THE CATFISH FAMILY ARIIDAE (TELEOSTEI) IN NEW GUINEA AND AUSTRALIA: RELATIONSHIPS, SYSTEMATICS AND ZOOGEOGRAPHY

by

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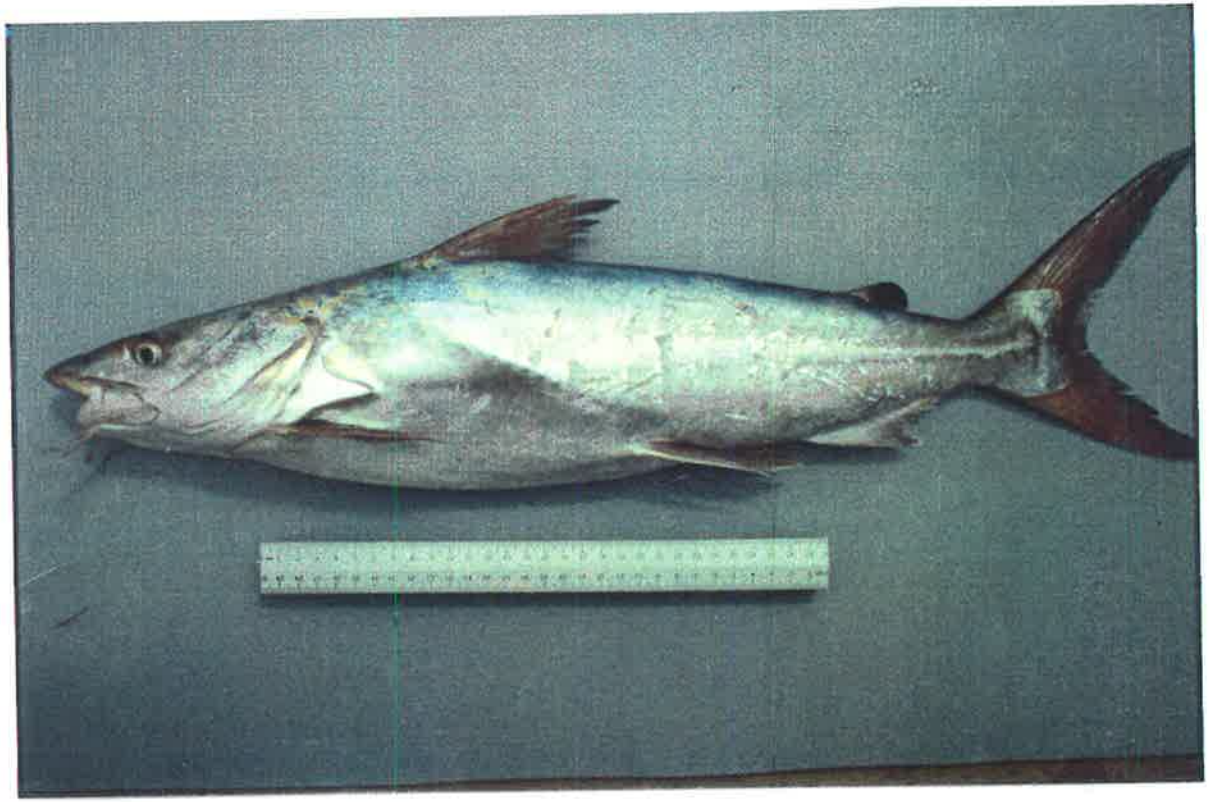

Frontispiece: "Arius" thalassinus (Ruppell); South China Sea specimen, 520mm SL (courtesy: K. Amaoka).

DECLARATION

This thesis contains no material accepted for the award of any other degree or diploma in this or another university.

To the best of my knowledge, this thesis does not contain material previously published or written by another person, except where due reference is made in the text.

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Patricia Joan Kailola

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SUMMARY

The highly speciose, circumtropical family of catfishes, the Ariidae (Pisces, Teleostei), are unique in their ability to tolerate a variety of water habitats, from fully marine to fresh, and in their reproductive strategy of producing few, large ova which are brooded by the male parent.

Although of considerable economic importance in many parts of their geographic range, the Ariidae has been the subject of little research. The studies undertaken investigated a range of traits, from reproductive strategy to diet and venom toxicity.

There has been no comprehensive systematic study of relationships between ariid taxa, and the phylogenetic position of the Ariidae within the suborder Siluroidei is unclear. My study sought to partly redress this problem using osteological and other morphological characters and comparing them with homologous characters in extralimital ariids and other siluroids. Phylogenetic relationships are constructed for within the Australo-Papuan ariids, and between them and other ariids. Problems in applying and interpreting suitable characters for a phylogenetic reconstruction of the Ariidae were encountered. A rationale for and manner of applying phylogenetic reconstruction rules in this study are explained.

The complete osteological description of the family is based on the type species "*Arius*" *arius* (Hamilton-Buchanan). The variation from the type, exhibited by the Australo-Papuan and extralimital ariids, provided a number of characters potentially useful in reconstructing a phylogeny. Problems of bone homology in the family are addressed. The osteology of Australo-Papuan "Arius" representatives is comparable to that of "Arius" arius. Sufficiently different from them are representatives of the genera Nedystoma, Cinetodus and Genus 1.

Morphological and meristic comparison enabled the recognition of 34 valid Australo-Papuan ariid species. Statistical analyses aided in differentiating between several pairs of morphologically similar taxa. Eight species were recognised as new to science, one of which (midgleyi) was described in 1988.

Fifty-seven characters were identified as potentially useful in a phylogenetic reconstruction. The states of these characters are compared within the Ariidae and with the outgroup, and polarity is assigned. Several of the characters are more-or-less "family" characters. I recognise the problems in the selection of outgroups for the phylogenetic study, in view of the generally poor comprehension of the relationships of all siluroid family groups. Nevertheless, the states of the 57 characters in 25 non-ariid taxa, including the plesiomorphic taxa Diplomystes and +Hypsidoris, are assessed. The outgroup taxa represented 11 nominal siluroid families. Extralimital (i.e. non Australo-Papuan) ariid taxa, representing nearly all remaining nominal ariid genera, were also compared and included in the OTU's for phylogenetic analysis.

Thirty-five other ariid characters were identified which could not be used reliably in a phylogenetic reconstruction, for several reasons. Some are autapomorphies for the Ariidae, others - such as meristic and morphometric characters - could not be polarised, and

others are ecologically adaptive. These characters are frequently homoplastic and correlated, examples including lip form, mouth shape and size, barbel length, gill raker number and buccopharyngeal pad development. In view of the not infrequent use of many of these characters in phylogenetic studies of other siluroids, their expression in the Ariidae is significant.

Cladistic analyses were performed using the PAUP program (Phylogenetic Analysis using Parsimony) (Swofford, 1986). The series of analyses a) supported the monophyly of the family, and b) revealed the high level of homoplasy - parallelisms, reversals and convergences - in the family. Although the high homoplasy engendered problems in interpretation (for example, clades are largely supported only by homoplasies, and OTU's frequently could not be resolved), several sets of taxa based on synapomorphies, consistently grouped on the cladograms. These groupings formed the basis for a revised classification of the Australo-Papuan ariids, and also clarified the systematics of some extralimital taxa.

Thus, only three of the 16 nominal genera previously recognised in New Guinea and Australia are valid. These are *Nedystoma*, *Cinetodus* and "*Arius*". A fourth distinct genus (Genus 1) is formally undescribed. *Pachyula* is a subgenus of *Cinetodus* and *Hemiarius*, *Hexanematichthys*, *Cochlefelis* and *Brustiarius* are subgenera of "*Arius*". Several synonymies are also recognised among the extralimital ariid genera: for example, *Hemipimelodus* is a synonym of *Cephalocassis*.

A complete presentation is given for each of the Australo-Papuan ariid species. This contains a primary synonymy, definition and description, statement of distribution, biological information, discussion and comparison, description of types, etymology and list of examined material.

The Ariidae has a long evolutionary history and is the earliest catfish family recognised in the fossil record - i.e. from the Cretaceous. The ariid ancestors probably moved onto the Sahul Shelf during the Late Miocene. The almost total absence of primary and secondary division freshwater fishes (*sensu* Myers, 1951) has enabled the adaptive radiation of the ariids in rivers and associated estuaries of Australia and New Guinea. The endemic freshwater and euryhaline ariids inhabit formally recognised drainage provinces, mainly the Leichhardtian, Riechian and Gaimardian. General ariid dispersal and speciation patterns, particularly of the *Netuma* species group, Genus 1 and northern New Guinea taxa, are postulated. The biogeographically defined Wallace's and Lydekker's Lines are seen as boundaries affecting the dispersal and hence speciation of ariids.

1 INTRODUCTION: THE FAMILY ARIIDAE

1.1 INTRODUCTION

The catfishes belonging to the family Ariidae are medium to large fishes having an elongate, robust body (Frontispiece). The head is conical to rounded and depressed. The mouth is terminal to inferior. The front and rear nostrils are usually close together, the rear (posterior) one more or less covered by a flap of skin. Usually six barbels are present around the mouth: a pair of maxillary, a pair of mandibulary and a pair of mental (inner) barbels (reduced barbel complements are exhibited by <u>Osteogeneiosus</u> Bleeker, <u>Bagre</u> Oken and <u>Batrachocephalus</u> Bleeker). The bony shield comprising part of the dorsal head surface is usually covered by thin skin, but in some taxa it is concealed by thick skin and muscle. The head shield is smooth, rugose, striate or granular and in most taxa its posterior portion (the supraoccipital process) extends caudad to meet the predorsal (nuchal) plate. The teeth are fine, conical and sharp, wedge-shaped or granular. Jaw teeth are arranged into narrow or broad bands; palate teeth (when present) are grouped into large or small patches. Teeth may be present on the parasphenoid. The gill membranes are joined together and attached to the isthmus, and the gill opening width varies from wide to restricted. There are 5-7 branchiostegal rays. The gill raker number on the anterior aspect of the first arch varies from 9 to more than 50. Rakers are always present along the posterior aspect of the 3rd and 4th arches, sometimes on the first and second arches.

The body is naked with a well-developed lateral line commencing near the upper part of the gill opening and terminating on the tail base by turning dorsad or bifurcating over the caudal fin lobes. The dorsal fin, situated before the mid-length of the body, consists of a very short, broad spine (or spinelet, buckler), a long, hard, usually serrated spine and seven branched rays. An adipose fin is always present and is situated above the spineless anal fin, which has 14-33 simple and branched rays. The pectoral fin is low-set and consists of a long, often serrated, hard spine and 8-13 branched rays. The pelvic (= ventral) fin has six branched rays and no spine and the shape of the inner (6th) ray is often modified in sexually mature females. The caudal fin is deeply forked, with 15 (7+8) principal rays, the outer ray of each lobe unbranched.

The most significant internal features are the large, free swim bladder, the Elastic Spring Apparatus (ESA) between the swimbladder and neurocranium, the extensive lamina of the 4th parapophyses which usually conceals the aortic canal, and the large auditory bulla containing an exceptionally large otolith.

Colouration is variable. The upper two-thirds of the body ranges from charcoal to pale blue and the paler lower body ranges from numerous fine, dusky stipples to white or cream. The upper body frequently bears a blue through coppery lustre, it may be dark blotched, or have a silvery lateral stripe. The fins are dusky yellow, often with dark margins or proximal areas, especially the dorsal aspect of the paired fins. The barbels are black, dark brown, creamy or white. The normally pale peritoneum and buccopharyngeal cavity may be dusky or charcoal-coloured.

1.1.2 Biology

Maximum attainable size ranges from 150mm SL (Doiichthys novaeguineae Weber) to about 1.5m SL (e.g. Sciadeichthys species, Hemiarius stormii [Bleeker]).

Fork-tailed catfishes consume a variety of food items including detrital matter and a range of invertebrates, plants and fish. Although most species are generally omnivorous, some (e.g. *Cinetodus froggatti* Ramsay and Ogilby) are specialised in dietary requirements. During periods of environmental adversity, ariids are frequently opportunistic scavengers.

The unique ariid method of reproduction makes them conspicuous among catfishes. A review of ariid reproductive strategy is given by Rimmer and Merrick (1983). The ova are large (up to 2.0 cm diameter) and fecundity is very low. The ova are extruded in a cluster by the female. They are then fertilised by the male and gathered up in his mouth where they are incubated. Brooding lasts for up to 6 weeks - the period it takes for the young to hatch and the yolksack to be resorbed. Spawning appears to occur during mass aggregations.

1.2 DISTRIBUTION AND ECONOMIC IMPORTANCE

The Ariidae, or fork-tailed catfishes, are distributed almost circumtropically (fig. 1) between about 35° N and S. ~~except in the central Pacific.~~ They are present along continental margins (often penetrating fresh water) ~~occur in~~ the western and eastern coasts of north, on central and south America, west Africa, south and east Africa including Madagascar, the Red Sea and the northwestern Indian Ocean, the Indian subcontinent including the Andaman Islands, the Thai-Malay Peninsula, the Indo-Malay Archipelago, the China Sea to southern Japan, the Philippines, New Guinea and the northern two-thirds of Australia. Despite records to the contrary (e.g. Weber and de Beaufort, 1913; Fowler, 1928; 1949) ariids do not occur around the Bismarck Archipelago, the Solomon Islands, New Hebrides and New Caledonia in the western

Pacific. Springer (1982) and Kailola (1983) dispelled the reports of *Arius dasycephalus* Günther in Hawaii and *A. thalassinus* (Rüppell) in Tonga; and *A. graeffei* Kner and Steindachner in Samoa.

The ariid catfishes inhabit marine, brackish and fresh waters of various turbidity. It is generally recognised that they, the Plotosidae and Aspredinidae (Myers, 1960; Mees, 1987) are the only siluroid families whose members tolerate this variety of ~~water~~ habitats (although Gosline [1975a] noted records for other individual siluroids). A few marine species within these families are widely distributed (e.g. *Arius thalassinus*, *Plotosus lineatus* Thunberg). Although groups of ariid species are usually associated with particular landmasses, some are wide-ranging within them (e.g. *Arius leptaspis* [Bleeker] in Australia and New Guinea) whilst others have a very limited distribution (e.g. *Potamarius* spp. in central America).

Ariids are abundant in coastal mangrove areas, estuaries and rivers within and beyond tidal influence as well as in freshwater streams and lagoons. Some species move along waterways far inland (e.g. *Arius gigas* Boulenger in central West Africa; *Arius leptaspis*, *A. graeffei* and *A. velutinus* [Weber] in Australia and New Guinea) and others inhabit (and breed in) almost isolated lakes (e.g. *Arius magatensis* Herre in the Philippines, *A. acutirostris* Day and *A. burmanicus* Day in Burma). At the other extreme, some marine ariids have been collected from depths to 150 m (*Arius thalassinus* and *A. dussumieri* Valenciennes) and more than 100 m (*A. heudeloti* [Valenciennes] [Tobor, 1969]).

In many parts of their range, the Ariidae are of considerable economic importance because of their usually large size, their local abundance, hardiness and flesh quality. They are the basis for substantial fisheries throughout India, Southeast Asia, south-central America and central West Africa. Examples of the economic value of ariids are provided in the following figures: nearly 53,000 tonnes were landed in the Western Indian Ocean (mainly India) in 1981 (Jayaram, 1984); 21,000 tonnes in West Africa in 1978 (Taylor and Van Dyke, 1981); 7,100 tonnes in central and northeastern South America in 1975 (Taylor and Menezes, 1977) and 11,560 tonnes in Indonesia in 1975 (Anon., 1980). "Kanduli" (mainly A. manillensis [Valenciennes]) are a major food source from Laguna de Bay, Philippines (Mane, 1929; Aldaba, 1931; Mercene, 1978). Ariids constitute 26% of all fish landings in Guyana (LeBail et al., 1984) and similar proportions are marketed in Brazil and Mexico (Reis, 1986; Yanez-Arancibia and Lara-Dominquez, 1988) and India (Sekharan, 1973; Pillai, 1978).

A variety of fishing gear is used to harvest these catfishes including bottom trawls, longlines, seines, castnets, traps and fixed bottom nets. They are frequently considered a nuisance in gill nets because of their rigid, erectile spines which tangle and tear nets and can inflict painful wounds.

The fish are marketed fresh, dried, brined, fermented before salting, or smoked. Inferior quality or small individuals are often made into fishmeal. High fat content around the annual breeding period raises the value of ariids as a food source to villagers along the Sepik River in northern New Guinea (Coates, 1983). The tough swimbladders of ariids are dried and used for isinglass in India (Jayaram, 1984) and in some areas, their cleaned neurocranium is sold as a crucifix. Although attempts to aquaculture ariids have so far proved unsuccessful (Kailola and Pierce, 1989), there is considerable interest in achieving this goal. This is especially so for species attaining large sizes where the amount and weight of bone would be offset commercially by flesh weight. In Mexico and central-south America ariids are raised in grow-out ponds (Yanez-Arancibia, 1977; Pinheiro *et al*., 1980).

1.3 PREVIOUS STUDIES

Despite their significance in human diet, their abundance and wide distribution, few studies have been conducted on the Ariidae. Mane (1929: 82) commented: "References relating to the study of the habits of catfishes in the Philippines are conspicuous for their absence", and in the subsequent 60 years, this situation has not changed.

Reproductive strategy has been investigated by several workers (e.g. Lee, 1937; Merriman, 1940; Dmitrenko, 1970; LeBail *et al*., 1984; and Rimmer, 1985; 1985a) and speculated upon by others (e.g. Day, 1877). Yet even now, the mode of spawning and fertilisation is unknown (Kailola and Pierce, 1989).

1.3.1 *Other studies* include:

Mucous property in *Arius thalassinus* and *A. graeffei*, investigated by Al-Hassan *et al*. (1985) and Di Conza (1970).

The mechanism and function of *sound production* in *Arius felis* (Linnaeus) and *Bagre marinus* (Mitchill), investigated by Tavolga (1962; 1971) and Breder (1968).

Karyological studies involving ariids, performed by LeGrande (1980), Rishi *et al*. (1983, cited in Fitzsimmons *et al*. (1988)) and Fitzsimmons *et al*. (1988).

Venom toxicity from ariid spines, investigated by Birkhead (1972).

Aspects of ariid *osteology*, described by several workers (Chapter 2, this report).

Studies pertaining to *diet* and *ecology*, performed in several parts of the family's range; e.g. by Tobor (1969), Haines (1979), Dan (1981), Lara-Dominguez *et al*. (1981), Marais (1984), Araujo (1984), Rimmer (1985b), Reis (1986a; 1986b) and Yanez-Arancibia and Lara-Dominguez (1988).

However, most publications on the Ariidae have been taxonomic: not so much comparative but more revisionary or record papers.

1.4 HISTORICAL REVIEW - AUSTRALIAN AND NEW GUINEAN ARIIDAE

Literature records 26 nominal species of ariid (including Doiichthyidae) from New Guinea and 19 from Australia (McCulloch, 1929; Munro, 1957; 1958; 1967; Whitley, 1964). Hoese and Hanley (1989) recorded 12 valid species.

Sir John Richardson (1845) published the first descriptions of catfishes actually collected in the Australasian region. Single specimens each of *Bagrus venaticus* and *Bagrus vertagus* (8½ and 3 inches long, respectively) were collected by Benjamin Bynoe off the "northwest coast of Australia" in 1842. Richardson deposited the two specimens (in very poor condition) in the Haslar Collection of the Naval Hospital at Portsmouth. Günther (1864) suspected that they had been destroyed and they could not be located on the occasion of the transfer of the collection to the British Museum of Natural History in 1855 (pers. comm., E. Trewavas, 1977). Munro (1957) hazarded their correct placement in Doiichthyidae ("*Doiichthys*(?) *vertagus*") and *Neoarius* ("*Neoarius*(?) *venaticus*"), and Whitley (1964) placed them in *Netuma* Bleeker. Despite subsequent extensive comparison of their meagre descriptions with material and descriptions of the other ten ariid taxa occurring in northwestern Australia, I am unable to ascertain their identity. Thus, as they lack types and sufficient description, I propose that *Bagrus vertagus* and *Bagrus venaticus* be considered *species dubia*.

The next taxon with an Australian type locality to be described is *Arius australis* Günther, 1867. The locality of Ash Island (Hunter River) is near the southernmost record for this species (fig. 177) which has the widest distribution of all the endemic Australo-Papuan ariids. Castelnau (1878) described its synonym *Neoarius curtisii* from Moreton Bay. DeVis (1884) and Ogilby (1898) described four more Australian ariids.

The first New Guinea ariid taxon described is *Hexanematichthys leptaspis* Bleeker (1862) from "southwestern New Guinea". Macleay (1884) described *Arius latirostris* from central Papua and the Royal Geographical Society's exploration of that region and the Fly River yielded further new species: *spatula*, *crassilabris*, *dayi* and *froggatti*, all described by Ramsay and Ogilby in 1886.

The remaining Australo-Papuan ariids were described between 1908 (*broadbenti* Ogilby; *velutinus* Weber) and 1978 (several Papuan taxa described by Roberts). Kailola and Pierce described another (*midgleyi*, 1988).

1.5 NOMENCLATURE AND COMPOSITION

The family Ariidae was first proposed by Regan (1911a).

A number of authors (e.g. Fowler, 1928; Jordan and Evermann, 1896-90; Chandy, 1953; Munro, 1958, 1967; Misra, 1976; Jayaram, 1984) have used the name Tachysuridae for this family, believing that *Tachysurus* Lacepède, 1803 (type = *T. sinensis* Lacepède) is the most senior genus applicable to this group of catfishes. However, most recent literature follows the decision of Wheeler and Baddokwaya (1981). These authors gave reasons why *T. sinensis* Lacepède cannot be referred to the Ariidae, concluding that it is an unrecognisable Chinese freshwater siluroid. In taking this stance, Wheeler and Baddokwaya confirmed Valenciennes' (1840), Regan's (1908), Ogilby's (1898a) and Gosline's (1975) opinion that the family should be termed Ariidae, based on *Arius* Valenciennes (type = *Pimelodus arius* Hamilton-Buchanan, 1822). (Inexplicably, Dhanze and Jayaram [1981] insisted that whereas "Ariidae" may be valid, *Tachysurus* Lacepède should still takes precedence over *Arius* Valenciennes.) Although appreciating that Lacepède's engraving of *T. sinensis* does not accurately portray an ariid catfish, I question some reasons given for rejection by Wheeler and Baddokwaya (1981). Caudal lobe shape, position of upper barbel and nape height may represent errors by the engraver; and freshwater habitat and blotched sides are not so rare in ariids as those authors supposed. However, further discussion on the appropriate name of the family (if it is worthwhile!) can only be continued after examination of Yangtse River ariids (ref. Wheeler and Baddokwaya, 1981; Fowler, 1932: pp. 251-2).

~~As at this time~~ Currently, 46 nominal genera (and two Kuhl and van Hasselt manuscript names) have been described for the Ariidae (Table 1). There is an uncertain number of nominal species, although valid species would number more than my earlier estimate of 90-100 (Kailola, 1986).

The family Ariidae belongs in the teleost suborder Siluroidei which itself belongs in the Superorder Ostariophysi.

1.6 PHYLOGENETIC POSITION OF THE ARIIDAE

1.6.1 Superorder Ostariophysi

Approximately 25% of all known fish species and 3/4 of the world's freshwater fishes are ostariophysans (Fink and Fink, 1981). The group possesses enormous ecological and evolutionary diversity. It occupies most freshwater habitats worldwide and to a lesser extent, coastal waters.

The Ostariophysi are characterised by the possession of a special and complex inner ear-swimbladder connection (otophysic connection) involving the modification of the first four or more vertebrae. Krumholz (1943) termed this feature the Weberian Apparatus and its possession indicates the phylogenetic integrity of this group (Rosen and Greenwood, 1970). Other features supporting the monophyly of the Ostariophysi are: possession of a swimbladder divided into distinct anterior and posterior chambers; a particular form of the caudal fin skeleton; fright cells and pheromones; and nuptial tubercles.

