had little time to play upon them, or because their lives were stable until their uplift".
Nalbant [1963] reviewed the geographic distribution of the Cobitidini, and he concluded that 'the present distribution of loaches, as well as their absence from North and South America, and Australia, and the greater part of Africa prove that it [the Cobitidae] is a more recent group than the carp-like fishes, but perhaps somewhat more recent than the Homalopteridae. In this thesis I have not been able to demonstrate the nature of the relationship between the cobitoids and cyprinids and I do not necessarily agree with Nalbant.

Banarescu & Nalbant [1964] proposed that Cobitis has an East Asiatic centre of origin, from which they proposed it has migrated through Siberia, and Middle Europe, and Banarescu et al. [1972] discussed the zoogeography of Sabanejewia as a subsidiary of the process.

Banarescu & Nalbant [1968] remarked on the discontinuous distribution of the noemacheiline genus of Oronectes, being present in Japan, the Amur basin, Korea, North and South China, and Indonesia, but absent from the Yangtse drainage, and Indochina. Banarescu [1977] offered an overall interpretation of cobitid zoogeography, and Jayram [1974] discussed particularly the Indian aspect of this. Menon [1974] and Jayram [1974] concluded that the major element in the fish fauna of Indian peninsula is of Indochinese origin, with the 'original' Indian fauna 'relict', and the Malay element poor.

Fang [1936] suggested that Botia issues from a centre of origin in the Indo-australasian archipelago, or Burma, or Thailand, with advanced forms spreading North and East,
while *B. macracantha* has spread independently South. The zoogeography of *Botia* has been the source of little subsequent discussion.

In conclusion to this thesis it seems appropriate to point out two particular areas of study towards which future research on the Cobitoidae might be directed. On the one hand a clearer understanding of the zoogeography of the group is required. On the other hand, with regard to the first section of this thesis, I would suggest that electromyographical work on the *m. rostralis* system coupled with time lapse photography of feeding activity, would be enlightening.
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