The Ostariophysi contains the catfishes (Siluroidei), the carp, minnows and loaches (Cypriniformes), the tetras (Characiformes), the knifefishes (Gymnotoidei) and the milkfish and knerids (Gonorynchiformes). Since Regan's (1911, 1911a) work, a classification of the Ostariophysi based on phylogenetic interpretations continues to take shape, and Greenwood _et al_. (1966), Rosen and Greenwood (1970), Roberts (1973), Gosline (1973; 1975), Novacek and Marshall (1976), Briggs (1979), Fink and Fink (1981), Fuiman (1984), Nelson (1984), Lauder and Liem (1983), and most recently Grande (1987) should all be consulted.

1.6.2 Suborder Siluroidei

Bleeker (1858) created the Order Siluri which he divided into four families (into six families in 1862). Gill (1870) replaced the name of the order Siluri with Nematognathi, a name used by Jordan (1923); Herre (1926, 1953); Shelden (1937) and Stigchel (1946).

Many early authors (e.g. Müller and Troschel, 1849; Castelnau, 1855; Günther, 1864; Day, 1877) placed all groups of catfishes as genera of the family Siluridae, although the loricariids were sometimes distinguished as a separate family (e.g. by Jordan and Evermann [1896-1900] and Regan [1908]).

Several authors (e.g. Regan, 1911a; Berg, 1940; Greenwood *et al.*, 1966; Roberts, 1973; Nelson, 1984 and Grande, 1987) have defined the Siluroidei.

There is vast morphological diversity in modern catfishes, although as a suborder it is unusually well-defined (Greenwood *et al.*, 1966). Rossi (1951; cited in Gosline, 1975) commented that siluroids are at the endpoint of a tremendous radiation. As a group, they are highly variable in morphology, habitat, behaviour and reproductive pattern. For example, members of at least two families (Clariidae, Heteropneustidae) possess air-breathing organs and others have highly vascularised organs (e.g. stomach) which enable aerial respiration (Loricariidae). Another (Malapteruridae) produces strong electrical currents. Some catfishes are known to possess venom glands (e.g. Plotosidae; *Noturus* spp.).

There are more families of catfishes than the combined total of other otophysan groups (Howes, 1983). Sixteen are endemic to South-central America, three to Africa and nine to Eurasia (eastern Europe to Southeast Asia). The Ictaluridae are endemic in North

America; the Bagridae, Schilbeidae and Clariidae inhabit both Africa and Asia. The Plotosidae are distributed from east Africa to the western Pacific and southern Australia (with freshwater representatives in the Celebes, New Guinea and Australia) (Berra, 1981; Nelson, 1984). The Ariidae is the remaining family, and it occurs in all major landmasses except Greenland and Antarctica (refer 1.2).

1.6.3 The Ariidae within the Siluroidei - historical perspective

The Ariidae were considered relatively primitive siluroids, "generalised in form and in fin structure" (Regan, 1911a: 556; also Jordan, 1923; Berg, 1940; Eigenmann and Eigenmann, 1890: as Tachisurinae) and slightly more primitive than the Doradidae, Plotosidae, Siluridae and Bagridae. These groups were followed in Regan's classification by the Ameiuridae (= Ictaluridae) and the Pimelodidae "which represent the Bagridae in South America" (Regan, p.557). Gregory (1933) and Breder (1935) speculated that the ariid skull was derived from an "ameiurid-like" ancestor.

Alexander (1965) grouped six of these families (except Siluridae) together as "unspecialised catfish", only a little more advanced than the plesiomorphic taxon Diplomystes (Diplomystidae), but all fairly primitive. Unfortunately, Alexander's treatment and allocation of this group may have been prejudiced by his deficient understanding of their natural history (refer Chapters 3 and 4).

Conceding that the pelvic girdle structure and associated musculature of ariids was highly specialised, Shelden (1937) viewed the Ariidae as an offshoot from the primitive stem (represented by Diplomystes).

Comparing the pectoral girdle of different siluroids from regional seas, Tilak (1963c) likened the form of the Ariidae with the Bagridae - although the ariid pectoral girdle is distinct in lacking a mesocoracoid. However, Tilak considered that the articular connection between the posttemporal bone and the skull in ariids was apomorphic to that of silurids, plotosids, schilbeids and bagrids. Tilak later (1965; 1967a) documented 19 characters of the osteocranium and Weberian Apparatus as evidence that the Ariidae are of a "higher grade of specialisation" than are the Siluridae, Bagridae, Plotosidae and Pangasiidae. Furthermore, the osteocranium and the Weberian Apparatus are plesiomorphic when compared with those of the Schilbeidae, Clariidae, Heteropneustidae, Loricariidae, Callichthyidae (both neotropical families) and the Sisoridae (Tilak, 1963b). Whilst some of the character distinctions cannot be upheld throughout the family, I consider that most of Tilak's observations are sound.

Greenwood et al. (1966: 386) seriously doubted that the Ariidae are primitive siluroids, stating that the Weberian Apparatus "of the related families Bagridae, Ictaluridae and Pimelodidae" appear to be more primitive. In addition, certain apomorphic caudal features in the Ariidae distinguishes the family from several of the generally regarded plesiomorphic siluroids (Lundberg and Baskin, 1969).

From his investigations of the palatine-maxillary mechanism in 19 siluroid families, Gosline (1975) concluded that the Ariidae, many bagrid fishes, the Doradidae, Pimelodidae, Schilbeidae and Pangasiidae share characteristics of a palatine-maxillary mechanism closest to the basic stock of modern siluroids.

Chardon (1968) concluded that the Bagridae and Ariidae closely resemble each other both in external morphology and form of the swimbladder and Weberian complex. In his superfamily Bagroidae, Chardon included the Bagridae, Cranoglanidae, Pimelodidae, Ictaluridae, Ariidae and Olyridae.

Yet another endorsement of the families more closely related to the Ariidae was presented by Bhimachar (1933) who considered that they have the most specialised skulls of five compared Indian siluroids (Schilbeidae, Bagridae, Plotosidae, Siluridae and Ariidae). Bhimachar concluded that the ariids have attained a high degree of specialisation - more so than have many other siluroid groups.

The Ariidae was considered neither plesiomorphic nor apomorphic by Nelson (1984) who placed it in the middle of the 31 siluroid families then believed valid.

1.7 STATEMENT OF THE PROBLEM

Despite the wide distribution and significance of ariids and the substantial taxonomic literature on them from almost every region, few studies have attempted to explore the interrelationships of ariid species and genera.

There are inherent problems in interpretation of ariid taxa due to their conservative phenotype. They exhibit an overall similarity in appearance which is emphasised by uniform colouration, habitat preference and biology. However, instead of addressing the question of why individuals appear morphologically similar yet distinct, when confronted with morphological differences most taxonomists found the "solution" by describing a new taxon. Failure to recognise ontogenetic, environmental and sexual changes combined with the lack of "traditional" teleost features (e.g. varied colouration and meristic features, body scalation) produced a plethora of nominal taxa from these earlier ~~pre-Hennigian~~ classifiers. Their practice extended beyond species to genera; and more genera came to include fewer species, such that any genealogical information about groups of species became lost. The 41 nominal species known in New Guinea and Australia alone prior to my study, had been placed in 15 nominal genera: an average of 2.7 per genus! (Table 2).

Early taxonomists were confused by the conservative ariid morphology and also failed to recognise ontogenetic changes. This is frequently illustrated by their selection of intraspecifically labile and adaptive features as being systematically important. For example, nominal genera are based on a range of characteristics such as lip thickness, mouth size, fin filament and snout groove development and dorsomedian fontanelle shape to gill raker, branchiostegal and barbel numbers, form and extent of dentition and width of branchial apperture.

The great ichthyologists of the last century (Valenciennes, 1840; Bleeker, 1858; Müller and Troschel, 1849 and the Eigenmanns, 1890) grouped ariids from different world regions into several common genera. But later authors (e.g. Gill, 1862; Bleeker, 1862; Jordan and Evermann, 1896-1900; Ogilby, 1898; Weber, 1913; Fowler, 1944; Whitley, 1940; 1941 and Hubbs and Miller, 1960) "regionalised" the taxa such that new genera were erected largely on the basis of geographical distribution of contained species. Consequently, the family is now classified into almost independent generic suites in Africa-Asia, Australia-New Guinea and the Americas.

Up until now, there has been no attempt to appraise the status of nominal ariid genera on a world-wide basis: to assess the characters, determine the number of valid taxa and compare the differences between them such that they can be "regrouped" in a classification reflecting their genealogical history rather than their global distribution.

The status and composition of some genera *have* been reassessed, but in isolation: *Tachysurus* Lacepède (see 1.5); *Felichthys* Swainson, *Ailurichthys* Baird and Girard (Jordan and Evermann, 1896); *Arius* Valenciennes, *Galeichthys* Valenciennes and *Ariodes* Müller and Troschel (Taylor, 1986); *Hemipimelodus* Bleeker (Desoutter, 1977); and Jayaram and Dhanze (1978) attempted a review of ariid genera. Unfortunately, my study has revealed inadequacies in these investigations. Higuchi, Reis and Araujo's (1982) question regarding the validity of using the genus *Netuma* Bleeker for neotropical ariids is however, a firm beginning to the process of phylogenetic assessment of the family.

Time restraints have prohibited an evaluation of all ariid nominal taxa. Nevertheless, although my study is primarily confined to ariids inhabiting the Australo-Papuan faunal region, it has extended considerably beyond.

I have five major objectives:

(1) to undertake a taxonomic revision of the Australian and New Guinean representatives of the Ariidae, which comprises a natural zoogeographic assemblage of taxa;

(2) to describe the osteological variation within this section of the family and compare it with that of the most widespread genus *Arius* Valenciennes;

(3) to describe the variability exhibited by morphological characters of New Guinean and Australian ariids, comparing it with homologous characters in other siluroids;

(4) to hypothesise the phylogenetic relationships within the New Guinean and Australian ariids and to compare phylogenetic information on homologous character states of other ariid taxa;

(5) to consider the zoogeographical pattern of ariid taxa in the study region.

These objectives are achieved through use of osteology (Chapter 2) and comparative morphology and some internal anatomy (Chapters 3, 4). A phylogenetic analysis was performed (Chapter 5) which resulted in a substantially revised classification scheme (Chapter 6). Zoogeography is discussed in Chapter 7. Study of osteology was preferred to myology because I considered it would provide a sounder basis for comparison with other catfish families (for which myology is largely undescribed). The inaccessibility of fresh material precluded a contribution to the phylogenetic analysis based on electrophoretic methods.

Despite problems involved in hypothesising the phylogeny of a section of the family, I consider my study as a real contribution to the advancement of knowledge of the Ariidae and with it, the relationships of this family to the remaining Siluroidei. In addition, because it is the most widely-dispersed catfish family (extant or extinct representatives known from 5 of the 6 continents) and tolerates a variety of water habitats, the phylogenetic information revealed will facilitate the development of hypotheses of comparative evolution and zoogeography of the entire Order Ostariophysi.

1.8 MATERIAL AND METHODS

Material for this study was collected from rivers and adjacent coastal waters of Australia, New Guinea, Asia, Africa and America.

Material from Australia and New Guinea is listed by political division. Such listings have no zoogeographic significance. Whilst recognising the zoogeographic distinction between northern and southern New Guinea however, the term "Australo-Papuan" is used ~~in discussion~~ throughout the text~~.~~ to refer to the combined regions of Australia and New Guinea.

Common abbreviations used throughout are:

SL - standard length: the straight line distance from the most anterior part of the snout or upper lip to the midbase of the caudal fin. In thick-skinned specimens, this distal point can be ascertained by flexing the rayed tail;

HL - head length: the distance from the most anterior part of the snout or upper lip to the hindermost point of the operculum (including the opercular margin);

C&S - cleared and stained: referring to osteological preparations.

LHS - left hand side;

RHS - right hand side.

Definition and counts of vertebrae are explained in Chapter 6.2.1.

Some revisionary work performed during the course of my study has been published prior to the thesis presentation. Hence, valid names for four taxa (*Arius graeffei*, *A. armiger* deVis, *A. thalassinus* and *A. bilineatus* Valenciennes) were established in Kailola, 1983 and 1986a; and the taxon *Arius midgleyi* Kailola and Pierce was described in 1988.

I have been unable to avoid using new name combinations revealed by phylogenetic analysis (Chapter 5), in earlier chapters of this thesis. Furthermore, the author of a taxon is named when the taxon is first stated, but after that, species and genus names stand alone. ~~subsequent to initial statement of authority, specific and generic epithets are frequently used without extension.~~

In the course of my research, I determined that conventional generic placement of some extralimital taxa was inappropriate. As further investigation was beyond the scope of my study, I have indicated the problem by placing the generic name for those taxa in inverted commas. The taxa involved are *dussumieri* Valenciennes (placed in *Ariodes* Müller and Troschel by Taylor, 1986); and the western hemisphere taxa characterised by restricted gill opening and molariform teeth in single patches on each side of the palate and on the mandible, which are usually referred to *Cathorops* Jordan and Gilbert.

1.8.1 Institutional abbreviations

Most specimens used in this study are deposited in the following institutions. Acronyms are those of Leviton, Gibbs, Heal and Dawson (1985), except for SAM and SAFRM, where I follow local use.

AMNH - American Museum of Natural History, New York;
AMS - Australian Museum, Sydney;
ANSP - Academy of Natural Sciences of Philadelphia;
ASIZB - Academy Sinica, Beijing;
BMNH - British Museum (Natural History), London;
CAM - Natural History Collection, Central Australian Museum, Alice Springs;
CAS - California Academy of Sciences, San Francisco (specimens bearing a prefix "SU" were previously in the Stanford University collection);
CSIRO - Commonwealth Scientific and Industrial Research Organisation, Fisheries Division's Ian S.R. Munro Ichthyological Collection, Hobart;
FMNH - Field Museum of Natural History, Chicago;
FUMT - Department of Fisheries, University Museum, University of Tokyo;
GCRL - Gulf Coast Research Laboratory Museum, Ocean Springs, Mississippi;
KFRS - Department of Fisheries and Marine Resources, Research Division's collection at Kanudi, Port Moresby, P.N.G.;
LACM - Los Angeles County Museum of Natural History, Chicago;

MAMU - Macleay Museum, University of Sydney;

MCZ - Museum of Comparative Zoology, Harvard University, Cambridge;

MNHN - Museum Nationale d'Histoire Naturelle, Paris;

MZB - Museum Zoologicum Bogoriense, Bogor, Indonesia;

MZUSP - Universidade de Sao Paulo Museu de Zoologia, Sao Paulo;

NCIP - Lembaga Oseanologi Nasional, Jakarta, Indonesia;

NHRM - Naturhistoriska Riksmuseet, Stockholm;

NMV - National Museum of Victoria, Melbourne;

NMW - Naturhistorisches Museum, Vienna;

NSMT - National Science Museum, Tokyo;

NTM - Northern Territory Museum of Arts and Sciences, Darwin;

QM - Queensland Museum, Brisbane;

RMNH - Rijksmuseum van Geologie en Mineralogie en Natuurlijke Historie, Leiden;

SAM - South Australian Museum, Adelaide;

SAFRM - South African Museum, Cape Province;

SMF - Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt;

TU - Tulane University Riverside Laboratories, Belle Chasse, Louisiana;

UMMZ - Museum of Zoology, University of Michigan, Ann Arbor;

USNM - National Museum of Natural History, Smithsonian Institution, Washington;

WAM - Western Australian Museum, Perth;

ZMA - Zoologische Museum, Universiteit van Amsterdam, Amsterdam;

ZMB - Universitat Humboldt Museum fur Naturkunde, Berlin;

ZMH - Universitat Hamburg Zoologisches Institut und Museum, Hamburg, Germany;

ZSI - Zoological Survey of India, Calcutta.

2 OSTEOLOGY

2.1 INTRODUCTION

There are no osteological data on endemic Australo-Papuan ariids, although the osteology of three marine taxa occurring there and beyond the region has been generally described by Tolentino and Clemente (1953) (*Arius thalassinus* (Rüppell), *A. bilineatus* (Valenciennes) and *A. leiotetocephalus* Bleeker (= *A. nella* Valenciennes)).

Other recent osteological studies published on certain Asian and American ariid taxa, are: the morphology of *Bagre marinus* (Mitchill) and *Galeichthys felis* (Linnaeus) (= *Arius felis*) from the western central Atlantic (Merriman, 1940); the entire skeleton of *Arius manillensis* Valenciennes from Philippine waters (Tolentino and Clemente, 1953); the Weberian Apparatus and associated structures of *Arius platystomus* Day from India (Karandikar and Masurekar, 1954); the skull and Weberian Apparatus of 14 nominal species inhabiting the seas around India (Tilak, 1965); the skull of *Tachysurus maculatus* (Thunberg) (= *Arius maculatus*) from India (Lenous, 1967); the entire skeleton of "*Cathorops*" *fuerthii* (Steindachner), *Guiritinga barba* (Lacepède), *G. planifrons* (Higuchi, Reis and Araujo), *Sciadeichthys troscheli* (Gill) and *Genidens genidens* Valenciennes from northern South America (Higuchi, 1982); the skull of *Arius tenuispinis* Day from India (Rao and Lakshmi, 1984).

Authors who have considered the ariids in detail when undertaking comparative or embryological studies among catfishes, include Regan (1911a), Starks (1926), Bhimachar (1933), Shelden (1937), Bamford (1948), Srinivasachar (1958), Chardon (1968) and Lundberg and Baskin (1969).

The type species of *Arius* Valenciennes is, I believe, the appropriate subject for osteological description of the family for the following reasons: Arius is by far the most speciose of all the ariid genera, it exhibits a substantial measure of the morphological diversity within the family (i.e. includes subgenera and species groups) and is represented throughout the family's range. Despite the status of this taxon, the skeleton of the type species Arius arius (Hamilton-Buchanan) has not been fully described, although it was generally discussed by Tilak (1965). The older valid ariid genera Galeichthys Valenciennes, 1840 and Bagre Cloquet, 1816 do not represent the majority of ariid species.

My purpose in describing the osteology of A. arius is to 1) provide a basis for comparison of osteological features between ariid taxa and other siluroids; 2) contribute towards a clarification of bone homology within the family and within siluroids; and 3) assess the extent of intraspecific variation.

In conjunction with this description, comparison is made with Australo-Papuan ariids. Any variation from the pattern and form of A. arius is noted for each series of sequential skeletal elements. This 1) provides a measure of the osteological diversity exhibited between ariids in the study region; and 2) describes states of characters for use in a phylogenetic analysis of ariid taxa (Chapter 5). The nominal genus and subgenus names given to the Australo-Papuan ariids here are those of recognised groups and are not meant to reflect a hierarchy.

2.2 METHODS

Skeletal preparations were made by clearing representatives of nearly all Australo-Papuan ariid taxa. The trypsin digestion methods of Taylor (1967) for single staining and Dingerkus and Uhler (1977) for double staining were largely employed; muscle tissue of some material was macerated in potassium hydroxide. Dry preparations of skulls and vertebral columns of several taxa were prepared by boiling the specimens before removing soft tissues.

After skinning and partial evisceration, the digestion (or maceration) time for larger specimens was reduced by cutting away flesh from the specimens' sides and by scraping muscle tissue away from the throat and sides of the head. Removal of the swimbladder intact was facilitated by several days' digestion.

Once clearing and staining was completed, observation of all aspects of the specimen was enhanced by removing the pectoral girdle, the hyoid apparatus and branchiostegals. In situ bone arrangements were drawn with the aid of the Camera Lucida attachment of a WILD M5 stereo-dissecting microscope.

To assess intraspecific variation in the form and structure of bony tissue in adults and juveniles, several specimens representing a graded SL range were processed whenever possible. Radiographs of specimens unavailable for processing (e.g. types) were also examined.

In the figures, cartilage is represented by diagonal bars or series of stipples; most fossa by cross-hatching. SL or HL of the drawn specimen is stated (scale not given).

2.2.1 Terminology

The homology of several bones is still debated and confused in ostariophysan literature (compare Weitzmann, 1962; Tilak, 1963; Harrington, 1955; Alexander, 1965; Patterson, 1975; Chardon, 1968; Nelson, 1969; Lundberg, 1975; Gosline, 1975; Arratia, 1987). Some recent authors have investigated the issue in study of parts of the skeleton. For example, Lundberg (1975a) examined the upper shoulder girdle; Lundberg and Baskin (1969) the caudal skeleton; Howes (1983) and Howes and Teugels (1989) the suspensorium; Jollie (1986) various skull bones.

Clarification of bone homologies is beyond the scope of this study. Nomenclature used here mainly follows that of Fink and Fink (1981) (who reviewed most of the ostariophysan skeleton) supplemented with observations and alternatives offered by Patterson (1975), Grande (1987), Jollie (1986), Schaefer (1987) and Vari (1989). Variations in bone nomenclature are discussed briefly in the following list of abbreviations.

aar, anguloarticular (and see Vari, 1989); **ac**, anterior ceratohyal (see Schaefer, 1987; Vari, 1989) (ceratohyal of previous authors); **af**, aortic foramen; **afle**, articular facet on palatine for lateral ethmoid; **afn**, anterior dorsomedian cranial fontanelle; **afp**, articular facet on lateral ethmoid for palatine; **alpp**, alary process ("wing") of parasphenoid; **apb**, anterior process of basipterygium; **arf**, articular facet; **atp**, autogenous tooth plate (considerable discussion in literature over the origin and hence correct terminology for the tooth-bearing plates, largely based on the position they occupy on the palate; i.e. approximating with neurocranial elements: "dermopalatines", "tooth-bearing ectopterygoids", "sesamoid bones", "ectopterygoid teeth" are some such names. [See Bamford, 1948; Tilak, 1965; Alexander, 1965; Roberts, 1973; Gosline, 1975; Howes, 1983a, 1985; Bailey and Stewart, 1984; Grande, 1987; Grande and Lundberg, 1988]. The name I select however, better reflects the situation that the plates occupy various positions on the palate); ~~[refer discussion in Nybelin, 1967]);~~
aub, auditory bulla; **ba**, basipterygium; **bb**, basibranchials;
bdl, ossified Baudelot's ligament (transcapular of Arratia, 1987;

ossified transcapular ligament of other authors; ref. Fink and Fink discussion, 1981); **boc**, basioccipital; **br**, branchiostegal rays; **c**, cartilage; **cb**, ceratobranchials; **cc**, compound centrum formed from first preural and first ural centrum ("hypural plate"); **cl**, cleithrum; **coc**, coronoid cartilage; **cop**, coronoid process; **cor**, coracoid; **cvc**, complex vertebral centrum; **d**, dentary; **dr**, distal radial; **ds**, dorsal spine; **eb**, epiphyseal bar; **ecpt**, ectopterygoid (additional pterygoid of Arratia, 1987; pterygoid of Bhimachar, 1933; Gosline, 1975; Howes, 1985); **crm**, coronomeckelian; **ep**, epural; **epb**, epibranchial; **epbtp**, epibranchial tooth plate; **epio**, epioccipital (epiotic of Tilak, 1963; Jollie, 1986); **es**, extrascapular (posttemporal of Alexander, 1965; Lundberg, 1975a); **ESm**, Elastic Spring Apparatus muscle; **exo**, exoccipital; **fofn**, foramen for the facial nerve; **fom**, foramen magnum; **fr**, frontal; **ha**, haemal arch; **hb**, hypobranchials; **hf**, articular facet for hyomandibular; **hh**, hypohyal (as anterior and posterior hypohyal in Rao and Lakshmi, 1984; ventral and dorsal hypohyal in Arratia, 1987); **hs**, haemal spine; **hy**, hypural; **hyo**, hyomandibular; **hyp**, hypurapophysis; **ih**, interhyal; **io**, infraorbital; **iop**, interoperculum; **isp**, ischial process of basipterygium; **k**, keel; **l**, lachrimal (Skelton, 1981; Grande, 1987) or antorbital (Arratia, 1987) or first **io** (<u>q.v.</u>); **lam**, laminar bone of the anterior fused vertebral complex; **leff**, lateral ethmoid-frontal fossa; **leth**, lateral ethmoid; **lg**, ligament; **lpb**, lateral basipterygium process or lateropterygium; **mklc**, Meckel's cartilage; **mdp**, mandibular pores; **mes**, mesethmoid (supraethmoid of Lundberg, 1982; supraethmoid + rostro-dermethmoid of Patterson, 1975; including internasal of Jollie, 1986); **mpt**, metapterygoid; **mspt**, mesopterygoid (endopterygoid of some authors. See e.g. Schaefer, 1987: 8; entopterygoid of Howes and Teugels, 1989);

Mur, Müllerian Ramus (anterior arm of 4th transverse process); **mx**, maxilla; **mxb**, maxillary barbel; **na**, nasal; **np**, nuchal plate ("predorsal plate" of ariid literature); **nra**, neural arch; **ns**, neural spine; op, operculum; **opf**, optic foramen; **os**, orbitosphenoid; pal, palatine (autopalatine of some authors; ref. Jollie, 1986: 371); **pas**, parasphenoid; **pc**, posterior ceratohyal (epihyal of previous authors) (Schaefer, 1987; Vari, 1989); **pcp**, posterior cleithral process; **pfn**, posterior dorsomedian cranial fontanelle; **pfr**, pectoral fin radial; **ph**, parhypural; **phb**, pharyngobranchial (infrapharyngobranchial of Lundberg, 1982; Jollie, 1986; Schaefer, 1987); **plr**, pleural rib; **pmx**, premaxilla; **pop**, preoperculum; **ppb**, posterior basipterygium process; **pro**, prootic; **prx**, proximal radial; **psp**, pectoral spine; **pt**, pterotic; **ptg**, pterygiophores; **pts**, pterosphenoid; q, quadrate; **r**, fin rays; **s**, suture; **scl**, supracleithrum (ref. Fink and Fink, 1981); soc, supraoccipital ("occipital process" of ariid literature); spl, dorsal fin spinelet (= first dorsal spine); **sph**, sphenotic; **svc**, subvertebral cone; **syc**, symplectic cartilage; **t**, teeth; **tf**, temporal fossa (opening between pterotic, sphenotic and exoccipital); **3fn**, third dorsomedian cranial fontanelle; **tgf**, trigeminofacialis foramen; **tp4**, expanded transverse process of 4th vertebra; **tp5**,**tp6**, transverse process of 5th/6th vertebra (called the 2nd and 3rd transverse processes by Mahajan [1966] after Regan [1911a]); **tr**, tripus; **ucp**, uncinate process of third epibranchial; **uh**, urohyal; un, uroneural; **v**, vertebra; **vo**, vomer; **vtp**, vomerine tooth patch.

2.2.2 Osteological study material

Specimens of all of the Australo-Papuan ariid taxa were available for study except *Cinetodus* (*Pachyula*) *conorhynchus*.

The list of material - where only specific names are used for taxa - states: the number of specimens, the institution register number (if any), locality and SL (or HL), preceded by the codes: ss = cleared and single stained (Alizarin); ds = cleared and double stained (Alizarin and Alcian Blue); dry = dry skeleton.

arius: ds - 2, LACM 38129-95, Sind, Pakistan, 112 and 190 mm SL.

armiger: ss - 1, AMS I.27418-001, Murganella Creek, 102 mm SL; ds - 1, unreg., Purari River delta, 176 mm SL; ss - 1, AMNH unreg., Victoria River, 87 mm SL (disintegrated); ds - 3, unreg., Murganella Creek, all approx. 24 mm SL.

argyropleuron: ss - 1, unreg., Cleveland Bay, Townsville, 71 mm SL; ss - 1, unreg., Shoal Bay, Melville Island, 49 mm SL; ds - 3, unreg., Gulf of Papua, 145, 162 and 190 mm SL; ds - 1, Arehava, 215 mm SL; ds - 1, unreg., Morowan, Ini Island, 338 mm SL.

augustus: ds - 1, NTM S.12352-001, mid Purari River, 185 mm SL; dry - 3, unreg., Strickland River, 160 mm HL (490 mm SL), 123 mm HL and 186 mm HL (570 mm SL) (only heads available).

berneyi: ss - 5, NTM S.12078-001, Hodgson River, 60, 61, 67, 67.5 and 78 mm SL; ss - 3, unreg., Wilton River, 84, 95 and 118 mm SL; ss - 1, AMNH 51648 (in part), Red Lily Lagoon, 157 mm SL.

bilineatus: ss - 3, unreg., Melville Island, 109, 124 and 128 mm SL; ds - 1, unreg., off northern Australia, 43.2 mm SL; dry - 1, unreg., NW Australia, (axial skeleton only), 380 mm SL.

carinatus: ds - 2, QM I.22654 (in part), mid Purari River, 237 and 320 mm SL; ds - 1, unreg., mid Purari River, 122 mm SL.

crassilabris: ds - 1, AMS I.27411-001, Kubipara, 308 mm SL; dry - 3, unreg., Strickland River, 80 mm HL, 136 mm HL (405 mm SL) and 175 mm HL (485 mm SL) (only heads available).

danielsi: ds - 1, AMS I.26972-002, Kubiri Creek, 139 and 154 mm SL; ds - 1, unreg., Aird Hills, 220 mm SL; ds - 1, unreg., mid Purari River, 355 mm SL.

dayi: ds - 1, AMS I.25992-002, Kibi Creek, Wabo, 200 mm SL; ds - 3, unreg., Wame River, 129, 158 and 225 mm SL.

froggatti: ds - 1, AMS I.27417-001, Gulf of Papua, 215 mm SL; ds - 1, unreg., Moinamu, 172 mm SL; dry - 1, unreg., Roper River, 109 mm HL.

graeffei: ss - 3, AMNH 57299, King River, 74, 100 and 118 mm SL; ss - 1, QM I.16734 (in part), Boyne River, 83 mm SL; ss - 3, AMS I.27419-001, Nourlangie Creek, 178, 179 and 184 mm SL; ss - 1, unreg., Jabiru, 91 mm SL; ss - 2, AMNH 57302(SW), lower Daly River, 86 and 93.5 mm SL; ss - 2, NTM S.12138-001 (in part), lower Daly River, 83 and 84 mm SL; ss - 2, AMNH 51637 (in part), Ashburton River, 84.5 and 107 mm SL; dry - 1, unreg. Roper River, 96 mm HL; ss - 1, unreg., Clarence River, 139 mm SL.

latirostris: ds - 1, KFRS F.4213-06 (in part), Ningerum, Ok Tedi, 119 mm SL (also as: AMS I.30114-001); ds - 1, KFRS F.4333-01, Laloki River, 90 mm SL (also as: AMS I.30113-001); dry - 3, unreg., Strickland River, 68 mm (220 mm SL), 147 mm and 155 mm HL (only heads available).

leptaspis: ss - 3, NTM S.12355-001, Jabiru, 67, 68 and 69 mm SL; ss - 2, NTM S.12356-001, Magela Creek, 137 and 137 mm SL; ds - 1, AMS I.27420-001, Jabiru, 174 mm SL; ds - 1, unreg., Jabiru, 131 mm SL; ds - 2, unreg., Canon Hill, N.T., both approx. 37 mm SL; dry - 3, unreg., tributaries of Strickland River, 78 mm HL, 128 mm HL (380 mm SL) and 162 mm HL (only heads available).

macrorhynchus: ds - 1, AMS I.25998-002, Kone, Wabo, 300 mm SL.

mastersi: ss - 2, NTM S.10319-001, Melville Island, 89 and 130 mm SL.

midgleyi: ss - 1, WAM P.28776-001, Lake Argyle, 166.5 mm SL; ss - 3, AMNH 51649 (in part), Victoria River, 103, 106 and 114 mm SL; dry - 1, unreg., Roper River, 107.5 mm HL.

nella: ss - 2, NTM S.11908-001 (in part), Melville Island, 147 and 149 mm SL.

novaeguineae: ss - 1, KFRS F02671, Balimo, 93 mm SL; ds - 1, AMS I.27416-002, Era River, 150 mm SL.

nox: ds - 2, WAM P.28225-001, Sepik River, 101 and 114 mm SL; ds - 1, AMS I.27407-002, Angoram, 192 mm SL.

polystaphylodon: ds - 1, AMS I.27412-001, Muarakarang, 165 mm SL; ds - 1, unreg., Vanimo, 160 mm SL.

proximus: ss - 1, NTM S.10060-003, Shoal Bay, Melville Island, 84 mm SL; ss - 1, unreg., Cleveland Bay, 158 mm SL.

solidus: ds - 1, KFRS F02815 (in part), Annanberg, Ramu River, 138 mm SL (also as: AMS I.30116-001); ds - 1, AMS I.27408-002, Angoram, 206 mm SL; ss - 2, unreg., Angoram, 230 and 247 mm SL; ds - 4, AMS I.27409-001, Magendo 2, Sepik River, 81, 113, 168 and 176 mm SL.

spatula: ss - 1, AMS I.25997-002, mid Purari River, 143 mm SL; dry - 3, unreg., Strickland River, 112 mm HL, 140 mm HL and 203 mm HL (only heads available).

taylori: dry - 3, unreg., Strickland River, 108 mm HL (305 mm SL), 79 mm HL and 108 mm HL (345 mm SL) (only heads available).

thalassinus: ss - 3, unreg., N of Darwin, 127, 137.5 and 142 mm SL; dry - 1, unreg., NW Australia, (axial skeleton only), 455 mm SL.

velutinus: ds - 1, RMNH 28815 (in part), Lake Sentani, 215 mm SL; ds - 1, unreg., Angoram, 55 mm SL; ds - 2, WAM P.27856-002, Lake Sentani, 149 and 156 mm SL; ds - 1, AMS I.27410-001, Angoram, 270 mm SL.

species 1: ds - 1, unreg., Gulf of Papua, 159 mm SL; ds - 1, KFRS F03992 (in part), Pie River, 89 mm SL (also as: AMS I. 30115-001).

species 2: ss - 1, SAM F.6254, Keram, Sepik River, 175.5 mm SL.

species 3: ss - 1, NTM S.10235-001, Shoal Bay, Melville Island, 90 mm SL.

species 4: ss - 1, NTM S.10190-002 (in part), Shoal Bay, Melville Island, 88 mm SL; ds - 1, AMS I.27414-001, Ini Island, 237 mm SL; ds - 2, AMS I.27413-001, Arehava, 108 and 151 mm SL.

species 5: ds - 1, KFRS F03302, Paiia Inlet, Gulf of Papua, 188 mm SL (also as: AMS I.30111-001).

species 6: ds - 1, unreg., Fly River delta, 59.5 mm SL.

species 7: ds - 1, KFRS F03995, Kambaramba, Sepik River, 237 mm SL (also as: AMS I.30112-001).

2.3 RESULTS - OSTEOLOGY OF _ARIUS ARIUS_ (HAMILTON-BUCHANAN)

The osteology of the Australo-Papuan representatives of _Arius_ is comparable to that of _A. arius_.

2.3.1 _Skull_

The skull comprises the neurocranium, infraorbitals, the splanchnocranium and suspensorium, opercular bones, hyoid and branchial apparatus.

2.3.1.1 _Neurocranium_

The surface of the neurocranium (fig. 2) is smooth to striate anteriorly and roughened posteriorly with numerous low granules and rugae. It is approximately rectangular in plan, albeit tapered anteriorly (mesethmoid), posteriorly (supraoccipital) and posterolaterally produced (pterotic-supracleithrum-extrascapular). The bones are well-ossified, with firm sutures between them.

In *Nedystoma* the neurocranial surface is smooth. In *Hemiarius* (species 5) it is smooth to well striated. A highly granular or rugose skull surface is present in *argyropleuron* (Genus 1) and in some *Arius* species (e.g. *mastersi*, *latirostris*) (refer figures of head rubbings, Chapter 6). The neurocranium in most ariids progressively strengthens and thickens with age (demonstrated by the dry skulls of adult *leptaspis* and *augustus*). The posterior neurocranial elements in *Cinetodus* are comparatively thick at any age. In contrast, the neurocranium of *Brustiarius* is thin. In adults of the extralimital genera *Hemipimelodus* and *Cephalocassis* (possibly also *Nedystoma novaeguineae*) cartilage persists at the junction of the supraoccipital, sphenotic and pterotic elements (fig. 3).

The MESETHMOID has a moderately wide neck and anterior cornua diverging at approximately right angles, separated by a deep median concavity. The smooth ventral surface of the cornua articulate with the dorsal surface of the premaxillaries.

The mesethmoid shape (fig. 4) displays considerable intra- and intergeneric variation. For example, in Genus 1: similar to that of *A. arius* in *argyropleuron* but broad and shallow-notched in *nella* and *polystaphylodon*. The median notch is more or less retained in most taxa although it is lacking in *Hemiarius*, *N. novaeguineae*, *A. thalassinus* and *A. macrorhynchus*. The last two taxa possess a convex fluted or heavily striated mesethmoid.

The NASALS are elongate and rod-like, turned outward anteriorly and somewhat curved following the line of the concave mesethmoid neck.

All taxa share this general form (sometimes broader; straighter; more curved) but for species 5 (in *Hemiarius*), *N. novaeguineae* and *A. macrorhynchus* which have a distinct, irregularly shaped nasal (fig. 5).

The LATERAL ETHMOID is well-developed and approximately triangular, with the prominent lateral wing rectangular or rhombic. The lateral ethmoid articulates with the frontal medially and by an outer caudad-directed process. The anterior cartilage-edged margin of the bone is turned ventrad, forming a facet for the palatine.

The form of the lateral ethmoid wing is highly variable in Australo-Papuan ariids (figs 6-8). For example, in *Pachyula* and two species within Genus 1 it is truncate and curves posteriad. In Genus 1 *argyropleuron* and *Brustiarius* it is strongly acute; in *A. thalassinus* the lateral ethmoid wing is much expanded distally and in *Nedystoma* it is rectangular (*dayi*) or shallow and curved.

The lateral ethmoid is extensive ventrally in *Cochlefelis* and two of the *Netuma* species group, thus obscuring the space between the frontal arms (figs 6D,E). In Genus 1 *nella* (and in the congeneric *dussumieri* Day from the western Indian Ocean) it is greatly expanded and cancellous in larger adults.

The FRONTAL is moderately elongate and bifurcates anteriorly. The median arm (bearing an upper tubular extension) articulates with the lateral ethmoid and the mesethmoid; the lateral arm extends beneath and sutures with the lateral ethmoid wing. The frontal articulates ventrally with the pterosphenoid.

In some *Arius* species (e.g. *bilineatus*, *mastersi*) and the extralimital *Bagre* the frontal is much expanded anteriorly in older individuals, dorsally overlapping its arms. In Australo-Papuan ariids, the frontal varies in shape from being broad and rectangular to narrow (figs 7,8).

The mesethmoid and the frontal bones form the margin of the elongate DORSOMEDIAN FONTANELLES. The anterodorsal surface of the orbitosphenoid forms the posterior margin of the triangular anterior fontanelle and the EPIPHYSEAL BAR connecting the frontals where the fontanelle is broadest, forms the posterior margin of the middle fontanelle. Caudad to the epiphyseal bar is a third fontanelle which tapers into a narrow median groove at the anterior part of the supraoccipital. In the larger specimen this fontanelle is relatively smaller.

The presence and/or size of the posterior (third) dorsomedian fontanelle is highly variable. In most Arius species it reduces with age, or is absent; but in armiger, species 4, species 7, taylori and macrorhynchus the fontanelle remains moderately large. This condition is also present in Pachyula and Nedystoma (fig. 8).

The SUPRAOCCIPITAL is a large, single bone suturing with the frontal, sphenotic, pterotic and extrascapular anterolaterally, and with the (first) nuchal plate posteriorly. The supraoccipital bears a coarse, median keel, is concave posteriorly and has a basal width (at the level of its median apex) approximately equal to its length from that point (fig. 9). The supraoccipital forms the dorsal margin of the foramen magnum.

The supraoccipital ranges from slender and rectangular (as in Nedystoma and species 5 (in Hemiarius) to very broad, often short (as in Cinetodus and Hexanematichthys), with or without a longitudinal median keel. In Genus 1 nella there is an ontogenetic shift of the slender supraoccipital into a broad oval shape.

The SPHENOTIC forms part of the roof and side of the cranium. It is rectangular above and attenuated adjacent to the termination of the 4th infraorbital bone. Laterally, the sphenotic bears a sharp longitudinal ridge, so forming most of an articular facet for the hyomandibular.

The articular facet is almost horizontal (fig. 15) and restricted to the sphenotic in about half the Australo-Papuan taxa. In the remainder it extends onto the pterotic - often only to just beyond the sphenotic-pterotic suture.

The PTEROTIC is square in two planes (above and laterally) and contains a deep concavity above an angular portion of the auditory bulla. It and the rounded EXTRASCAPULAR form the dorsal and lateral borders of the ovate lateral TEMPORAL FOSSA situated dorsad to the supracleithrum. This fossa is reduced in larger individuals (fig. 10).

The temporal fossa remains large and conspicuous in adults of *Cinetodus*, *Hemiarius* and some other species (including members of *Arius*; e.g. *taylori*). However, in *Hexanematichthys*, *Brustiarius* and *A. bilineatus* (all within *Arius*) and *Nedystoma* the fossa ranges from being moderately reduced (and elliptical) to virtually absent (fig. 11).

The SUPRACLEITHRUM is very thick; dorsally wedge-shaped, ventrally extending below the skull as a transverse arm (the ossified Baudelot's ligament) to articulate with the basioccipital.

The supracleithrum extends dorsally in some taxa (e.g. *Cinetodus*, *Nedystoma*) posterior to the extrascapular (figs 11B,19A,38B).

The head of the VOMER is triangular, the short arms deeply serrated distally. The long posterior extension interdigitates with the several tapering anterior processes of the parasphenoid. The vomer is edentate.

There is some interspecific variation in the shape of the vomer anteriorly (e.g. crenulate; rounded) and the arm length (fig. 12). In Genus 1 the vomer is almost club-shaped, the lateral arms very short.

The flat, dilated ORBITOSPHENOID, forming the anterolateral wall of the neurocranium, underlies the frontal and overlays the parasphenoid anteriorly. Posterolaterally it shelves slightly outward and unites with the (anterior) wing of the parasphenoid.

The long PARASPHENOID shelves anteriorly ventral to and sutures with the orbitosphenoid; it sutures posteriorly with the basioccipital (fig. 13). At about mid-length, the parasphenoid is expanded broadly dorsolaterally into a thin shelf attenuating to form two spurs or wings (Bhimachar, 1933). The flange sutures with the anteroventral margin of the pterosphenoid.

In some taxa the alary processes ("wings") of the parasphenoid exhibit an ontogenetic increase. There is also considerable variation among _Arius_ and other genera in Australia and New Guinea in the number and shape of the processes (fig. 14).

Midlaterally on the neurocranium, and bounded by the orbitosphenoid apex, the parasphenoid, frontal, sphenotic and prootic, lies the small PTEROSPHENOID. It is irregularly ovate-elongate and has a long ventral shelf suturing with the parasphenoid. The posterior extremity of the pterosphenoid surrounds the large trigeminofacialis foramen. The optic foramen occupies an area between it and the orbitosphenoid.

The pterosphenoid ranges from being narrow and wedge-shaped in some taxa (e.g. _Cochlefelis_) to broad and ovate (e.g. _A. augustus_) (fig. 15). Ventrally it may be produced into spurs independent of the parasphenoid wings.

The PROOTIC is moderately large and ovate, forming the ventrolateral wall of the cranium. Posteriorly, it bulges outward as part of the AUDITORY BULLA. The prootic is bounded by the sphenotic, pterosphenoid, parasphenoid, basioccipital, exoccipital and pterotic. The last two bones also contribute to the auditory bulla.

The stout BASIOCCIPITAL sutures laterally with the ossified Baudelot's ligament of the supracleithrum (figs 16,18A). Posteriorly it sutures tightly with the superficial bone over the compound vertebral region. Together these elements extend ventrally as a SUBVERTEBRAL CONE, which is truncated and tipped with cartilage. The rounded anterior opening of the aortic tunnel (aortic foramen) lies on the basioccipital at the anterior base of the cone. The basioccipital posteriorly forms the ventral margin of the foramen magnum.

The size of the subvertebral cone varies (fig. 17) within *Arius* in Australia and New Guinea and among other genera. For example, it is very prominent in *Cinetodus*, *Nedystoma* and *Arius armiger*.

The smooth EXOCCIPITAL forms the posterolateral wall of the skull. Its ventral aspect sutures with the basioccipital and bears two short, connecting struts. The exoccipital forms the lateral margin of the foramen magnum (fig. 18B).

The EPIOCCIPITAL is moderately large and lies in two planes, the anterior forming the dorsal posterolateral part of the cranial roof and the posterior diverging from it at a 45°-60° angle. The upper surface closely articulates with the supraoccipital, the extrascapular and the pterotic. Posteriorly the epioccipital shares a long, median articulation with the ventrolateral extension of the fourth neural spine and thereby sutures to the dorsal surface of the compound vertebral region laminar bone (fig. 17).

Whereas in most ariid taxa the anterior of the epioccipital lies below the extrascapular, in some it is exposed and forms part of the neurocranial dorsal surface. This situation exists in two

Australo-Papuan *Arius* species (*proximus*, species 6) and two Genus 1 species. In *Cinetodus*, where the epioccipital and extrascapular form a unit, the epioccipital could also be interpreted as a neurocranial roofing bone (figs 11A,19,38).

Extending the median length of the lateral ethmoid plus mesopterygoid is a triangular, elongate AUTOGENOUS TOOTH PLATE (one each side of palate). It is not articulated with any bone. The tooth plates are finely pitted and ridged on the dorsal surface and the teeth on the ventral surface are stout, blunt and conical.

The presence/absence and disposition of autogenous tooth plates is highly variable in ariids, particularly within *Arius* (fig. 20). In all Australo-Papuan *Arius* species possessing such plates at some life stage they are located on the anterior half of the palate lateral to the vomer. The plates are usually ovate, sometimes triangular (in species 6, *A. graeffei* and the *Netuma* species group). *A. mastersi*, *A. thalassinus* and *A. bilineatus* possess a second, more posterior tooth plate on each side. Palatal tooth plates are also present in Australo-Papuan *Hemiarius*, Genus 1, *Cinetodus* *Cinetodus* and *Nedystoma novaeguineae*.

2.3.1.2 Infraorbitals

There are four infraorbital bones, each somewhat tubular. The first infraorbital (or lachrimal) is a simple, oblong plate with triangular processes diverging from each corner. It occupies the space between the nasal, lateral ethmoid and maxilla. The remaining infraorbitals are simple tubes as follows: 2nd slightly convex and not closely articulated with the lachrimal; 3rd almost straight and at the midorbit level; 4th ascending and longest, having a strong anteriorly inclined angle (or sigmoid form) and terminating opposite the forward angle of the sphenotic (fig. 21A).

All Australo-Papuan ariids except for N. novaeguineae have four infraorbitals (fig. 21B) and they are more or less arranged as in A. arius. The lachrimal form varies slightly between taxa, being noticeably narrower with blunt or acute processes in taxa such as Nedystoma novaeguineae, Arius macrorhynchus and two species within Genus 1 (fig. 22).

2.3.1.3 Splanchnocranium

The premaxillae and mandibles are dentate, constituting the functional biting elements.

The PREMAXILLA is thin and broadly rectangular. Its lateral border is concave (formed by the extended upper and lower corners) and the median border is straight. The premaxilla lacks a low crest dorsolaterally. There are 9 or 10 irregular series of slender, villiform teeth covering the entire ventral surface (figs 20,25).

The shape of the premaxilla is approximately similar in Australo-Papuan Arius species but for species 4 in which it is shorter with an almost truncate lateral margin. This form also occurs in Cinetodus and Genus 1. The premaxilla is wider in broad-mouthed taxa. In Nedystoma it is elongate-oval with irregular margins. The bone is thin in Brustiarius and Nedystoma.

The number of tooth rows and type of teeth is highly variable, ranging from a broad band of 15 series in Cochlefelis (within Arius), to a narrow band of 1-4 series in Nedystoma.

The MANDIBLE consists of elongate, toothed dentary, anguloarticular and coronomeckelian bones. In a groove on the inner surface lies the MECKEL'S CARTILAGE; and on the outer lateral surface are perhaps 5 shallow or poorly developed mandibular foramina or pores. The relative thickness and amount of striation on the mandible is consistent with that of the neurocranium. The mandibular pores are large in Australo-Papuan *Hemiarius*, *Nedystoma novaeguineae*, *A. armiger* and *A. augustus* (fig. 23).

The DENTARY is thick and depressed in its anterior two-thirds with a blunt or truncate median border. It bears 4 or 5 series of villiform teeth. Posteriorly, it is elevated and extends ventrally below the anguloarticular.

The ANGULOARTICULAR is wedge-shaped, with a broad, thickened facet posteriorly to accommodate the quadrate. It is elevated anteriorly to form a moderately-developed coronoid process with the dentary. The CORONOMECKELIAN is small and irregularly pitted: an ovate portion overlays the junction of the CORONOID CARTILAGE and Meckel's cartilage, and a narrow, wedge-shaped portion inserts posteriorly into a crevice on the inner surface of the anguloarticular. The coronoid cartilage extends only slightly dorsad to the CORONOID PROCESS.

There is interspecific variation in the height and shape of the coronoid process among Australo-Papuan ariids, i.e. more flattened or tapered, well-elevated or shallow. This variation cannot be quantified.

The palatine and maxilla are excluded from the gape in ariids. The MAXILLA in *A. arius* forms a support for the maxillary barbel. It is wedge-shaped with a proximal constriction anterior to a short, bilobed termination articulating with the palatine.

Most Australo-Papuan ariids have a similarly shaped maxilla; in some (e.g. *Brustiarius*) the proximal section is almost unilobula.

The PALATINE is elongate, truncate anteriorly and tapered distally. The extremities are cartilaginous, the anterior tip articulating solely with the maxilla, the posterior tip slightly projecting beyond the lateral ethmoid wing. There is a short articular facet for the lateral ethmoid two-thirds along the length of the palatine (fig. 24).

There appear to be differences between several species groups of Australo-Papuan ariids in the *length* of the palatine (e.g. longer in species 4). A long lateral ethmoid articular facet is present in the subgenus *Brustiarius* and the genera *Nedystoma* and Genus 1.

2.3.1.4 *Suspensorium*

This group comprises the hyomandibular, preoperculum, quadrate, metapterygoid, mesopterygoid and an ectopterygoid (figs 25,26).

The ECTOPTERYGOID is a small, sickle-shaped bone, the anterior part articulating with the palatine at about the level of the lateral ethmoid articular facet, and the posterior with the ventral surface of the posterolateral arm of the mesopterygoid.

The MESOPTERYGOID is triangular, with a concave distal margin. A ligament from the ventral face of its apex inserts onto the lateral ethmoid before or on the tip of the vomer arm, and a second ventral ligament inserts anterodorsally on the metapterygoid.

The mesopterygoid shape is mostly comparable between ariids in the study region, although in *A. thalassinus* and *A. bilineatus* it is almost crescentic.

The METAPTERYGOID is roughly square, narrowing ventrally. It sutures with the quadrate ventrally and ventroposteriorly with the hyomandibular. A short elongate process underlies the mesopterygoid anteriorly. The sutures are serrated, and symplectic cartilage fills the unossified space the three bones share with the preoperculum.

Australo-Papuan *Arius* species *macrorhynchus*, species 4 and *Brustiarius*, as well as *Cinetodus carinatus*, *Hemiarius* and Genus 1 have a large metapterygoid extending beyond the quadrate, often to above the hyomandibular (fig. 26D).

The QUADRATE is approximately triangular. Its posterior portion is compressed with a convex border; anteroventrally it is thickened and forms a concave facet to accommodate the anguloarticular. The ventral border of the quadrate articulates with the anterior of the preoperculum.

The HYOMANDIBULAR partly overlaps and partly articulates with the preoperculum along its ventral margin. Approximately oblong, it broadly articulates dorsolaterally with the sphenotic via the long, ventral facet. The dorsoposterior part of the hyomandibular is extended to form a rounded spur beyond the articulation of the hyomandibular and the opercular facet.

The narrow PREOPERCULUM's extensive contact with the ventral border of the hyomandibular is interrupted by a foramen for the facial nerve. Anterolaterally the preoperculum overlaps the ventral part of the quadrate. It is tapered and cylindrical dorsolaterally. When viewed laterally, the considerable space separating the preoperculum from the sphenotic is apparent.

2.3.1.5 Operculae

The INTEROPERCULUM is expanded posteriorly, its concave posterior margin accommodating the operculum. The stout ventroanterior part of the interoperculum is ligamentously attached to the anguloarticular bone.

The OPERCULUM is broadly triangular with a convex dorsal angle and truncate ventral margin.

There is interspecific variation between the shape of the adjacent operculum and interoperculum margins and the dorsoposterior angle of the operculum (fig. 27), e.g. between A. thalassinus and A. bilineatus. Tilak (1965) used these features in distinguishing ariids of the seas around India. The operculae are smooth and venulose in Hemiarius.

2.3.1.6 Hyoid apparatus

The INTERHYAL is a small, oblong bone attaching the hyoid arch (through ligaments) to the skull at about the position of the hyomandibular-interoperculum interface. It is not sutured to the broad and stout triangular POSTERIOR CERATOHYAL. Strong sutures unite this bone with the ANTERIOR CERATOHYAL across a synchondral space. The anterior ceratohyal is cylindrical, yet expanded at each extremity (fig. 28).

The HYPOHYAL is in two parts: the ventral (anterior) hypohyal sutures with the anterior ceratohyal and the slightly smaller dorsal element articulates with both bones. Cartilage occupies the space between the bones.

There are six BRANCHIOSTEGAL RAYS. The four proximal rays are associated with the ventral edge of the anterior ceratohyal, the fifth with the cartilage between it and the posterior ceratohyal, and the last with the ventroanterior tip of the posterior ceratohyal. The proximal four rays are slender, the remainder somewhat expanded distally, such that the last is twice as broad at its end as at its origin. The tip of the 5th ray slips dorsad to the 6th ray's tip.

In *Brustiarius*, *Nedystoma* and species 5 (in *Hemiarius*) the branchiostegals are slender and elongate. Those of *Cinetodus* and Genus 1 are stouter and reasonably short. The two outer rays (numbers 5, 6) are very broad in Genus 1. One *Cinetodus* species, *A. thalassinus* and *A. bilineatus* have only 5 branchiostegals; Australo-Papuan *Hemiarius* and *A. augustus* have 7 (fig. 29).

The UROHYAL is moderately elongate and elevated medially. Anteroventrally it is oblong and emarginate with a short median groove; posteroventrally it is triangular with two lateral processes diverging off a slender median extension. Dorsomedially, the urohyal forms a high, convex crest.

The form of the anterior margin and the length or width of the posterior processes of the urohyal exhibit considerable inter- and intrageneric variation in Australo-Papuan ariids (fig. 30).

2.3.1.7 Branchial apparatus

The branchial apparatus (figs 31,32) consists of two basibranchials and (on each side) two osseous and two cartilaginous hypobranchials, five ceratobranchials, four osseous and one cartilaginous epibranchials and three pharyngobranchials.

The median BASIBRANCHIALS are situated between the two anterior hypobranchials. They are mushroom-shaped, the first resting on the dorsal surface of the urohyal.

The osseous HYPOBRANCHIALS are triangular and associated with the first two ceratobranchials. Hypobranchials associated with the proximal tip of ceratobranchials III to V are cartilaginous.

The first four CERATOBRANCHIALS are long, slightly curved and rod-like, articulating via cartilage with the four osseous epibranchials. The medially situated, fifth ceratobranchial is proximally J-shaped and expanded to form a thin shelf bearing 2 to 6 series of villiform, sharp teeth. This ceratobranchial bears a long cartilaginous distal extremity.

The four osseous EPIBRANCHIALS and remaining elements form the dorsal part of the "branchial basket". The first two are elongate and approximate closely at their distal, cartilaginous tip and the first has an expanded "elbow" or protruberance mid-dorsally. The third epibranchial bears an angular UNCINATE PROCESS which overlaps and is connected by ligament to, the broad mid-section of the 4th epibranchial. The cartilaginous (5th) epibranchial intersects at a right angle with the distal extremity of the 5th ceratobranchial and the cartilage between the 4th ceratobranchial and the 4th epibranchial.

The first PHARYNGOBRANCHIAL is an elongate bone attached proximally to the expanded portion of the first epibranchial. The third pharyngobranchial is elongate and angular, lying transversely between the tips of the 2nd and 3rd epibranchials. The 4th pharyngobranchial is an ovate disc supported by a plate of cartilage, between the tips of the 3rd and 4th epibranchials. It is capped ventrally by an osseous tooth plate bearing many slender teeth and having two dorsal extensions.

There is no 2nd pharyngobranchial. The small cartilaginous structure between the apices of the 1st and 2nd epibranchials is recognised as such by Fink and Fink (1981) and Skelton (1981) but I concur with Rao and Lakshmi (1984) and C. Ferraris (pers. comm.) who dispute its homology with a pharyngobranchial. Its presence within the family is inconsistent.

Pharyngobranchial IV and ceratobranchial V are the only toothed elements of the branchial skeleton.

GILL RAKERS line the anterior and posterior margins of the first four epibranchials and ceratobranchials, and the anterior margin of the 5th ceratobranchial. Gill filaments extend along the outer face of the first four ceratobranchials and proximally on their opposing epibranchials.

All Australo-Papuan ariids possess a branchial apparatus resembling that of *A. arius* (fig. 31). The cerato- and epibranchials may be comparatively longer (e.g. *Brustiarius*) or shorter. The uncinate process is rhombic (Genus 1) or elliptic (*Nedystoma*). In *Nedystoma* it overlaps the proximal part of the 4th epibranchial; in *Brustiarius* it articulates with or abuts that epibranchial. The only other substantial variation exhibited is the shape and position of the 1st pharyngobranchial (fig. 33): in *N. novaeguineae* and species 5 (in *Hemiarius*) this elongate bone is attached near the distal tip of the 1st epibranchial; and in *Cinetodus Cinetodus* is either lost or fused with the expanded portion of the 1st epibranchial. The 1st pharyngobranchial is ovate in Genus 1. Finally, the gill raker complement and presence/absence of rakers on the trailing edge of the arches, is specifically related.

2.3.2 The axial skeleton

2.3.2.1 Weberian Apparatus and anterior vertebrae

The anterior vertebrae in *Arius* (numbers 1 to 6 or 7) are rigidly united to form the COMPOUND VERTEBRAL REGION (figs 34,36). A part of this, termed the COMPLEX VERTEBRA, is a single composite centrum formed by the fusion of the second to 4th vertebral centra. Ventrally, the centra are covered by a sheet of superficial (or laminar) bone which envelops and encloses the aorta in a tunnel. The narrow proximal portion of the laminar bone is produced ventrally to form a thick subvertebral process or cone (q.v.). This process is suturally united with the produced ventral process of the basioccipital.

The composition of the ariid complex centrum is described in detail by Karandikar and Masurekar (1954), Tilak (1965) and Chardon (1968).

The SUPERFICIAL (LAMINAR) BONE forms a pronounced ridge along the midline of the vertebral centra and is emarginate medially over the free 6th or 7th vertebra. The laminar bone is more extensive in larger individuals, an ontogenetic change evidenced in most taxa.

Through all life stadia, the laminar bone is less extensive in Australo-Papuan Hemiarius and more extensive in some Arius (species 4, macrorhynchus), Genus 1 and Nedystoma.

I partly dissected the bone-encased FIRST VERTEBRA on my specimens. It appears to be similar to that of A. platystomus Day, which Karandikar and Masurekar (1954) reported lies hidden within the subvertebral cone, is small and consists almost wholly of the discoidal centrum.

The VERTEBRAL COLUMN is firmly attached to the skull in four places: 1) at the subvertebral cone; 2) the articulation of the 3rd neural spine with the exoccipital and the supraoccipital at the dorsal wall of the foramen magnum; 3) the articulation of the long medial border of the epioccipital with the flange of the 4th neural spine; 4) the tip of the 4th neural spine with the nuchal plate thence the posterior termination of the supraoccipital, all in turn rigidly attached to the first pterygiophore of the dorsal fin.

The extensive TRANSVERSE PROCESS (or parapophysis) OF THE 4TH VERTEBRA is a moderately thin, arched bony plate. Posteromedially it underlaps the transverse process of the basally thickened 5th vertebra; and anteromedially it terminates in a hook-like knob (which is attached in turn by ligament to the superficial bone at the base of the subvertebral cone). Anterolaterally, the 4th transverse process projects outward and downward, forming the MÜLLERIAN RAMUS. The Ramus is attached by specialised muscle bundles (Elastic Spring Apparatus) to the posterior wall of the neurocranium.

The Müllerian Ramus in all Australo-Papuan ariids is tapered. In Pachyula, Nedystoma and some Arius (midgleyi, augustus) it is longer than in other taxa. The Ramus in species 5 (Hemiarius) is unique, being abbreviated and directed at a right angle. In this species also, the reduced bony plate of the 4th transverse process bears large openings (fig. 36F).

The 5th vertebra has a proximally-expanded transverse process. It is directed obliquely backward. In Nedystoma dayi, species 5 (Hemiarius) and two species in Genus 1 the processes remain at right angles to the 5th centrum. The 1st pleural rib emanates from near the tip of the 6th vertebra's transverse process.

The four WEBERIAN OSSICLES (scaphium, intercalarium, claustrum and tripus) are morphologically similar to those of other ariids (fig. 35). Description of form and arrangement is given in the references cited above. Ossicles from Australo-Papuan ariids were not compared.

The strong NEURAL SPINE of the 4th vertebra is bifid distally and receives the expanded pterygiophore of the first dorsal spine. It bears low median and lateral ridges or flanges. The 5th, 6th, 7th and 8th vertebrae lack a neural spine (figs 37,41).

The flange(s) of bone from the neural spine is (are) well-developed in some ariids. Furthermore, a third flange may be present from the anterodorsal portion of the spine, articulating with the supraoccipital (fig. 38). In *Cinetodus* the flanges are particularly high (fig. 19B).

2.3.2.2 Median fins and supports

The CENTRA of the vertebral column posterior to the compound vertebral region are approximately square, a little higher than long and of similar size (fig. 39).

The Australo-Papuan ariids exhibit interspecific morphological differences in the vertebral centra which are difficult to quantify, e.g. size of the anterodorsal spur, situation of foramina. In *Cochlefelis* and *Brustiarius* a bony lamina extends well above each centrum. However, two features can be clearly demonstrated: the anterior caudal centra in *A. thalassinus* are considerably enlarged; and the posterior caudal centra in Genus 1 are shortened and extended vertically.

Posterior to the 6th (or 7th) vertebrae comprising the fused vertebral region, 12 (11) vertebrae form the THORACIC or TRUNK REGION. The vertebrae in the anterior and trunk sections are termed PRECAUDAL vertebrae (they have open haemal arches). The HAEMAL REGION - where the transverse processes from each vertebra is joined to its partner to form the haemal arch - consists of 4 (5) vertebrae. Each of the remaining 29 (30) vertebrae (including the hypural plate) have single haemal and neural spines. The haemal, caudal and hypural together form the CAUDAL VERTEBRAE. The transverse processes of the 6th to 18th (19th) vertebrae bear slender pleural ribs.

There are inter- and intrageneric differences in the number of centra in each section of the vertebral column. For example *Cinetodus* with 3-4 haemal centra *cf.* Genus 1 with 6-7 and some regional members of *Arius* (*midgleyi*, *graeffei*, *velutinus*) with 6-8; also *Hemiarius*, *A. mastersi* and *A. leptaspis* with 20-24 precaudal centra *cf.* 13-15 in *Nedystoma* (and refer fig. 76).

CAUDAL FIN SKELETON. The first preural and first ural centra are fused, forming a COMPOUND CENTRUM (HYPURAL PLATE). A free, rather thickened EPURAL lies above the well-developed neural arch of the compound centrum and the penultimate centrum. This neural arch lacks a spine. The vertebra next anterior possesses reduced neural and haemal spines. The PARHYPURAL is fused to the compound centrum and free from the first hypural. HYPURALS 1 + 2 are fused together and to the compound centrum. These three elements (Hy 1 + 2, parhyp.) are overlain proximally by the combined ridge of the PRIMARY and SECONDARY HYPURAPOPHYSES (fig. 40).

Hypurals 3 + 4 are attached. Their proximal termination is cartilaginous and abuts the middle of the compound centrum. The 5th hypural is free, its dorsolateral margin closely approximating the ventrolateral margin of the URONEURAL. There is no trace of a 2nd ural centrum at the base of hypurals 3 to 5.

In the *Netuma* species group of *Arius* and in *Pachyula* and Genus 1 *nella* the parhypural is fused with the 1st hypural. Apart from this, the only noteworthy caudal skeletal difference of Australo-Papuan ariids from *Arius arius* is the slightly variable form of the secondary hypurapophysis (margin knobby; straight) in most taxa although it is clearly expanded and flattened in Genus 1 *argyropleuron*. A neural spine is usually present on the penultimate vertebral centrum and its size -

along with nearby neural and haemal spines - appears to be individual or ontogenetic expression. Some variability is present in the size of the epural proximally and its level of association with the neural spines (e.g. broad and square-based in Cinetodus). Quantitative assessment of such features however, cannot be made.

The caudal fin has 15 principal segmented rays, the outer two being unbranched. It is forked, 7 principal rays associated with the upper hypurals, 8 with the lower. The number of PROCURRENT RAYS varies, but two specimens examined have 21 and 23 associated with the upper lobe, 19 and 22 associated with the lower lobe.

There are 7 + 8 principal caudal rays in ariids, whereas the number of procurrent rays exhibits considerable interspecific variation.

The DORSAL FIN is supported by two enlarged PTERYGIOPHORES associated with the spines, five slender pterygiophores and a double pterygiophore (fig. 41).

The 4th neural spine, which receives the tip of the 1st pterygiophore, extends shortly below the crescentic collar of the (first) nuchal plate (fig. 37). This plate is sutured with the shelf of the second pterygiophore which in turn forms a facet for the dorsal spine base. The first dorsal spine is wedged between the two plates. The next five pterygiophores each have slender arms and an expanded distal portion, and are separated by a cartilaginous radial from the soft fin rays. The expanded dorsal part of the last pterygiophore has a broad, truncate ventroposterior portion in addition to the slender ventroanterior arm and supports the 6th and 7th branched fin rays.

There are 7 or 8 simple and 13 to 15 branched rays in the ANAL FIN. Simple, slender pterygiophores support all of them except for the first two - which share a single pterygiophore - and the last ray which has an expanded pterygiophore bearing two dorsal arms (fig. 42). A cartilaginous distal radial separates each pair of elements.

There is interspecific variation among Australo-Papuan ariids in the number of anal fin rays, from 15-17 in *A. thalassinus* to 31-33 in *N. novaeguineae*.

2.3.2.3 Girdles

PECTORAL GIRDLE AND FINS. The CLEITHRUM is large and in two planes: on the dorsal aspect it is broad and flat and meets its partner medially at a broad, straight symphysis; on the lateral aspect it is heavily ossified at the angle, thence produced into two ascending and one caudally-directed (= "humeral process") arms (fig. 43). Ventrally there is a long pouch in the bone. The two ascending arms of the cleithrum articulate with the skull through the socket of the supracleithrum. Each expanded CORACOID joins its partner on the midline through about 12 interdigitations. Laterally, the coracoid ventral keel turns slightly upward.

The pectoral symphysis is noticeably wider in some ariids. In the *Netuma* species group, species 6, *Brustiarius*, *A. mastersi*, *graeffei*, *berneyi* and species 4 (all in *Arius*) it is approximately 9% or more of the SL. The girdle is noticeably shelving and thin in *Brustiarius*. In *Cinetodus* the girdle is very stout and well-curved, with a short median "shelf", the most apparent of the interspecific variation in girdle curvature and size exhibited within the Australo-Papuan ariids.

The cleithral process is moderately large in most *Arius* in New Guinea and Australia, although in the *Netuma* group it is somewhat broad. *Nedystoma* and *Arius armiger* have reduced processes *contra Cinetodus* in which the process is long, almost horizontal and thickened.

The 10 or 11 PECTORAL RAYS are supported by 3 radials: two osseous, one short and cartilaginous. The pectoral spine terminates in a large socket at the angle of the cleithrum. The number of pectoral rays varies from 8 (Brustiarius) to 12 or 13 (Genus 1). The pectoral spine - as with the dorsal spine - displays considerable inter- and intrageneric variation in thickness and armature, from being almost smooth and margined with few or low series of serrae to highly rugose with strong dentae or large serrae.

PELVIC GIRDLE and FINS. The broad BASIPTERYGIUM (fig. 44) is produced to form two long, acute processes anteriorly and a curved, expanded process posteromedially. A neural foramen pierces the middle of the basipterygium. The basipterygia meet synchondrally along the midline and each has a short anterior prominence. The tips of the inner, long processes do not touch each other. The outer processes have a strong ridge and at their base is a short, upturned spur. Six branched segmented rays abut the basipterygium posterolaterally. The base of each ray is split into halves; and there are no radials.

There is little variation in the form of the basipterygium among Australo-Papuan ariids. The posterior process may be more slender (e.g. Cochlefelis) or rounded (e.g. Nedystoma) and the short upturned lateral spur may be longer or shorter. The number of 6 branched segmented rays is constant in the family.

3. CLASSIFICATION SCHEME AND CHARACTER ANALYSIS OF AUSTRALO-PAPUAN ARIIDS

3.1 RATIONALE

The search for patterns of organismic descent and arrangement of groups of taxa to form the basis for a sound classification scheme has been undertaken by three main methods. The evolutionary relationships defined in this thesis are determined by the phylogenetic or cladistic method as expounded by Hennig, ~~1950;~~ 1966; Wiley, 1976; 1979; 1981; Ax, 1987). I believe this method is preferrable to evolutionary systematics (defined by Simpson, 1961; Mayr, 1963; 1969) and phenetic analysis (following Sneath and Sokal, 1973).

Phylogenetic classification is based on genealogical descent, i.e. heritable characteristics of organisms are passed from ancestral to descendant species to form a hierarchy (Wiley, 1979; Brooks and Wiley, 1985). Such species are recognised as having combinations of ancestral (plesiomorphic) and derived (apomorphic) traits.

Using this method, evolutionary relationships between groups of natural taxa are based on shared, derived character states or synapomorphies. Such groups of natural taxa are defined as monophyletic ("holophyletic" by Ashlock, 1971) and it is only these groups that can indicate phylogenetic relationships (Wiley, 1976).

The phylogenies are reconstructed using the following processes: selection of characters for comparison whereby misleading and irrelevant ancestral states held in common (symplesiomorphies)(Patterson, 1982) and uniquely derived states (autapomorphies) are eliminated; and the determination of character states as ancestral and derived (= polarity assessment) by outgroup comparisons or through ontogenetic transformation series.

To enable meaningful application of phylogenetic methods to hypotheses of evolutionary relationships in the Ariidae, several intrinsic problems pertaining to character choice, had to be addressed. These, and other conceptual terms, are discussed below.

3.1.1 Characters

The need for osteological description of the Ariidae was outlined in Chapter 2.1. Other ariid morphological features have generally received scant attention (Merriman, 1940; Alexander, 1965) apart from those pertaining to reproduction (Rimmer and Merrick, 1983: review) and pre-Hennigian classification schemes (e.g. Bleeker, 1858; Weber and de Beaufort, 1913; Munro, 1967; refer Chapter 1).

To be utilitarian, a character should satisfy two important criteria: it should have a genetic rather than an environmental basis, and it should be independent of every other character (Richardson, et al., 1986). Heritable characters may be modified during genealogical descent but in phylogeny there are no true character reversals (Wiley, 1976). Distinction between concepts of character, character-variable and character-states has been reviewed (Colless, 1967; Ghiselin, 1984; Colless, 1985).

Character recognition is a problem in the Ariidae and other catfish groups. There is a great lack of information on the biology and morphology (functional and descriptive) of catfishes and, considering the size of the suborder, comparative studies have been undertaken for only a few families (e.g. by Lundberg and Baskin, 1969; Gosline, 1975; Howes, 1983; Schaefer, 1987). Howes (1983) pointed out that the anatomy of even the largest families have been considered in only meagre literature and that of others has not been described. Arratia (1987) believed that her study of the Diplomystidae was hampered by lack of comparative information and that a base for future phylogenetic interpretation of the relationships within the Siluroidei requires detailed ontogenetic studies on various structures in different siluroid groups. Leaving Chardon's (1968) problematic attempt (Roberts, 1973; Arratia, 1987) to arrange the siluroids into higher categories, the scientific community has still not produced sufficient knowledge on this massive suborder "so much that a cladogram could be produced which includes most of the families." (Arratia, 1987:82).

Largely because of this, Howes (1983) and Arratia were unable to apply cladistic methods to interpret relationships of the subjects of their studies albeit Howes (1983a) proposed one for the loricarioid fishes ~~(following Baskin, 1972)~~ - even based on an incomplete "genera" set.

3.1.1.A. Only homologous characters can be compared in studying relationships among taxa. Characters are homologous if they are transformation stages (states) of the same original character present in the common ancestor (Wiley, 1975; and see Bock, 1973). In practice, homologues are decided on the basis of similarity in location, structure and ontogeny (Arnold, 1981). Problems in ascertaining character homology rarely arose in the ariids (fin spine form, neurocranial ossification and palatal dentition may be exceptions). However, homologues in my outgroup were sometimes not so clear-cut (see 3.1.2).

3.1.1.B. The effect of incorporating correlated characters into a phylogenetic analysis can produce quite different interpretations in reconstruction (Felsenstein, 1982). Yet detecting these characters all too frequently depends on functional analysis of the study group. Other than authors such as Gosline (e.g. 1975), Alexander (1965; 1970) and

Schaefer and Lauder (1986) such a task has been largely ignored in the Siluroidei. Furthermore, Maddison et al. (1984) drew attention to the problem that characters labile in an outgroup may be equally labile in the ingroup and so cannot confidently be used to resolve the ingroup. The ariids possess a number of correlated characters (e.g. those pertaining to the trophic and habitat requirements). Recognition of firm, independent, non-osteological characters proved to be a particularly vexing problem.

3.1.1.C. Homoplastic characters (sensu Clark, 1986) are structurally similar characters which have arisen independently of each other (Wiley, 1981). Homoplastic characters do not contribute to the reconstruction of a phylogeny (Farris, 1983) and they comprise what have been known as "reversals", "convergences" and "parallelisms" (Wiley, 1981; Arnold, 1981; Ax, 1987). Homoplastic characters can be recognised as features with phyletic distribution incongruent with the final most parsimonious phylogenetic reconstruction (Hennig, 1966; Vari, 1983; 1989). Panchen (1982) and Neff (1986) pointed out that by calling incongruent characters reversals or convergences, one is actually only negating data which questions the central currently held, cladistic hypothesis! Vari (1983; 1989) recognised two types of homoplasies (internal, external) and investigated whether they are innovative or reductive with a meaningful pattern in the final hypothesis of relationship. Although acknowledging the value of his work for the Ariidae, I did not pursue it in my study of this family section.

3.1.2

Polarity assessment relies on hypotheses of evolutionary change between character states. Stevens (1980) and Arnold (1981) comprehensively reviewed criteria used to assign evolutionary polarity.

They concluded that the most satisfactory is outgroup comparison, i.e. comparison of homologous characters between ingroup taxa and its sister group plus at least one more cladistically ancestral taxon (together forming the outgroup). A character state occurring only in the outgroup or related groups is assumed to be plesiomorphic. Polarity has sometimes been decided by using the "commonality principle" (a character state common to most terminal taxa is deemed to be plesiomorphic) but this principle has been criticised by Watrous and Wheeler (1981), Arnold (1981) and other authors (yet see comments by Farris, 1974).

Hypotheses of outgroup relationships have an effect on ingroup character polarity, which are themselves hypotheses. For example, Markle (1989) arrived at different character polarity in gadoid fishes through the use of alternative outgroups.

Therefore, a recurring problem with the use of outgroup comparison for determining character polarity is the requirement that the interrelationship of the ingroup and outgroup is known, something not always available (Colless, 1967a), and certainly not for the Ariidae - as explained below. Selection of outgroups for any catfish family can best be described as haphazard. Less than half of the known catfish families have been systematically reviewed since Regan (1911a) and those that have constitute the larger, or "more specialised", or more accessible groups. The almost circumtropical presence and apparently conservative nature of the Ariidae have made outgroup selection an even greater predicament, as almost all catfish families could be nominated as outgroups to the Ariidae under those "guidelines" (refer Chapter 1; 3.1.1 above). Thus, because polarity assessment is more robust the closer and more comprehensive the outgroup, polarities in this study are necessarily more vulnerable (Maddison *et al.*, 1984).

Not only that, but if species used as an outgroup in fact belong to the taxon under study, completely erroneous conclusions will be drawn; i.e. an ingroup comparison would have been made. For this reason, extralimital ariids cannot form an outgroup of the Australo-Papuan ariids - even if one were to view the species from the study region as an entity. Employing "extralimital ariids" as an outgroup is inappropriate because of this family's overall homogeneous composition throughout its wide range. However, representatives of twenty ariid taxa not occurring in the region are included in the phylogenetic analysis in a different (i.e., not outgroup) role, viz: to provide support for homologous character recognition; to indicate homoplastic character states between geographically distant groups of endemic terminal taxa; and to enhance formulation of classification schemes for Australo-Papuan ariids by providing information on sister species groupings.

Resolution of this matter to permit outgroup comparison in this study resulted in:

(A) Selection of a functional outgroup (fide Watrous and Wheeler, 1981; Arnold, 1981) on several levels, following the examples of Lundberg (1982), Weitzman and Fink (1985), Arratia (1987), Schaefer (1987), Starnes (1988) and Vari (1989), viz: a generalised outgroup of siluroids, ostariophysans and plesiomorphic teleosts (e.g. Fink and Fink, 1981) under the assumption that the state of an homologous character most widespread among them (but not including all or part of the ingroup) is plesiomorphic. This comparison is not made at the level of terminal taxa in the classification hierarchy (Maddison et al., 1984). Recourse to this "wider net" of taxa was particularly helpful when only equivocal polarity assessment was reached from comparison with presumably more closely related taxa.

(B) Assessment of the character state in eight *possibly closely related families* (*fide* early classifications; Chapter 1), *viz*: the Bagridae, Pimelodidae, Doradidae, Synodontidae, Siluridae, Pangasidae, Ictaluridae and Schilbeidae. Time restraints meant that I examined few representatives of each family - which in itself could have influenced my decisions. For example, only 13 taxa were directly compared in the Pimelodidae and Bagridae, the largest currently-recognised catfish families. Furthermore, studies by Howes (1983a; 1985), Nelson (1984) and Lundberg *et al*. (1988) questioned the holistic nature of nominal catfish families.

(C) Comparison with the two recognised sister groups to the Siluroidea (Grande, 1987): the Diplomystidae and the extinct +Hypsidoridae.

Despite examination of these specimens and comprehensive information in recent literature, I recognise my total outgroup is incomplete. It could well be that siluroids more closely related to the Ariidae are among those catfish families still awaiting investigation.

(D) Polarity assessment was sometimes facilitated by the "predominant-states" method (Kluge and Farris, 1969; Arnold, 1981; Maddison *et al*., 1984).

3.1.2.1

Transformation series correlation or *Character trends* is to some extent dependent on polarity assignment. Many criteria exist for hypothesising the direction of such trends (Meacham, 1984) and those one is sure of facilitate interpretation of direction in other character trends. Howes (1983a) and Arratia (1987) attempted an apo-plesiomorphic *analysis* of some catfish families by comparison with known character states of some groups and supposed *trends* within the siluroids.

3.1.2.2

The historically-recognised parallel between ontogeny and phylogeny suggests that ontogenetic transformation will provide insight into phylogenetic history (Fink, 1982). The ontogeny criterion is based on von Baer's concept. Furthermore, the ontogenetically later stage in a transforming lineage is more apomorphic relative to its homologue in a nontransforming group (Vari, 1983). Whilst some advocate the importance of ontogeny as a "theory-neutral" method of polarising character states (e.g. Nelson and Platnick, 1981; Fink, 1982; Nelson, 1985) others consider that it requires certain assumptions which can only be tested if character polarity and phylogeny are already known (e.g. Lundberg, 1973; Maddison *et al.*, 1984; Kluge, 1985; Brooks and Wiley, 1985; Alberch, 1985; de Queiroz, 1985). Although acknowledging the value of ontogenetic information, Arnold (1981) believed it may often be unreliable because of heterochronic and homoplastic processes (see also Lauder, 1981; Wiley, 1981; and reconsider Nelson, 1978). Fink (1982) allayed such concerns by pointing out that reference to the same set of characters would enable appropriate polarity recognition, and that ontogenetic analysis may occasionally facilitate detection of homoplasy.

Use of ontogenetic transformation series in the ariids was restricted because few very small specimens were available. (This reflects the parental care phenomenon and the male's habit of disgorging young from his mouth upon capture.) Only four mouth juveniles (3 species, min. SL 24mm) were obtained. This shortfall was partly obviated by comparing specimens of different sizes in each taxon and by evaluation of Srinivasachar's (1958) work. I am therfore confident that character state polarities arrived at on these specimens are correct as far as available information has allowed.

Ontogenetic precedence was the sole polarity criterion when morphological homologues were absent in outgroups (e.g. subvertebral cone development; palatal dentition; and consider ventral fin pad development in mature females).

The problem of distinguishing ancestral and derived character states in phylogenetic reconstruction of the ariids can be overcome by applying the methods of Lundberg (1972) and Farris (1970). These authors devised ways of performing analyses whereby states are not explicitly polarised. Their overall method is primarily useful when some of the character states in available outgroups are unknown or when polarity is equivocal (see also Farris, 1983). Meacham (1984), Maddison et al. (1984) and Colless (1985a) recommended this method of rooting "Wagner" trees as the safest and best method for phylogenetic reconstruction. It obviates misinterpretation of character states in outgroups, a problem which can produce a phylogeny not reflecting the actual genealogical history of the group under study (see above).

3.1.3 Parsimony

Through inadequacies in polarity assignment of character states, outgroup information, incongruence and homoplasies, two or more hypotheses of relationship derived from the same data may compete. The most feasible interpretation may be achieved however, by applying the powerful, general criterion of parsimony - the principle of simplicity. This criterion presupposes that evolution is simple. It is to be preferred over its alternatives (e.g. of character weighting based on information content; phenetic character distribution)(Wiley, 1975; 1981; Farris, 1982; 1982a) and can yield a decision even when seemingly distant outgroups are employed. Taken a step further, global parsimony finds the phylogeny requiring the fewest hypotheses of convergence and reversal within the ingroup and among outgroups (Maddison et al., 1984) and by this process, homoplastic characters are indicated.

The influence of parsimony in arriving at an acceptable phylogenetic reconstruction is debated by systematists, among them Popper (1968, cited in Sober, 1985), Beatty and Fink (1979), Sober (~~1983;~~ 1985) and Felsenstein and Sober (1986). Felsenstein (1978; 1982) argued that parsimony methods in phylogenetic analyses are justified only when rates of evolution are assumed to be small or equal among lineages; and Sober (1985) attempted to provide a likelihood justification of parsimony independent of homoplasies.

Despite Panchen's (1982) criticisms, I have leant heavily on the concept of parsimony in this study, seeing it as a key to providing meaningful interpretation of ariid cladograms. Panchen discounted the parsimony assumptions on correlated characters, that homologous characters predominate over homoplastic characters, and that the number of synapomorphies and homoplasies in a phylogenetic reconstruction reflects the numbers actually present yet undetected, in the study group.

Because homoplasies frequently defy attempts to recognise beforehand (see above; also Farris, 1982; Watrous and Wheeler, 1981) some systematists attempt to devise methods of detecting them prior to undertaking a phylogenetic analysis - for example, to streamline the process.

Such a method is character weighting. This assumes that in parsimony, independent characters should be weighted based on whether they are evolutionarily labile or conservative (Sober, stated in Weitzman and Fink, 1985). Arnold (1981), Meacham (1984) and Neff (1986) appraised the arguments (of Hecht and Edwards, 1976) on a priori and *a posteriori* weighting. Recognising that characters are themselves hypotheses, Neff suggested one can evaluate the degree to which each character has been tested and corroborated in character analysis. Thus, those which are more internally consistent, extensive and complete would be weighted more heavily than would labile and correlated characters.

Despite the *concept* of weighting being overtly rejected by many systematists, it *is* performed - by omitting from analysis characters which show great intraspecific variability, are affected by ecological shifts, are difficult to score, are present in distantly-related taxa and which appear to be highly labile in both outgroup and ingroup (Arnold, 1981). I am doing it in this study, as has Markle (1989). Nevertheless, I state (Chapter 4) the reasons why the "improved" data set produces a "better" phylogeny (Arnold, 1981) and why I do not incorporate the characters in the analysis.

As outlined above, there are many problems involved in attempting to hypothesise the phylogeny of the Australo-Papuan ariids. Nevertheless, pending a more comprehensive understanding of siluroid interrelationships, I consider it is a worthwhile undertaking. I agree with Hull (1979) that it is better to clearly and unambiguously represent some aspects of a phylogeny rather than none at all. The level of correspondence between biological reality and my assumptions will be demonstrated in the final results.

3.2 MATERIALS AND METHODS

Lists of material examined are in Chapter 5.3, Chapter 6 (Systematics) and Appendix A (Extralimital ariids).

Section 4.5 summarises the characters described in this study. The first 57 were used for phylogenetic analysis, although some of them are correlated (e.g. Characters 16, 17, 33 and 43), or relevant to an assessment of the whole family (e.g. Characters 1-10, 30, 37, 42, 44, 45 and 56), or are probably autapomorphic (Characters 40, 41).

The nomenclatural convention I adopted in these three chapters (3, 4 and 5) is a) specific epithets only for all Australo-Papuan ariids and other ariid OTU's which are not type species of nominal genera; and b) generic names for type species of genera (and see Chapter 1.8).

The Character number is used consistently throughout the text. A "+" sign used before a name indicates that it is a fossil (extinct) group.

3.3 CHARACTERS USED IN PHYLOGENETIC RECONSTRUCTION

In this and Chapter 4, characters which exhibit morphological variation among Australo-Papuan ariids are described and evaluated. This is the primary aim, as I consider that a clear understanding of ariid morphology is a firm and valuable prerequisite to the phylogenetic analysis.

1. Oral incubation - low fecundity

The habit of orally incubating eggs and young is unique within the Siluroidei. Oral incubation is well described for many genera (Rimmer and Merrick, 1983; Rimmer, 1985) and the presence of few, large-sized ova in mature females clearly indicates the phenomenon of parental care (Oppenheimer, 1970). Parental care practised in some other catfish families (e.g. Loricariidae, Aspredinidae, Ictaluridae) only involve protection (e.g. carrying the eggs on the body) and external incubation (Breder, 1935).

Mature females of some Australo-Papuan species were not available in this study. However, I am confident that they are mouth brooders after comparing the number and size of immature ova, season of capture, gonad form and ventral fin shape, with mature females of known mouth brooders.

2. Mesocoracoid

The mesocoracoid is absent from the pectoral girdle of the ariids, bunocephalids and doradids (Regan, 1911a; Tilak, 1965; Greenwood *et al.*, 1966). In the bagrid *Rita*, this bone is represented by a short hook-like process (pers. obs.; Bailey and Stewart, 1984). Loss of the mesocoracoid is a derived feature as it is present in all other siluroids, including the +Hypsidoridae and Diplomystidae.

3. Epioccipital extension

In the Ariidae, the epioccipital is produced posteriorly into a long process which articulates more or less with the dorsal aspect of the superficial laminar bone of the anterior fused vertebrae. In *Galeichthys*, the bone is only slightly produced.

The only other siluroids sharing this derived state are the Auchenipteridae and the doradid genus *Pterodoras* (Regan, 1911a; Gosline, 1975; C. Ferraris, pers. comm.), although the form of the bone posteriorly is not homologous with that in the ariids (see also, Character 23).

4. Aortic tunnel

In the Ariidae, the superficial bone of the complex and subsequent vertebrae spreads over the aortic canal, so forming a tunnel. In *Ancharius*, the aortic canal remains open; in *Galeichthys* it is only partially covered. In my few small ariid specimens (50mm SL; 3 species) the canal is open.

Concealment of the canal in adults - often by a thick sheet of bone - appears to be derived within the catfishes. Only in *Pimelodus* (outgroup material; C. Ferraris, pers. comm.) and 11 other pimelodid genera (Howes, 1983) is the canal largely concealed.

5. Supraoccipital - nuchal plate articulation

The primitive condition in catfishes is presence of one or more supraneurals between the nuchal plate and the supraoccipital (Arratia, 1987; Grande, 1987). The supraneural is prominent in bagrids, many pimelodids (J. Lundberg, pers. comm.), doradids and *Synodontis* (pers. obs.).

In all ariids except *Galeichthys*, the supraneural is not exposed in the dorsal surface and the supraoccipital rigidly articulates with the nuchal plate (and see Character 72). Only *Pimelodus* in my outgroup material shares this derived condition.

6. Lateral ethmoid - frontal articulation

In the vast majority of catfishes the lateral ethmoid articulates with the frontal by one facet. The Ariidae and Pangasidae exhibit a derived condition within the Siluroidei in which there are two facets: articulations of two processes from each bone. A posterior arm of the lateral ethmoid articulates with a forward extension of the frontal.

The sturdiness and length of the lateral arm varies within the family, from thin and long to very stout and short.

There is some intrafamilial variation however: *Ketengus* possesses only one frontal - lateral ethmoid connection; and in *Bagre* and *Ailurichthys* a long process from the mesethmoid makes a third posterior connection with the frontal. Tilak's (1965) alusion to *A. sagor* having only one facet is an error engendered possibly by the broad spread of the frontal over the lateral ethmoid in large individuals (see Character 48).

7. Otolith size and auditory bulla

The auditory bulla and lapillus otolith are exceptionally large in ariids. The bulla is formed by swelling of part of the prootic, pterotic and exoccipital. Characiforms also have a pronounced bulla (Fink and Fink, 1981).

All other catfishes have a much reduced otolith and bulla when compared with the ariids (Chardon, 1968; Regan, 1911a; other authors; pers. obs.). The ariid(?) *Ancharius* has a reduced otolith and shallow bulla.

8. Elastic Spring Apparatus (ESA)

The ariids possess a special set of muscles which form an Elastic Spring Apparatus (or Mechanism) which functions to produce a gas resonance (see also Character 9). Tavolga (1962) presented an excellent description and functional analysis of the ariid ESA; Howes (1983) and Alexander (1965) suggested possible homology and phylogenetic implications.

An ESA is found in several catfish families (Regan, 1911a): Doradidae (then including the Ageneiosidae and Auchenipteridae), Mochokidae, Malapteruridae and Pangasidae, as well as the Ariidae. Royero (1988) confirmed that the ESA is structurally homologous in all of these families except the Pangasidae and Malapteruridae.

9. The Müllerian Ramus

The Müllerian Ramus is the anterior limb of the 4th vertebral parapophysis (or transverse process). In the Ariidae, it is free from the supracleithrum and curves ventrad to contact the tunica externa of the swimbladder. Muscles from the anterolateral arm of the Müllerian Ramus attach to the neurocranium and anterior vertebrae to form the Elastic Spring Apparatus (ESA) (see above).

A relatively primitive, smoothly curved configuration of the transverse process lamina is present in the Ariidae, the Diplomystidae, Ictaluridae, +Hypsidoridae (Grande, 1987), some bagrids and pimelodids (Lundberg and McDade, 1986). Variation in the form of the Müllerian Ramus - away from one moderately long and more-or-less curved ventrad - is exhibited within most of these families. In other siluroids, the Ramus is often much expanded and disclike.

The Ramus in the ariids appears to be comparatively long in species 1, species 4, *froggatti*, *carinatus*, *crassilabris* and *dayi*. It is long and angular in species 5 (fig. 36). In the freshwater Madagascan taxon *Ancharius*, the Müllerian Ramus is enlarged to form a rounded disc turned at right angles to the swimbladder (fig. 45) - a shape not dissimilar to that in *Synodontis* (Mochokidae).

I have not detected any connection between the length of the Ramus and the form of the swimbladder in the ariids, although in species

5 this organ is extremely flattened. Both swimbladder form and shape of Ramus tip are autapomorphies of this taxon.

10. *Subvertebral cone*

The laminar bone over the first and complex vertebrae is well elevated anteromedially in *Schilbe* and the plotosid *Neosilurus* and low in most other catfishes. Only the Ariidae have a sheet of bone concealing the fusion of the basioccipital and the anterior vertebral complex. The first vertebra is completely (or almost) concealed and the laminar sheet forms a "subvertebral cone" at the fusion site, a condition I consider derived.

11. *Subvertebral cone shape*

Not only is there a strong suture uniting the basioccipital and the laminar bone, but the subvertebral cone is variably projecting. The tip may be bifurcate and is often cartilage covered (fig. 16). In the genera *Galeichthys*, *Ancharius* and *Bagre* the subvertebral cone is low, with a deep median excavation (aortic tunnel incomplete) in the first two taxa. The subvertebral cone attains its most extreme development in "*Cathorops*", *Cephalocassis* and *Hemipimelodus* (extralimital taxa), *armiger*, *froggatti*, *carinatus*, *dayi* and *novaeguineae*. I consider this high, stout cone as the apomorphic condition.

In taxa having a low cone, the basal *aortic foramen* opens downward. With increasing length and expansion of the cone, the foramen comes first to open obliquely, then to open forward from a position in the angle at the anterior base of the cone.

12. 4th neural spine - epioccipital flange

The transverse process of the complex centrum is broadly expanded in a horizontal plane and together with the fused neural arches, forms a roof over the neural canal. Tilak (1965) placed considerable importance on the disposition and height of the ridges or laminae on the dorsal surface of the so-formed shield in ariids (termed the "pars sustentaculum"): the transverse flange of the 4th neural arch, the median ridge forward from the neural arch and the diagonal ridge associated with the epioccipital laminar extension. Higuchi (1982) also noted the specific differences in the form and elevation of the laminae and I have observed a variety of expressions in ariids from Australia, New Guinea and elsewhere. The flanges may function as a strut in support of the dorsal fin-skull articulation, and they fall into 4 general groups:

(1) The lateral and the forward ridges (or laminae) of the 4th neural spines are low and concave, especially the former. However, in species 6, *crassilabris*, *dayi*, *carinatus* and *froggatti*, the lateral ridge is high, extending half-way up the neural spine (fig. 19B). Several other taxa have a moderately elevated lateral ridge (e.g. *augustus*, *thalassinus* and *spatula*). "*Cathorops*" (fig. 46) has an exceptionally high transverse lamina.

(2) The forward ridge from the 4th neural spine to the 3rd is moderately elevated in some Australo-Papuan ariids, e.g. species 1, *augustus*, *thalassinus*, *bilineatus*. *Galeichthys*, *Ancharius*, *platypogon* and *Bagre* are some extralimital ariids in which the forward lamina is very high.

(3) The posteromedian flange of the epioccipital attaches to the dorsal surface of the complex centrum or its lamina in most ariids. In

some species however, it abuts the lateral ridge or lamina of the 4th neural spine and may be very well-elevated, e.g. in species 7, dayi, crassilabris, armiger, froggatti, carinatus, species 6 from Australo-Papuan taxa. Extralimital ariids having this condition are Bagre, "Cathorops" and rugispinis (figs 38,46).

(4) Several ariids have a median lamina extending from the ventral surface of the supraoccipital. This is present in froggatti, carinatus, Galeichthys and Ancharius.

The plesiomorphic condition for these four expressions appears to be low ridges or laminae. Diplomystids, +Hypsidoris and many other catfishes share this feature. Howes (1985) remarked that the space between the cranium and the 4th neural spine has almost disappeared in advanced siluroids. Lundberg and McDade (1986) and Ferraris (1988) reported that the elevated lamina is also found in some pimelodids and bagrids. Elevated, thin laminae as in conditions 2 and 4 above only, are present in the bagrids Bagrus, Mystus, Bagrichthys and Chrysichthys (all very high), Schilbe, Pylodictus and Ictalurus punctatus (Ictaluridae) and Neosilurus (all high). The laminae are low in Synodontis and Pimelodus. In doradids, only conditions 1 and 2 seem to be present - not the epioccipital, condition 3. Rita (Bagridae) has a very high transverse ridge.

Lundberg (1982) implied that the vertical lamina is a phenomenon associated with large species size (i.e. for strength), but this supposed correlation is not supported in the Ariidae where it occurs in taxa attaining quite a range of maximum sizes (e.g. dayi to thalassinus); neither is it evident in some taxa with thicker and heavier bones (e.g. Batrachocephalus).

The various developments of laminae in the nuchal region I consider here as one character, and the trend towards increasing height of (any) ridge or flange is apomorphic.

13. First pharyngobranchial

There are four separate, ossified pharyngobranchials of similar length in the Diplomystidae (Arratia, 1987) and *Rita* (pers. obs.) which is the supposed primitive condition. Many catfish families have three pharyngobranchials: e.g. some bagrids (Skelton, 1981; Tilak, 1965a), Schilbeidae (Tilak, 1964); and others have two: e.g. Amblycipitidae (Tilak, 1967b), Sisoridae (Tilak, 1963b), some plotosids (Tilak, 1963), Trichomycteridae (Arratia and Menu-Marque, 1984), loricariids (Schaefer, 1987) and Chacidae (Brown and Ferraris, 1988). In my outgroup material, *Rita* and *Neosilurus* have a long, basally situated first pharyngobranchial and a cartilaginous 2nd pharyngobranchial. The pimelodids have a similar 2nd pharyngobranchial, but the first pharyngobranchial in *Pimelodus* is long and situated midway along the epibranchial, in *Rhamdia* it is short and at the epibranchial angle. The doradids appear to lack the first pharyngobranchial and often the second (C. Ferraris, pers. comm).

Most ariids have three pharyngobranchials: the first elongate (ovoid in one group of species), lying parallel and dorsal to the first epibranchial; third rectangular to "v"-shaped, lying between the 2nd and 3rd epibranchials; fourth almost square, between the 3rd and 4th epibranchials and forming a base for the tooth plate (fig. 32). I could not distinguish an autonomous 2nd pharyngobranchial between or before the contiguous cartilaginous ends of the first two epibranchials in any Australo-Papuan ariids (refer 2.3.1.7), but it may be present in *Ailurichthys*.

The *position* of the first pharyngobranchial varies in the Australo-Papuan ariids (and see above). In two ariid taxa it lies close to the distal end of the epibranchial, representing a supposed plesiomorphic state shared with extralimital taxa *Bagre* and "*Cathorops*". A position exhibited by many taxa, is more proximal, adjacent to the epibranchial angle. The most derived state is displayed by *froggatti* and *carinatus* in which the element is either missing or united with the epibranchial at its expanded, thin angle (fig. 33).

A trend to lose this element in the Ariidae is evident. Similar expressions of this character appear to have arisen independently within the siluroids.

14. Posterior cleithral process

The posterior cleithral process (or "humeral process") is present and well-developed in diplomystids, ictalurids (Lundberg, 1982), bagrids, +*Hypsidoris* and other "diverse neotropical catfishes" (Stewart, 1986a:669). In +*Hypsidoris* it is long and ornamented with bony tuberculations (Grande, 1987); in *Rita* and *Bagrichthys* the process is very large (pers. obs., Bhimachar, 1933); in +*Astephus* (Ictaluridae) it is long and sculptured (Grande and Lundberg, 1988); in the doradids and mochokids I examined it is long and smooth or tuberculated. The pimelodids, *Schilbe*, plotosids, silurids and *Pangasius* have a medium to short process. In *Brochis* and *Dianema* (Callichthyidae) it is very extensive.

Tilak (1963c) compared the size and shape of the posterior cleithral process in representatives of eight families.

Lundberg (1970~~; 1982)~~, cited in Lundberg, 1982) defined four basic conditions of size and ornamentation of the cleithral process among catfishes: long and unornamented; long and ornamented; short and unornamented; absent. The long and unornamented form is probably the most plesiomorphic (Lundberg, 1982), being common among catfishes (see above), including fossils and diplomystids. Lundberg believed that the other two conditions are derived in divergent ways (and see Bailey and Stewart, 1984).

Most Australo-Papuan ariids have a moderately large, often rugose posterior cleithral process, usually anteroventrally thickened. The extremes are displayed by froggatti, carinatus, conorhynchus and crassilabris where it is very long and strong, and armiger, dayi, nox and the extralimital "Cathorops" and Hemipimelodus (e.g.) where it is very short.

15. Eye covering

Arratia (1987) cited examples of siluroids having either covered or naked eyes, and observed that the traits can vary within the one family. The diplomystids have a naked eye as do most ariids and most bagrids. Representatives of several pimelodid genera (e.g. Microglanis, Pseudopimelodus, Heptapterus, Horiomyzon) lack a free eye margin (Gosline, 1941; Stewart, 1986; Mees, 1974); as do the silurid and doradid taxa in my outgroup material.

Bailey and Stewart (1984) concluded that the loss of a free orbital rim in the African bagrid Bathybagrus was apomorphic; and a subcutaneous eye has been derived independently in some gymnotiform groups (Lundberg and Mago-Leccia, 1986).

The primitive ostariophysan condition is one of a free orbital rim (Lundberg, 1982; Lundberg and Mago-Leccia, 1986). The covered eye of several unrelated lineages probably has developed in response to habitat preference.

The nominal ariid genus *Hemipimelodus* is diagnosed as having a subcutaneous eye, a condition which also exists in two Australo-Papuan ariids - *novaeguineae* and species 5. The eye in *Cephalocassis* is partly subcutaneous.

16. *Extent of gill opening*

Several character states are exhibited by the Ariidae in the freedom of the branchiostegal membrane and the extent of the gill opening. In some taxa (e.g. species 6, *danielsi*, *midgleyi* and species 5) the gill openings extend well forward on the isthmus; and the branchiostegal membrane margins are broad and free, meeting medially in an acute angle, often overlapping. In other taxa (e.g. *berneyi*, *proximus*) the openings are moderately wide and the broad, free membranes meet on the isthmus at approximately a right angle; or they may form an obtuse angle or concave fold. The last state is where the gill openings extend only to the sides of the isthmus or slightly further; with the narrow-margined membranes joining broadly across the isthmus; or the membranes folding into the isthmus (e.g. in *froggatti*) (figs. 84B, 242B).

Gosline (1973) expanded on Woskoboinikoff's (1932, cited in Gosline, 1973) explanation of the opercular "sleeve"'s function during inspiration and expiration. During feeding employing suction in large-mouthed catfishes, the throat is extended downward and forward and a broad, extensive branchiostegal membrane is needed to overlap the isthmus. On the other hand, in catfishes with smaller mouths and more compressed head, the throat drops less, the membrane is shorter and the opercles contribute more in the exhalation of water. These conditions occur in the Ariidae, where the size of the gill openings is well-correlated with head height and mouth width (figs 47,48; Table 3).

The usual, plesiomorphic condition among catfishes is of an unrestricted gill opening. This is in contrast to the condition in the ostariophysans Cypriniformes and Characiformes which usually have a compressed head and more restricted gill opening (Gosline, 1973). Lundberg (1982) observed that branchiostegal membranes fusing with each other across the throat is an advanced feature, but one which has arisen independently in several catfish lineages (e.g. doradids, auchenipterids, callichthyids - Alexander, 1965; Mees, 1974; pers. obs.).

17. Buccopharyngeal pads or flaps

Nedystoma dayi is distinguished in systematic literature partly by the large pads or flaps hanging from the rear of the buccal cavity and attached to the posterodorsal aspect of the anterior gill arches (figs 49; also 243D). Roberts (1978) observed that such structures function very effectively in sorting fine food items. Several Amazonian fishes possess similar structures for straining minute organisms from mid-water (Roberts, 1972) (see also Characters 84 and 91).

I assessed the pads and/or flap development in other Australo-Papuan ariids over a scale of 1 to 3. Whereas a few taxa have moderately developed structures, species 4 has flaps substantially identical to those in *dayi*. Furthermore, *nox* (less so *solidus*) has convoluted flaps and extensions on the upper gill arches which almost certainly function in a similar manner. Of these taxa, species 4 is the only coastal inhabitant, probably feeding in the stronger currents associated with river mouths.

In some taxa (e.g. *leptaspis*, *proximus* and *solidus*) pads are moderately developed at juvenile stadia and much reduced in adults. This structural change appears to be correlated with a change in dietary preference from finer to larger food items. Retention of well-developed pads in ariid taxa at adult stadia appears to be derived.

Lundberg *et al*. (1987:81) drew attention to the "additional advanced features" of the feeding apparatus in the planktivorous gymnotid *Rhabdolichops zareti* which appear to be homologous with the structures present in *dayi*, *viz*: fleshy, suspended pads and valves on the gill arches and buccopharyngeal roof. *R. zareti* occupies swiftly flowing waters, has numerous gill rakers and a quadrangular mouth gape (and see Characters 84 and 88).

The planktophagous catfish *Hypophthalmus edentatus* has a strong, membranous flap on the hind edge of some arches (Roberts, 1972) and the pimelodid *Rhamdia* has well-developed flaps. Vari (1989) drew attention to the numerous, probably functionally homologous, lobulate protruberances extending from the mouth in some curimatids (Characiformes). He surmised that these structures can promote an increase in the amount of buccal mucus, an adaptation possibly correlated with the species' microphagous and detritivorous diet.

18. Mesethmoid shape

The plesiomorphic shape of the siluroid mesethmoid is elongate and 'T'-shaped, usually with a median notch (Lenous, 1967; Tilak, 1965; Howes, 1983; 1983a; Arratia, 1987; others) or excavation (e.g. in *Schilbe*). This form is present throughout the Siluroidei: Diplomystidae to Trichomycteridae (Arratia, 1987; Schaefer, 1987). The lateral arms, or cornua, can be exceedingly produced (e.g. *Trogloglanis* - Lundberg, 1982; Chacidae - Brown and Ferraris, 1988).

Howes (1983) described several derived states of the siluroid mesethmoid: poorly ossified ("papyraceous", as in

Hypophthalmus); expanded; curved ventrally; greatly depressed and expanded laterally; flattened with divergent cornua (and presumably no median notch); cavitous with medially grooved surface.

Most of these states are exhibited in outgroup material and some in the Australo-Papuan ariids. Although some ontogenetic change is apparent, the mesethmoid form is consistent within each ariid taxon. There is a trend in the group towards loss of the median notch and a general broadening of the mesethmoid (fig. 4). Species 1, novaeguineae and species 5 have an expanded, convex mesethmoid without a median notch; spatula, danielsi, armiger, nella and polystaphylodon have a broad mesethmoid with very shallow notch. In thalassinus (and to a lesser extent, grandicassis from America), the termination is convex and fluted or ridged while in macrorhynchus the short cornua are partly enveloped in a median, convex prominence turned ventrad. I interpret these conditions as autapomorphies. The ventral mesethmoid surface in spatula (and species 5?) becomes concave with ontogeny.

Ariids lack the mesial processes on the cornua present in ictalurids and "various catfishes in other families" (Lundberg, ~~1970;~~ 1982:31) which is a derived condition among catfishes.

19. Nasal bone shape

The nasals are simple, slender tubes in +Hypsidoris, the Diplomystidae (Arratia, 1987) and many other catfishes (Lundberg, 1982; pers. obs.).

Simple tubes, often broader anteriorly where they tend to bifurcate, and lying longitudinally on the cranium, appear to represent the plesiomorphic condition in the ariids. In the Australo-Papuan ariids, there is a trend for the nasals to curve parallel to the concave mesethmoid neck and come to lie over or cradle into its margin (most apparent in those taxa where that bone is broader). The expanded, irregular nasal form in *novaeguineae*, *Batrachocephalus* and, to a lesser extent species 5, is further derived. [Schaefer (1987) noted a stout, broad "nasal" in the loricariid *Hypostomus*.]

20. First infraorbital (lachrimal) shape

A simple lachrimal is present in diplomystids (Arratia, 1987), *Trichomycterus* (Arratia and Menu-Marque, 1984) and *Malapterurus* (Howes, 1985), suggesting that this form has been independently derived in several lineages. Apomorphies are exhibited in other groups; for example *Rhamdia* has an elongate lachrimal; in doradids it is considerably enlarged and irregularly-shaped; and in *Neosilurus* the lachrimal is broadly crescentic or moon-shaped.

In Australo-Papuan ariids, the anterior-most bone of the infraorbital series is generally rhombic or "axe"-shaped with anterior and posterior processes well-produced. This is the characteristic and presumably plesiomorphic form in other ariids and many siluroids (Higuchi, 1982; also Schaefer, 1987; Howes, 1983). This shape varies in some ariids, however. In six Australo-Papuan taxa the lachrimal is more ornately-shaped: narrow with extremely-produced angles. An almost rectangular lachrimal is present in *novaeguineae* and the extralimital ariids *Bagre* and *Batrachocephalus*.

21. Shape of the vomer

A 'T'- or arrow-shaped vomer is present in many siluroids, including +*Hypsidoris* (Grande, 1987; Grande and Lundberg, 1988; Lundberg, 1982; pers. obs.). A rhombic, enlarged vomer is a unique derived feature of the Diplomystidae (Arratia, 1987). Vomer size varies and in some groups (e.g. *Hypophthalmus* - Howes, 1983; loricariids - Schaefer, 1987) it may be needle-like with or without greatly reduced lateral arms.

In the ariids, the vomer is usually 'T'-shaped. The vomer arms are slightly abbreviated in some taxa and/or the medial "head" of the bone is dentate; but the intraspecific variability I have observed suggests that these forms do not represent independent character states. The general "T" condition is lacking in *nella*, *polystaphylodon* and *argyropleuron* however, in which the head is enlarged and the arms are very short. I consider this the apomorphic state of this character.

22. Mandibulary pores

The openings of the mandibulary sensory canal lie along the anteroventral aspect of the mandible. Lundberg (1982) believed that there are six openings primitively, and higher counts are derived. The foramina can be clearly seen on +*Hypsidoris* and +*Astephus*; and Arratia (1987) illustrated those in *Diplomystes*. Pores appear to be absent from the loricariids (Schaefer, 1987). In *Prietella* (Lundberg, 1982), plotosids and some bagrids the pores are large (pers. obs.), not so in *Synodontis*, pimelodids, *Parasilurus* and *Schilbe*.

The Australo-Papuan ariids display variability in the number (4 to 7) and size of the foramina. Because I experienced difficulty in counting the pores nearest the symphysis in some osteological preparations due to bone convolutions, I cannot arrive at a real pore number for each Australo-Papuan ariid taxon.

However, the *size* of the foramina may be used in phylogenetic reconstruction. The ariids *armiger*, species 1, *augustus*, species 5 and novaeguineae have noticeably large openings at all stadia, compared to danielsi, spatula, carinatus and others wherein the openings are quite small. The extralimital ariids Bagre, "Cathorops" and Hemipimelodus have large foramina and Batrachocephalus has very small (or no?) openings. The majority of ariids have moderate-sized foramina which I suggest is the relative size in +Hypsidoris and many other ariids. Nevertheless, I am unable to suggest the direction of change for this character.

23. Epioccipital

The epioccipital lamella extends well posterior to the skull in most ariids (not Galeichthys). In many ariid taxa, the proximal part of the bone - which forms a major portion of the posterior wall of the neurocranium - closely underlies the extrascapular and the posterolateral arm of the supracleithrum. In four (possibly 5 or 6) Australo-Papuan taxa and extralimital ariids sona, Sciadeichthys, Ailurichthys and "Cathorops", the epioccipital invades the skull roof, that portion matching in ornamentation the other dermal bones. Lundberg (1975a) reported a similar situation for the doradids and auchenipterids, but the condition in ariids is of an additional dermal skull bone (contra Character 24, doradids, auchenipterids).

No other catfishes (and ostariophysans) have the epioccipital invading the skull roof, besides retaining the extrascapular.

24. Extrascapular

The status of the plate-like bone between the supraoccipital and the supracleithrum has often been debated (see Lundberg, 1975a; Grande, 1987 for scope; also Howes, 1985). It is usually present in the diplomystids (Arratia, 1987) and at least nine other catfish families including Mochokidae, Bagridae, Ariidae and Doradidae. There is a pronounced trend towards its division (e.g. in some ictalurids - Lundberg, 1975a; 1982) or independent loss (Arratia, 1987) a number of times within the siluroids. Lundberg further suggested that the lost extrascapular is the source of dermal bone material on the underlying epioccipital in taxa where it is exposed in the skull.

In most ariids, the extrascapular is well-developed. It lies over the epioccipital, is closely sutured to the neighbouring dermal skull bones yet can be clearly identified with careful skull examination. In three Australo-Papuan taxa however, the extrascapular appears to have amalgamated with the anterior portion of the epioccipital which is thus exposed in the skull roof (cf. Character 23).

These three ariids have highly ossified skulls, especially posteriorly. It is possible that the amalgamation of the two bones acts to reduce weaker sites on the skull (as, for e.g., sutures) in response to achieving strength in that area.

25. Temporal fossa

Many ariids possess a large fossa at the intersection of the supracleithrum, pterotic and extrascapular. Such a fossa is not common in catfishes, at least in adults where, if it is present, it is largely overlain by the extrascapular. Diplomystids have a reduced fossa; pangasids, schilbeids and some sisorids also have a fossa (Tilak, [1963b; 1964]; pers. obs.; Bhimachar [1933]). I consider its presence in adult ariids as plesiomorphic because: (a) it is present in the characoids (although variably present in cyprinoids) (Roberts, 1973); (b) the fossa is much reduced or even absent in some ariids, especially at adult stadia (e.g. dayi, nox, novaeguineae and the extralimital Hemipimelodus and "Cathorops"); and (c) it indicates the space between the neurocranium and pectoral girdle in taxa where the supracleithrum is only ligamentously attached or where both arms of the supracleithrum are not strongly sutured to the skull (e.g. in Schilbe and some ariids including taylori). In contrast, Howes (1985) considered a loose connection of the supracleithrum and neurocranium to be apomorphic.

26. Metapterygoid position

The metapterygoid sutures ventrally to the quadrate and posteriorly to the hyomandibular. In primitive characins the ectopterygoid and mesopterygoid are well-developed and large components of the suspensorium (Alexander, 1965; Fink and Fink, 1981). With their substantial reduction in catfishes, the metapterygoid has moved forward to occupy the vacated space and in turn, the hyomandibular has extended anteriorly to fill the space left by the forward movement of the metapterygoid. This condition exists in many catfish families (e.g. diplomystids, ictalurids, many bagrids, pimelodids, +Hypsidoris, schilbeids, Clarias, some sisorids, doradids - various references) and most ariids.

In these catfishes, the posterior margin of the metapterygoid lies above or before (well before in pimelodids and Chrysichthys) the middle of the quadrate. Some ariids, including the extralimital Potamarius and Osteogeneiosus however, have a somewhat enlarged metapterygoid where the hind border extends posteriorly to lie in line with the hind border of the quadrate - or even beyond it (fig 26B,D). This condition is shared (extremely) by Malapterurus (Howes, 1985). A general elongation of the suspensorium in the region between the articular condyle for the quadrate and the hyomandibular accompanies the posterior progression of the metapterygoid. I consider this condition derived, although it mirrors the gonorhynchiforms (Fink and Fink, 1981). The metapterygoid has again assumed a posterior position in the gymnotoids (*ibid*).

27. Metapterygoid - hyomandibular suture

The metapterygoid is united with the anterodorsal portion of the hyomandibular. The breadth of the suture varies in the Ariidae from very broad (fig. 26) to narrow. Such variation was also observed by Brown and Ferraris (1988) in the Chacidae. A broad suture extending the length of the hyomandibular-metapterygoid interface is present in +*Hypsidoris*, *Diplomystes* (Fink and Fink, 1981), +*Astephus* and other ictalurids (Lundberg, 1982) and several other catfish families (several references; pers. obs.). I consider a broad, sutural contact the plesiomorphic condition in catfishes.

28. Skull ornamentation

Primitively, much of the dorsal surface of the catfish skull is covered with heavy exostosis - of tubercles, ridges, granules, grooves and rugae (~~Lundberg, 1970;~~ Grande, 1987; Stewart, 1986a). The families in which strong ornamentation of the skull is exhibited are the Ariidae, Bagridae, Pimelodidae, Doradidae, Auchenipteridae, Sisoridae, Clariidae and many Characiformes (Lundberg, 1975). I confirm this trend and, based on my outgroup material, add *Synodontis* (Mochokidae) and *Neolisurus* (Plotosidae). +*Hypsidoris* has a heavily sculptured head (Grande, 1987), as does the ictalurid +*Astephus* (Grande and Lundberg, 1988).

Ornamentation continued to the skull roof above the hyomandibular occurs because the cheek muscles (adductor mandibularis) are restricted to the cheek - as in most ostariophysans and lower teleosts (Grande and Lundberg, 1988). Extensive cranial attachment of jaw muscles (recognised in skeletal material by smooth bone surfaces) has probably evolved independently in several catfish lineages. In the ariids, *Galeichthys* may display this condition, although all Australo-Papuan ariids display the plesiomorphic condition.

Nevertheless, there is consistent variation in the relative smoothness of the cranial surface among the ariids, unrelated to cheek musculature. Some taxa (e.g. *mastersi*, *latirostris*, *argyropleuron* and *Sciadeichthys*) have very granular and rugose skull surfaces whilst others (e.g. *novaeguineae*, *dayi* and *Bagre*) have very smooth skulls. I recognise three states for this character in the Australo-Papuan ariids, despite some problem with accounting for ontogeny and intraspecific variation in my assessment. The considerable ornamental diversity present precludes unequivocal qualitative description (see also Character 68).

29. Shape and position of adipose fin

Alexander (1965) mentioned the compensatory values of large and small adipose and anal fins, the former seemingly useful in swim stability. Gosline (1971) suggested that the adipose fin is chiefly significant in juvenile stadia and discussed the use and advantages of different dorsal fin forms in locomotion.

Fink and Fink (1981) hypothesised that the adipose fin is lost independently in several ostariophysan lineages, e.g. some Auchenipteridae (Mees, 1974; Ferraris and Fernandez, 1987; Curran, 1989). Vari and Ortega (1986) described intraspecific variability for the presence or absence of the short-based adipose fin within some populations of *Helogenes* and noted similar events in other ostariophysans. Skelton (1984) found variation in adipose fin size and shape in some species of *Amphilius*.

The long anal-finned *Hypophthalmus* has a small adipose fin placed far posterior (Howes, 1983). Many characoids and non-ostariophysan adipose-fin possessing fishes have a small adipose fin. The usual form and position of the adipose fin in catfishes are of a moderately high and free fin smoothly rounded posteriorly, situated approximately over the middle of the anal fin.

The adipose fin of ariid catfishes varies in size and position. Some ariids, notably *carinatus*, *crassilabris*, *froggatti*, *spatula* and *conorhynchus*, have a long-based adipose, its base longer than that of the anal. They share this fin form with a number of "generalised" catfishes including the diplomystids, +*Hypsidoris* (Grande, 1987), bagrids, many pimelodids (Alexander, 1965; Stewart, 1986; 1986a; pers. obs.) and the ariid(?) *Ancharius*. I consider this condition plesiomorphic (see also Gosline, 1971). The derived condition - of a small-based adipose fin situated above the posterior half of the anal fin - is exhibited in the sea-inhabiting *thalassinus*, *proximus* and several freshwater taxa such as *nox* (fig. 50).

30. Barbel number

The number and situation of sensory barbels in catfishes is haphazard and opinions vary concerning their phylogenetic information. Fink and Fink (1981), Roberts (1973) and Lundberg and Baskin (1969) considered possession of a maxillary pair of barbels only, as primitive. This state is not singular to the primitive diplomystids however, occurring also in the phylogenetically more advanced loricarioid group. Howes (1985) believed that possession of nasal barbels may be plesiomorphic: present (e.g.) in Schilbeidae, *Malapterurus*, plotosids, some bagrids and *Anadoras* species.

I incline to Fink and Fink's view (1981) that barbels other than the maxillary barbels, have been independently derived within the Siluroidei.

Within the ariids, six is the plesiomorphic number: a pair of maxillary, mandibulary and mental. A barbel complement other than six is probably derived within the Ariidae. The S.E. Asian taxon *Batrachocephalus* has a pair of mandibulary barbels only and *Osteogeneiosus* has a pair of maxillary barbels only. *Bagre* and *Ailurichthys* lack mental barbels. The ariid(?) *Ancharias* has a pair of short and fine nasal barbels, a feature unknown in any (other) ariids. A barbel complement other than six is probably derived within the Ariidae. (See also Character 75.)

31. Barbel position

The issue of barbel homology within the Ostariophysi has been discussed by several recent authors (e.g. Roberts, 1973; Arratia, 1987; Fink and Fink, 1981). Alexander (1965) and Gosline (1975) interpreted the movement and function of the barbels in different ostariophysans.

The position of the mandibulary barbel bases is worthy of attention. In some taxa (e.g. *dayi*, *polystaphylodon*, *froggatti*) they lie close together, are approximately transversely aligned and near the mandibulary symphysis. Howes (1983) and Stewart (1986a) drew attention to several pimelodid taxa sharing this barbel position; also aspredinids

(Mees, 1987). In other ariids (e.g. species 5, spatula and danielsi) the condition of well-spaced, staggered barbel bases is displayed (figs 126B, 130B, 137B). In the majority of catfishes however, the barbel bases are moderately separated and staggered. Variations from this condition, as in the above taxa, appear to be derived (see also Curran [1989] for auchenipterids).

32. Lateral line at tail base

The form of the lateral line at the tail base in catfishes appears to be stable (see also Character 78). A lateral line curving slightly either dorsad or ventrad at the tail base is probably the plesiomorphic condition, as it is present in this form in diplomystids (Arratia, 1987) and many Australo-Papuan ariids. In a large subset of ariids from the study region, the lateral line turns sharply dorsad. Some ariids however (e.g. thalassinus, bilineatus, nella, polystaphylodon, argyropleuron and Hemipimelodus) possess a bifurcate lateral line at the tail base. This apomorphy also occurs in some other catfishes, e.g. pangasiids, schilbeids, some sisorids, pimelodids, auchenipterids, some doradoids, Hypophthalmus and Cranoglanis (Lundberg and Baskin, 1969; pers. obs.) as well as in the chanoid Gonorhynchus (Lundberg and Baskin, 1969).

Bleeker (1858) partly based his genus Hemipimelodus on the bifurcate nature of the lateral line.

33. Shape of the swimbladder

The relatively primitive catfish swimbladder is large and sack-like or "heart"-shaped, with smoothly rounded margins (Stewart, 1986a), covered with a silvery peritoneal tunic. This is the common and presumably plesiomorphic shape in ostariophysans (ref. Alexander, 1964).

Most catfishes have only the anterior chamber of the swimbladder. The plesiomorphic condition of two chambers connected by a ductus pneumaticus is retained in several siluroid groups however, such as *Malapterurus*, *Pangasius*, ictalurids and schilbeids; possibly some pimelodids (Howes, 1985; Roberts, 1973; Stewart, 1986a); and *Rita* (pers. obs.). *Sciadeichthys* is the only ariid taxon sharing this condition.

The rounded *Diplomystes* swimbladder is internally divided into two chambers by a thick transverse septum (Arratia, 1987), a condition shared by all Australo-Papuan ariids except species 5. In ariids, the posterior section is further divided by 2 to 4 irregular pairs of incomplete septae linked to a median longitudinal partition (figs 51-54). Alexander (1964; 1965) noted that the flattened shape of catfish swimbladders is maintained by the internal partitions, and Tavolga (1962) surmised that the ariids use the septae for channelling sound.

In some ariid taxa (e.g. *novaeguineae*, *nox*) the bladder is almost rounded; in most, it is heart-shaped or ovate and in species 1, *Ketengus* and *Batrachocephalus* it is almost triangular. The edges or sides of the swimbladder are usually smooth and entire. In *nella* and *polystaphylodon* the sides are deeply creased internally (fig. 53); in several Australo-Papuan taxa as well as the extralimital *Osteogeneiosus* and *truncatus*, the sides are scalloped externally and internally (fig. 54). This condition is also found in some pimelodids (Stewart and Pavlik, 1985; Stewart, 1986a). Species 5 has a long and oval, board-like swimbladder (fig. 55) internally divided by numerous septae.

As the Weberian Apparatus functions to transmit vibrations from the bladder to the inner ear, the form of the bladder must either (a) have some effect on the type of vibrations transmitted or

(b) provide efficient reception of sound vibrations from the preferred ~~water~~ habitat of different taxa (and see Tavolga, 1962; 1971). Correlation between bladder shape, vibrations and habitat could be revealed with further study.

Howes (1983) noted a trend for more derived siluroids to have reduced and encapsulated swimbladders (e.g. loricaroids, callichthyids, trichomycterids). This trend is directed towards a demersal existence (Alexander, 1965) wherein a greater variety of environments can be exploited (see Gee, 1976). However, compensation of the effect of low swimbladder volume can also be achieved by active swimming, a phenomenon observed in juvenile ariids, at least. The larger, high-volumed swimbladder hence appears to represent the plesiomorphic condition.

During immature growth stadia, most ariids inhabit the lower water column. Although actual fatty deposits are built up only cyclically in relation to spawning and brooding activity in adults, I suggest that the body tissue becomes increasingly buoyant from oil and fat deposition as growth proceeds. Support for this statement comes not from analysis, but from two observations: (1) the high oil content of large ariids caught and marketed in Java makes them unsuitable for air drying *per se* without prior heavy salting; (2) adult (i.e. larger) individuals of some ariids *do* inhabit the middle water column, e.g. *thalassinus*, *bilineatus* and *midgleyi*.

34. Pads on the ventral fins

A noticeable feature of female ariids is the gradual thickening of the sixth (and occasionally fifth) ventral ray with advancing sexual maturity. Rimmer (1985), working with *graeffei*, was able to demonstrate that the pads develop synchronously with ripening of ova and regress post spawning (see also Smith, 1945; Lee, 1937).

Day (1877:457) observed that the ventral rays are thickened "by a deposit of fat, whilst the innermost one has a large similar pad attached to its posterior edge". The fin pads (fig. 56) can be expanded into a "cup-like surface, the use of which may be to receive the eggs as they are extruded". Day's observations are supported by those of later authors (see Rimmer and Merrick, 1983: summary). Hardenberg (1935) believed that the male attaches to the female by thick hooks formed by the pad (in *Arius maculatus*) to fertilise the ova.

Whereas comparatively large and few ova are produced by all ariids, not all taxa develop pads. For example, *Sciadeichthys* and *Osteogeneiosus*, *crassilabris*, *carinatus*, *froggatti*, *dayi* and *novaeguineae* lack them. In "*Cathorops*", the innermost rays are doubly thickened. Presence/absence of pads is unrelated to the maximum attainable SL. For example, pads are present in *thalassinus* (SL to 1.3m) and *leptaspis* (SL to 55cm); and absent in *carinatus* (SL to 52cm) and *Sciadeichthys* (SL to 80cm).

Possession of a padded ventral fin in mature females is a unique ariid feature and I am bound to assign plesiomorphy to the absence of pads (*fide* outgroup, other siluroids). Nevertheless, *if* the function of the pad is to hold up the egg mass until all of it is extruded and/or fertilised (see above) the pad-less taxa could have developed some other method of supporting the ova (e.g. by expanding the paired fins). The ova produced by these taxa, as far as I have been able to determine, are no smaller nor lighter than those of other ariids. Nor are there differences in fecundity and maximum SL. Clearly, evidence of pad function is a prerequisite to a firm statement of polarity.

Regrettably, I cannot present a complete statement for Australo-Papuan ariids as mature female specimens of some taxa were not available.

35. Vomer dentition

A large, toothed vomer appears to be the primitive condition in catfishes (Bhimachar, 1933; Grande, 1987; Grande and Lundberg, 1988). Vomerine teeth are borne on firmly attached plates or in definite patches in diplomystids, some bagrids, *Pangasius*, +*Hypsidoris*, some silurids, +*Astephus*, *Neosilurus*, clariids, schilbeids and some pimelodids (not *Rhamdia* and *Pimelodus*) (various references; pers. obs.). They are also present in many primitive non-ostariophysans (Fink and Fink, 1981) and Ostariophysi other than catfishes (Grande and Lundberg, 1988). Teeth are lacking in *Synodontis* and the doradids, callichthyids and the three silurid genera in my outgroup series; also loricariids.

I concur with Bhimachar (1933) that an edentate vomer or one with very small tooth patches represents an advanced condition. Such conditions are found in diverse catfish groups (e.g. see above) and occur in most ictalurids although the primitive condition is present in the genus +*Astephus*. Not infrequently, both states may occur in the one catfish family or genus (e.g. *Gephyroglanis* - Skelton, 1981). There is little doubt that vomerine dentition has been lost more than once among siluroids.

Within the Ariidae, the expression of teeth on the vomer is similarly highly variable although most taxa exhibit the plesiomorphic condition. Fourteen of the 34 Australo-Papuan species lack vomerine teeth at any life stage and I have found no evidence that ariids lose these teeth with increasing age (*contra* Grande and Lundberg, 1988).

36. Vomer dentition - stability

The vomerine tooth patches expand slightly in several Australo-Papuan ariid taxa, the most extreme expressions being where the two oval patches coalesce and form a median "butterfly"-shaped patch (berneyi, nox) or a very large median patch (solidus - fig. 57). Rarely, graeffei individuals may lack one patch.

The tendency for tooth patches to alter in shape and number during ontogeny is derived within the ariids and may be neomorphic. Study of extralimital ariid taxa suggests that this phenomenon may occur in several different lineages.

37. Infraorbitals

The infraorbital series in ostariophysans is primitively represented by bony, often ornamented plates (Fink and Fink, 1981; Scnaefer, 1987). In the siluriforms, the series usually consists only of the canal-bearing portions of the bones, which are often elongate and lacking ornamentation (above authors; Roberts, 1973; Howes, 1983). Taxa in some catfish lineages exhibit homoplasy in that the infraorbitals have expanded: e.g. loricarioids, Malapterurus (Howes, 1983), clariids (Tilak, 1963a), the ariid Batrachocephalus and some doradids (pers. obs.).

The number of infraorbitals varies from 4 to 12, ~~(Lundberg, 1970)~~, the primitive number being 5 (Lundberg, 1982, with proviso: i.e. 4 plus lachrimal). This number has increased in several lineages. In ictalurids the "lowest and primitive" number of 6 occurs in two extant genera, and the fossil +Astephus has 6 (Grande and Lundberg, 1988). Contra Lundberg however, Grande (1987) concluded that 6 is the primitive siluriform number of infraorbitals as it is the number common to most teleosts (Nelson, 1969, cited in Grande, 1987) and also occurs in many catfish families. In the outgroups at my disposal, 4 and 5 are the common numbers. *Rita* has 5 or 6, the posterior ones being small and possibly fragmented. My two *Neosilurus* specimens have a derived count of 8: all fibrous except for the ossified lachrimal and the last enveloped by the sphenotic. Diplomystids have 7 to 9 (Arratia, 1987) including the lachrimal. Arratia partly interpretted the high number as a derived condition, against the trend in fishes to reduce or lose infraorbitals.

The dominant number in Australo-Papuan ariids is 4, including the lachrimal. The seven infraorbitals present in *novaeguineae* appear to be the result of fragmentation to accommodate its low eye. Four is the dominant number in extralimital ariids, with *Hemipimelodus* and *Cephalocassis* having 5 (the second is quite small) and *Ailurichthys* having 6. Bearing in mind the variation displayed in this character throughout the Siluroidei and the possible trend towards reduction, I interpret 4 (including the lachrimal) as the plesiomorphic condition in the ariids.

38. Peritoneal colour

and

39. Buccopharyngeal cavity colour

The ariids are not known for their brightness of hue, compared to the patterned body of other siluroids (e.g. auchenipterids, mochokids, loricariids). The body colour of Australo-Papuan ariids is generally uniform, although "piebald" individuals of some taxa occur in northern Australian fresh waters. Not infrequently, colour intensity and hue varies, making a match with the colour of the surrounding water. All ariids are darker on the upper two-thirds of the body.

The Australo-Papuan ariid *mastersi* has a dark or dusky brown peritoneum, sometimes darkly spotted. The taxa *nox* and *solidus* have a dark buccopharyngeal cavity, the colour extending over the gill rakers (cavity occasionally dusky in species 4 also). Dark blue or brown pectoral fins are present in *carinatus*, *froggatti* and *crassilabris*. Of extralimital taxa examined, *Cephalocassis* has distinct dark patches on the pectoral, anal and caudal fin lobes; a pair of broad bands pass along the sides in *Galeichthys peruvianus*; and the peritoneum of the ariid (?) *Ancharius fuscus* is brown, flecked regularly with cream.

The expression of definite colour in the ariids appears to be sporadic. In an attempt to determine whether it reflected synapomorphies in a phylogenetic relationship or was independently derived within the family, peritoneal colour and buccopharyngeal colour were scored for analysis.

Any selective "advantage" taxa may achieve through having definite colours has not been investigated.

40. Secondary hypurapophysis

The "Type C" hypurapophyses of Lundberg and Baskin (1969) (of combined hypurapophyses and secondary hypurapophysis extending over the parhypural and first two hypurals) is an advanced character state among catfishes (*ibid.*). This condition is exhibited by all ariids. Some minor variation is apparent among Australo-Papuan taxa.

A more derived secondary hypurapophysis is exhibited in the ariid *argyropleuron*, in which the structure is flattened and "teardrop"-shaped (fig. 40D).

41. Size of caudal vertebrae

Ariids exhibit some interspecific variation in size and form of vertebrae. Although objective comparison between form proved unreliable in my C&S material (figs 39,40) the size ratio between the randomly-chosen 10th penultimate vertebral centrum and the 7th-8th trunk vertebral centrum, was used to quantify observed size difference.

The marine ariid thalassinus has enlarged anterior caudal centra. They are twice as wide as centra in other parts of the column, including the last centrum and a mid-trunk vertebral centrum (figs 39B, 147) (Kailola, 1986a).

Whereas in most other ariids the penultimate 10th centrum is 10-40% wider than the last centrum, it is not in nella, polystaphylodon and argyropleuron. In them, the distal caudal vertebrae are shortened and extend vertically such that the last centra are 50% shorter than the penultimate 10th.

Among extralimital ariids, the posterior caudal centra of quadriscutis are considerably elongated.

42. Size of nuchal plate

In the majority of siluroids, the nuchal plate is a narrow crescentic bone at the proximal base of the first dorsal spine or buckler and it forms a rigid supporting connection between the skull and the dorsal fin elements. In the ariid Sciadeichthys the nuchal plate is noticeably enlarged, apparently at all growth stadia (examples also in Taylor and Menezes, 1977). This character state is also present in some pimelodids (Lundberg et al., 1988).

In Hexanematichthys sagor, the nuchal plate expands during ontogeny, an apomorphic phenomenon shared with the Australo-Papuan taxon mastersi (fig. 140).

43. Rakers on posterior or trailing edge of gill arches

Presence of posterior rakers on all four gill arches was considered plesiomorphic by Stewart (1986) because rakers are present in this situation in the primitive family Diplomystidae. Many of my outgroup taxa have such rakers. I prefer however, to follow Skelton's (1981) caution not to allocate polarity. He observed that the character is difficult to evaluate and appears to have a complex distribution within the Siluroidei, likely associated with functional demand.

Members of the Ariidae have or lack ~~have not~~ gill rakers on the posterior faces of the first two gill arches (fig. 58) (Taylor, 1964; 1986; Roberts, 1978; Kailola, 1983). The rakers are confined to the dorsalmost part of the arches in some taxa. I have found considerable intraspecific variability in the presence of rakers on the second gill arch in the Australo-Papuan ariids and am accordingly somewhat uncertain of the characters' stability. (See also Character 91.)

44. Ventral fin elements and pelvic musculature

According to Lundberg (1970~~)~~, cited in Grande, 1987 and Grande (1987), primitively there are six segmented rays in the catfish ventral fin. In my outgroup material, the number of fin elements decreases from 11-13 in *Neosilurus* and *Parasilurus* and 9 in *Wallagonia* and *Pylodictus*, to 5 in the loricariids (see also Grande, 1987, Table 2).

All ariids have six segmented rays. The fin lacks a spine and the two halves of the divided innermost ray are widely separated proximally.

In conjunction with the low ray count, ariids have a very complex and highly specialised pelvic musculature, described by Shelden (1937). These muscles have a powerful grasping function consistent with the development and possible function of ariid secondary sex characteristics. Moreover, it is not lacking from males and "pad-less" female taxa (and see Character 34).

The combination of complex muscle form, low segmented ray number and basipterygium shape (Shelden, 1937; Character 62) is derived for the Ariidae.

45. Caudal elements

The most primitive caudal ray count of 9+9 occurs in the Diplomystidae within the Siluroidei. Other ostariophysans and primitive teleosts have 10+9 rays (Lundberg and Baskin, 1969; Arratia, 1987). +*Hypsidoris* and the majority of siluroids have 17 (8+9) principal caudal rays (Grande, 1987; Lundberg and Baskin, 1969). The ariids have a derived count of 7+8, only loricarioids and amphilids having a more derived (= lower) regular count.

Lundberg and Baskin (1969) determined that the number of principal caudal fin rays is constant within catfish taxa having forked tails (as e.g. the Ariidae).

46. Posterior dorsomedian fontanelle length

In +*Hypsidoris* the dorsomedian fontanelle is long, extending behind the supraoccipital-frontal articulation at all stadia (Grande, 1987). Lundberg (1970~~)~~, cited in Grande, 1987 observed that the open dorsomedian fontanelles are present in all catfishes but tend to close (at least partially) during ontogeny. Howes (1985) considered that absence of a posterior cranial fontanelle is a common phenomenon in siluroids and thought that the condition could be derived; but if so, it must have developed independently in several lineages.

The Ariidae also exhibits the trend towards closure. In them, the double dorsomedian fontanelle in juveniles usually extends from the mesethmoid to the region of the supraoccipital-frontal articulation; and the posterior fontanelle tends to reduce or be absent in adults. The presence of an elongated, well-developed posterior fontanelle extending to, just short of, or beyond the supraoccipital-frontal articulation and remaining open in adults, appears to be plesiomorphic.

47. Shape of posterior dorsomedian fontanelle

In most catfishes the fontanelle is elongate-rectangular. I agree with the following contributors that this is the plesiomorphic condition: Tilak, various papers; Lundberg, 1982; Arratia, 1987; Grande, 1987. An irregularly-shaped or rounded posterior fontanelle appears to be derived; for example Lundberg proposed this for the Ictaluridae. *Chrysichthys* and several ariids have a small, heart-shaped fontanelle, including *Hemiarius*, *dayi*, *Hemipimelodus*, *taylori* and *novaeguineae*. Species 4 and *armiger* have irregularly-shaped fontanelles.

48. Size of the frontals

Arratia (1987) interpreted a narrowing of the frontal posteriorly as a derived feature, although the siluroids she cited as sharing the presumably plesiomorphic condition (i.e. broader posteriorly) are generally considered more phylogenetically derived (Nematogenyidae, Trichomycteridae, Plecostominae, ...).

The forward spread of the frontals is influenced by growth in some ariids. For example, the space between lateral ethmoid and frontals is considerably reduced in larger individuals of *Hexanematichthys*, *Sciadeichthys* and *Ailurichthys* (Higuchi, 1982; pers.

obs.). Based on my assessment of this condition in the Australo-Papuan ariids and outgroups, I conclude that a broader frontal posteriorly with an anterior narrowing is the derived condition in the ariids. Two extreme character states in addition to the general form exist: (i) broad anteriorly and tapered to moderate or narrow posteriorly, arms moderately wide; (ii) broad posteriorly with tapered, narrow arms anteriorly (e.g. "*Cathorops*", *dayi*, *armiger*). In the former state, the lateral ethmoid-frontal space is reduced and in the latter it is much enlarged. (This space is "derived" from the foramen for superficial ophthalmic branches of cranial nerve V and VII: J. Lundberg, pers. comm.).

49. Laminar bone on anterior vertebrae

The laminar bone ventral to the fused vertebrae is usually continuous medially in ariids (except in *Galeichthys* and *Ancharius*; and see Character 11). The excavation of the laminar bone posteromedially and the overlapping of the transverse process bases laterally however, is variable (figs 34,36) and is fairly extensive in the four bagrid taxa (not *Rita*) and *Pimelodus* I examined.

The laminar bone in other siluroids extends laterally over the first 4 to 6 vertebrae to a greater or lesser degree. This and their open condition, suggests that in the ariids, a minimal cover over the aortic groove is plesiomorphic. I interpret this in Australo-Papuan ariids as exposed transverse process bases and a deep median excavation below the vertebrae.

Some ariids possess apomorphic modifications in the laminar shelf: depressions (e.g. *dayi*, *Guiritinga barba*, *froggatti*) or median keel (e.g. high and acute in *Batrachocephalus*, *armiger*).

50. Additional palate dentition

The teeth often present on the siluroid palate are borne on autogenous tooth plates. Examples of catfishes bearing such plates are +*Hypsidoris*, +*Astephus*, some bagrids (Bailey and Stewart, 1984; Skelton, 1981; Tilak, 1965), *Schilbe*, *Pangasius*, *Ompok* and *Wallago* (pers. obs.) several pimelodids (Schultz, 1944; Grande and Lundberg, 1988; Mees, 1974) as well as ariids. Fink and Fink (1981) regarded their presence as neomorphic because tooth-bearing plates are also present in some groups of characiforms (see also Gosline, 1975). In lower teleosts such as *Elops* (Elopiformes) tooth plates are likely to form in any part of the mouth roof where a firm backing can be found, provided they are needed (Nybelin, 1967, cited in Gosline, 1975). Roberts (1973) implied that these plates arose independently in characins and catfishes.

The presence of fixed tooth plates on the parasphenoid and/or orbitosphenoid in *Sciadeichthys* (fig. 59) is an autapomorphic character, possibly secondarily derived within fishes (see Gosline, 1971). Similar, independent apomorphies have been recorded elsewhere: fixed toothed plates in a schilbeid (Tilak, 1961); tooth plates below or attached to the palatine (Arratia, 1987 and Azpelicueta, 1988 in diplomystids; Mo, 1988 in *Chrysichthys*).

The possession of autogenous palatal tooth plates is plesiomorphic in the Ariidae. When present in the Australo-Papuan ariids they are either ovate, elongate-oval or roughly triangular.

The expression of this character is labile in *velutinus* however, individuals of which very occasionally having one or two toothed plates (fig. 20C).

51. Position of palatal tooth plates

The form and position of the tooth plates, constant within an ariid taxon, have been used almost solely as defining characters in taxonomic works on the family (e.g. by Weber and de Beaufort, 1913). There may be one plate on each side of the palate adjacent to the vomer teeth (or edentate vomer) and lying ventral to the anterolateral aspect of the lateral ethmoid; or lying more posteriorly over the metapterygoid on each side (as in *Arius arius*); or the plates may be paired, forming a toothed triangle with the vomerine teeth (e.g. in *thalassinus*, *bilineatus* and *mastersi*); or even of anterior small and posterior large patches, the latter extending as far back as the hyomandibular. In some taxa, the palatal dentition is "broken" into several patches on each side (e.g. *genidens*, *planifrons*). Further, some individuals may develop "extra" tooth plates, a phenomenon I have observed in *nella* and the extralimital ariid *dispar*.

I regard the anterior plate position as plesiomorphic.

52. Dentition on palatal tooth plates in females

Gosline (1975) drew attention to several siluroids having larger teeth on the vomer than in the jaws (e.g. *Rita*, *Neosilurus*). The form of palate dentition in ariids is probably associated with feeding specialisations (see also Gosline, 1975): fine and villiform, conical, acute, small and curved, "peg"like and molariform. I cannot see that any meaningful phylogenetic relationship can be inferred from comparison of tooth form. Where palate teeth of ariid taxa are granular or globular, they are noticeably larger than the jaw teeth but, apart from sea urchins (echinoderms) in the gut of juvenile *nella* (pers. obs.) and *tenuispinis* Day (Al-Hassan *et al*., 1988), very little information on the diet of such taxa is available.

However, the presence or absence of teeth on the tooth plates is variable in ariids, independent of diet. As there are usually teeth on the palatal tooth plates in catfishes, I consider its presence as plesiomorphic.

The males of some taxa having granular palatal dentition (e.g. maculatus, nella) shed many teeth during the spawning (= brooding) period (pers. obs.; Willey, 1911) (fig. 60A). Individuals of solidus of various sizes, maturity and either sex also shed teeth, the cause of which is undetermined. In species 4, the tooth plates are never toothed (fig. 60D).

53. Fin spine thickness

The presumed plesiomorphic condition of the fin spine in catfishes is: well-ossified with strong and/or relatively few well-developed, retrorse serrations along the posterior and often anterior margin(s), plus a functional locking mechanism. This is the condition in many siluroids - e.g. ictalurids except Prietella (Lundberg, 1982), +Hypsidoris, diplomystids, many bagrids (Bailey and Stewart, 1984; pers. obs.), some pimelodids, auchenipterids (Mees, 1974), doradids, Synodontis and loricariids. The derived form of the fin spine is: relatively slender and often flexible with serrations along the posterior margin. Stewart (1985; 1986; 1986a), Buckup (1988), Ferraris (1988) and Lundberg and McDade (1986) discussed the phylogenetic implications of this apomorphy in the Pimelodidae. Hypophthalmus and several other siluroids possess thin fin spines. The loss of spines altogether and absence of a dorsal fin (Fink and Fink, 1981; Howes, 1985) appear to be related apomorphies.

The Ariidae display interspecific variability (see also Character 74) in spine thickness and serrature and spines often thicken with age. They range from usually being hard and stout with strong serrae or dentae (as in *carinatus*) to thin and finely serrated as in *nox*.

54. Branchiostegal number

There is considerable variation in number of catfish branchiostegal rays. Alexander (1965), Roberts (1973) and Lundberg (1982) believed that a higher number is probably advanced and associated with a flattened head in catfishes; but Gosline (1973) ~~and Woskoboinikoff (1932)~~ doubted there is any correlation with head shape. Gosline argued that the branchiostegal number is related to the tightness-of-fit of the gill cover or "sleeve" over the gill chamber during inspiration. Opercles and branchiostegals support the sleeve as it spreads over the gill chamber: opercles for flat surfaces, branchiostegals for rounded surfaces. The two authors reasoned that the number of rays (or struts) is positively associated with the length of the sleeve's anteroventral portion. The struts unfold like a fan to overlap the isthmus: more to cover a larger area, fewer to support a sleeve spanning a shorter distance. Working mostly on *Chanos*, Gosline (1967) found there is often a three-way relationship between fewer branchiostegal rays, a broadly-united gill membrane and shorter lower jaw.

The plesiomorphic combination of higher number of branchiostegals, extensive gill opening and broad membrane is exhibited in many catfishes. Grande's (1987) summary agrees with McAllister's (1968), and of the 18 families he listed (Table 1), the more phylogenetically apomorphic families possess fewer rays. Overall, the numbers range from three (Callichthyidae) to 20 (Siluridae).

Surprisingly, the Ariidae have *fewer* branchiostegal rays than do other catfishes having gill openings of comparable size (e.g. pimelodids, silurids, hypophthalmids) and so appear to be reasonably apomorphic in this character. Four Australo-Papuan taxa have 7 branchiostegals, only three of them also having wide gill openings. Most (with both wide and restricted gill openings) have 6 rays; and three taxa have 5 (one with restricted openings, the others with wide openings) (Table 3). Tilak (1965) recorded 7 rays in only one of the S.E. Asian ariids he studied. I hesitate to hypothesise a trend for this character in ariids.

Catfishes lack a suboperculum. Gosline (1973) considered that this element originally functioned as a branchiostegal ray, the upper ray in siluroids characteristically occupying the space left by the absent suboperculum (McAllister, 1968). Maybe in catfishes its loss has been compensated for by the relatively more numerous branchiostegals (*cf.* characins, cyprinids). In all ariids, the first two (outer) rays are broader than the remainder and, as Tilak (1965) and Lenous (1967) surmised, they may act as a suboperculum. The first ray in *argyropleuron*, *nella* and *polystaphylodon* is exceptionally broad (fig. 29C), as it is in the extralimital ariids "*Cathorops*" and *Ketengus*. I suggest this apomorphy has been independently derived in these species groups.

55. Abdominal cavity length

There is considerable variation in the length of the abdominal cavity in Siluriformes. *Sensu* Lundberg and Mago-Leccia, 1986, I determined this indirectly from the number of precaudal vertebrae (i.e. fused vertebrae of the anterior complex plus those with an open haemal arch). ~~(see Lundberg and Mago-Leccia, 1986).~~

The percentage of the vertebral column this comprised was then calculated (Table 4) (assuming all vertebral centra of equal size).

In the ariids, the number of precaudal vertebrae ranges from 12 in *quadriscutis* to 27 in *dowii*; in Australo-Papuan ariids, from 13 in *dayi* and *novaeguineae* to 24 in *mastersi* and species 5. In other catfishes, the range is 9 (*Hypostomus*) to more than 19 (*Pterodoras*, diplomystids, +*Hypsidoris*, some ictalurids including +*Astephus*, and *Clarias*). The range in percentage of the vertebral column of all catfishes I examined is 22 to 47 (see also Character 82).

Lundberg (1970~~)~~, cited in Lundberg and Mago-Leccia, 1986 concluded that a longer abdominal cavity is derived in ictalurids. Conversely, Lundberg and Mago-Leccia (1986) suggested there is a trend in gymnotoids towards reduction in the length of the abdominal cavity, an apomorphy associated with reduction in the size of the swimbladder. Albeit I found no clear correlation between swimbladder size and cavity length in catfishes examined, it is possible there is one (from evaluation of outgroups; long swimbladder in species 5 associated with long abdominal cavity) and a trend towards reduction of the abdominal cavity may exist.

56. Naked body

A scaleless body is a derived condition in the ostariophysans. Most cypriniforms, characiforms and most primitive teleost and gonorhynchiforms possess scales on all or part of the body. The majority of catfishes (including ariids) and gymnotoids lack scales although they are often represented by ossified lateral line tubes (Roberts, 1973; Fink and Fink, 1981).

It is possible the "armature" in catfishes are not homologous with the body scales of other ostariophysans (Roberts, 1973; Fink and Fink, 1981).

57. Gonad reduction

Most ariids possess paired gonads of an unlobed, hollow type (Rimmer and Merrick, 1983), a condition which prevails in Australo-Papuan ariids. The exceptions are *dayi* and *novaeguineae*. In these taxa, the gonad forms a single, ovate unit having an internal incomplete septum. In species 4 and *truncatus*, the proximal third of the ovaries are united (fig. 61).

The reduced size of the gonad may be associated with the maximum attainable SL of the taxa (recorded at 300 and 150mm SL respectively). In these oral incubating fish, the number of mature ova produced at each spawning appears to be directly related to the number the male parent's mouth can accommodate: i.e. the smaller the male parent, the less capacity has his mouth. Production and fertilisation of more ova than can be viably accommodated might be interpretted as a "waste" of reproductive effort. One solution could be to produce more *smaller* ova, although for fishes hatching large, precocial larvae (Fuiman, 1984) as do the ariids, there must be a minimum amount of yolk required in the ovum (ref. Breder and Rosen, 1966). The alternative, of reducing the gonadal epithelium such that *fewer* ova are produced, appears to be the *modus operandi* in these small ariids. Welcomme (1967) reported a similar relationship in the mouthbrooding *Tilapia* (Cichlidae), where the number of ova produced approximately equals the square of the total length (cm) of the parent fish.

4 ANALYSIS OF CHARACTERS NOT EMPLOYED

4.1 RATIONALE

Many characters potentially useful in demonstrating the phylogeny of the Australo-Papuan ariids were revealed by my study. Fifty-seven of them were used in a phylogenetic analysis (Chapter 5) after evaluating homology and polarity.

In view of the poor definition of ariid features in systematic literature and the often flimsy basis for generic nomination exposed, I consider that the clear character descriptions and evaluations in the previous chapter should be continued here. By this means, the merit of characters upon which earlier taxonomic descriptions are based can be assessed.

In my opinion, a real contribution to a future, broader assessment of the family's relationships in the suborder Siluroidei, is made by redescribing homologous and uniquely derived features of ariid morphology along the lines established by recent studies of other siluroids (e.g. by Lundberg, 1975a; 1982; Howes, 1983; 1985; Vari and Ortega, 1986; Arratia, 1987; Schaefer, 1987).

Furthermore, comparison of homologous characters and ecological adaptations with those of other siluroids provides additional supportive evidence on the role of environment in speciation.

There are a variety of reasons why I considered the remaining characters unuseable in an analysis.

(1) They are hard to qualify or quantify, either through examination of suboptimal C&S preparations or through perceived or suggested changes with ontogeny;

(2) The character was obscured, damaged or probably altered by poor preservation;

(3) Assumptions about character states were required for different-sized individuals unavailable to me;

(4) They present no phylogenetic information. For example, unique character states (autapomorphies) were generally excluded (but note Characters 40, 41 and 52). Such individually derived characters are described in Chapter 6.

(5) Compared to their successful use in phylogenetic reconstruction in other catfish families, many characters in the Ariidae are either highly labile or very stable, exhibiting only intraspecific variation or parallel ontogenetic modifications (e.g. caudal skeleton form; shape of vertebral centra).

(6) The characters are either meristic or morphometric (section 4.3). The problem with meristic and morphometric characters is that because most states occur in an outgroup and no disjunction is evident, polarity cannot be determined (Chernoff, 1986). Morphometric characters are often correlated with habitat and diet.

(7) Ecologically adaptive characters are frequently homoplastic and correlated. In the ariids for example, mouth size, gut form, lip thickness, gill raker number, buccopharyngeal pad development, gill arch papillae, form, number and mobility of jaw teeth are all highly correlated with diet. Although generally unuseable on these bases, some characters (numbers 15?, 16, 17, 29?, 31?, 33, 38?, 39?, 43, 55?) were scored and included in the character matrix for analysis; for example, buccopharyngeal pads (Character 17) and abundance of posterior gill rakers (Character 43). Haines (1979), Roberts (1978), Coates (1983) and Kailola and Pierce (1988) recorded the food items of various taxa in Australia and New Guinea, which I have supplemented in my study (refer Table 3; Chapter 6).

The 35 characters discussed here fall into three approximate groups (compared to the overlapping among the first 57). The reasons why some of the equivocal and problematic characters (4.2) could have contributed to a phylogenetic reconstruction are discussed. Ariids possess few meristic characters (4.3), and Character 55 (abdominal cavity length) may also be one. Although many adaptive characters are discussed in section 4.4, others were included in the phylogenetic analysis (e.g. Characters 16, 17) partly because they are obvious and characteristic taxonomic features.

All characters are summarised (4.5).

4.2 EQUIVOCAL, UNSTABLE OR PROBLEMATIC CHARACTERS

58. Pectoral girdle

A reinforced girdle is considered advanced in the substrate-dwelling loricariids (Schaefer, 1984), matching Howes'(1985) observation that a rigid girdle is lacking in midwater, shoaling fish. The coronoid process height is significant in +Hypsidoris (Grande, 1987). A short keel is plesiomorphic in ictalurids (Lundberg, 1982).

In the Australo-Papuan ariids, the pectoral girdle (fig. 43) curvature varies from being shallow and/or thin (e.g. in nox, species 1 and 5, augustus, danielsi and spatula) to strong, stout and compact (e.g. in latirostris, froggatti, carinatus, dayi, nella and macrorhynchus. The coracoid keel is strong and very clearly defined in froggatti, carinatus and crassilabris.

Although marked differences could be recognised, differences in height of the coracoid keel and coronoid process and amount of curvature of the girdle between different taxa, could not be quantified because of ontogenetic variation and fallible measurement of curvature.

The TYPE of girdle is related to feeding habit (Gosline, 1977). In most predaceous forms, the girdle is broader compared to the stout girdle of non-predaceous catfishes. Gosline's conclusions (partly based on the ariid *Potamarius*) seem applicable to the Australo-Papuan suite of catfishes.

In the ariids, cleithrum and coracoid are broadly united for most of their lengths. At the midline, the coracoids and part of the cleithrum are joined by 5-7 pairs of interdigitations. Such a joint provides strength and rigidity to the girdle (Roberts, 1973). In *+Hypsidoris* the coracoids are simple at the midline. A complete midline connection between the coracoids is widespread and probably plesiomorphic in catfishes (Howes, 1985). The derived ictalurid *Trogloglanis* has a broad symphysis compared to that in confamilials (Lundberg, 1982). *Schilbe*, *Synodontis*, *Pimelodus*, the doradids and some bagrids have extensive girdle shelves, a feature lacking in the Siluridae and Helogenidae (Alexander, 1965).

I attempted to measure the observed variation in symphysis width in the Australo-Papuan ariids on C&S material. About one-third have a broad symphysis, >/= 9% SL (e.g. *nox*, *thalassinus*, species 4) and, at the other extreme, six taxa (e.g. *crassilabris*, *macrorhynchus*, *latirostris* and species 5) have a symphysis </= 7.5% SL. Unfortunately, these ratios could not account for the girdle's curvature (see above). Although a broad pectoral symphysis is probably apomorphic in ariids, I am unable to justify this postulation because of irregularities in measurement of the curved girdle.

59. Caudal skeleton

In all Australo-Papuan ariids, the caudal skeleton consists of: parhypural; hypural 1 + 2; hypural 3 + 4; hypural 5; epural (fig. 40). In many of my specimens (C&S material; juveniles) the hypurals are imperfectly ossified and sometimes the 3rd and 4th hypurals are incompletely fused. The parhypural is clearly sutured with the hypural 1 + 2 in nella, thalassinus, crassilabris and proximus. The significance of the trend for caudal elements to unite or ossify as growth proceeds could not be assessed here because of differences in SL. Lundberg and Baskin (1969) recorded variation in element fusion in different-sized ariids (including unfused in a 400 mm SL specimen of Potamarius!).

The limited variation exhibited in the EPURAL size and position (C&S material) could not be adequately quantified. Lundberg and Baskin (1969) and Arratia et al. (1978) noted a trend towards loss of this element in the Trichomycteridae, and it is specifically polymorphic in the Pygidiinae (Arratia, 1983).

60. The hyomandibular articular facet

This facet lies on the sphenotic (fig. 15), extending over the sphenotic-pterotic suture in many taxa. Occasionally (e.g. in species 1 and 3, nella, argyropleuron and species 6) it reaches the front of the pterotic, a condition shared with other siluroids such as the Bagridae, Schilbeidae, Pimelodidae and Siluridae. This character's significance in the ariids cannot be accurately assessed from my C&S material and a few dry skulls, however. There may be a trend for the facet size to reduce in catfishes: for example, it is shorter in some phylogenetically apomorphic groups (see Schaefer, 1988; Brown and Ferraris, 1988).

61. 5th parapophyses

In most Australo-Papuan ariids the parapophyses emanating from the 5th vertebra are directed posterolaterally. In dayi, species 5 and the extralimital Osteogeneiosus they are directed at right angles to the centrum. This condition also exists in the Ictaluridae (Lundberg, 1982). In "Cathorops" and Potamarius the 5th and 6th parapophyses are united and angled forward. The parapophysis form appears to be highly variable.

62. Pelvic girdle

Shelden (1937) suggested that absence of a posterior (or ischiac) process is plesiomorphic in catfishes. Grande (1987) (and see Roberts, 1973) pointed to the correlation between lack of a process and higher number of ventral fin rays (more than 7) in about six catfish families.

There is very little qualifiable difference in pelvic girdle form in ariids, Tilak's (1967) records probably being only of intraspecific variation. In some taxa (e.g. "Cathorops") the basipterygium has an extensive, rounded posterior process.

Juveniles (at least) of many ariid taxa possess a rudimentary lateral process or lateropterygium. The significance of this structure was discussed by Shelden (1937) and Howes (1985).

63. Urohyal

A triangular urohyal (when viewed ventrally) is common in catfishes, although considerable variation in this character is displayed throughout the Siluroidei. In some groups the urohyal is slender, e.g. in the Schilbeidae, some bagrids, some silurids, the pimelodid Rhamdia and some ariids. Conversely, it is broad and triangular in the derived ictalurid *Trogloglanis* (Lundberg, 1982), the bagrids *Gephyroglanis* (Skelton, 1981), *Bagrichthys* and *Rita* (pers. obs.), Chacidae (Brown and Ferraris, 1988), *Trichomycterus* (Arratia and Menu-Marque, 1984), *Pimelodus* (pers. obs.) and the loricariid *Hypostomus* (Schaefer, 1987). In diplomystids it has short anterior processes and a long, median posterior extension (Arratia, 1987), and in +*Hypsidoris* and +*Astephus* it has three small, diverging anterior processes (Grande, 1987; Grande and Lundberg, 1988).

The urohyal in the Ariidae is often narrow, the posteromedian and lateral arms long and tapered (fig. 30). In *crassilabris* the urohyal is broad and anteriorly truncate; in *nox*, *solidus* and *novaeguineae* the lateral arms are very slender and tending to bifurcate distally. Although Lundberg (1982) suggested that a narrow urohyal is more primitive in catfishes, my findings in the Ariidae do not endorse this. Unfortunately, the 5-6 character states in the Australo-Papuan ariid urohyal (narrow, stout and oblong, broad and short, etc.) are difficult to define unequivocally. Ontogenetic and intraspecific variation is apparent in some taxa.

64. Otoliths

When fresh material was available, the lapillus otolith (Arratia, 1987) was extracted from the utriculus region of the skull and examined in an attempt to recognise and compare interspecific variation in form. However, the otolith shape is extremely uniform in the ariids and I found no assessable changes, except those associated with growth.

65. Weberian apparatus

Fink and Fink (1981) analysed the development of the Weberian Apparatus in the ostariophysan suborders. Apparatus features are useful in classifying the families of catfishes, but of limited use for finer resolution (Chardon, 1968). Krumholz (1943) found that ossicles differed in form between various North American ostariophysans; and Tilak (1965) attempted to show they do in ariids. The form of this Apparatus in ariids has been described in detail by Tilak (1965) and Chardon (1968).

Chardon (1968:69) perceived some variability in the shape of the "osselets" in catfishes but attributed them to skeletal strength and other general adaptations. I also found no substantial differences in these structures in ariids. Moreover, as they are very small and easily damaged when extracting, I consider that any differences I perceived cannot form a reliable expression of interspecific (even intergeneric) distinction.

66. Axillary pore

The pore (of the axillary gland) is located just ventral to the posterior cleithral process in most catfishes. In *Diplomystes chilensis* the opening is rounded or elongate, most individuals having two openings in each axil (Arratia, 1987). Lundberg (1982) observed that the pore is variable in the Ictaluridae, frequently lost with growth and absent in the apomorphic genus *Trogloglanis*. Generally in ariids, the opening is moderately small. In *carinatus*, *froggatti*, *crassilabris* and *conorhynchus* however, it is enlarged and ovate, and in other taxa (e.g. *velutinus*) it is tiny.

My attempts to quantify pore size proved unreliable, particularly on preserved material.

67. *Ascending parasphenoid "wings" (alary processes)*

These are present in most catfishes (Bhimachar, 1933). They suture with the pterosphenoid and thereby separate the optic foramen anteriorly from the trigeminofacial foramen. *Diplomystes* lacks the bony "wings", as does *Trogloglanis* and some trichomycterids (Lundberg, 1982).

The alary processes are frequently well-developed in ariids and their shape - ranging from slender, long spurs (e.g. in *augustus*) to broad, low flanges (e.g. in *dayi* and *carinatus*) (fig. 14) - appears to be characteristic of groups of taxa. However, I found considerable intraspecific and ontogenetic variation in the "wing" shape which precluded their meaningful contribution to a phylogenetic analysis.

68. *Ossification*

The well-ossified neurocranium of diplomystids and many other siluroids appears to be plesiomorphic. Thinning of the skull bones and/or presence of persistent cartilage in adults is a derived condition often apparent in taxa achieving a small maximum (adult) size. *Satan* and *Trogloglanis* (Ictaluridae) are such taxa (Lundberg, 1982) where the poorly ossified skeleton appears to be paedomorphic.

The ictalurid situation is mirrored in the Ariidae. Weak cranial ossification occurs in *novaeguineae*, *Bagre*, *Hemipimelodus* and *Cephalocassis* and there is a tendency towards it in *nox*. All attain a small maximum size. Cartilage persists in adult stadia between the sphenotic, pterotic and supraoccipital in *Hemipimelodus* (fig. 3) and *Cephalocassis*.

I also recognise a second derived condition in *carinatus*, *froggatti*, *crassilabris*, *Batrachocephalus*, *Osteogeneiosus* and possibly *augustus*. In them, the skull is heavily ossified, especially posteriorly. A superficially bony skull is apomorphic among catfishes (Bhimachar, 1933) just as is a thinly-ossified skull.

Stewart (1986) and Howes (1983) described poorly ossified cranial bones of some pimelodids as 'honeycomb texture with the frontal papyraceous' or 'appearing extremely porous'. Such phenomena occur in *Ailurichthys* and *Bagre* (frontal bones), "*Ariodes*" *dussumieri*, *nella* and *Osteogeneiosus* (lateral ethmoid expansion) and *nella* (expanded supraoccipital process).

69. *Premaxillary thickness*

Although the premaxillary is usually well-ossified in Australo-Papuan ariids, it is reduced and thin in some taxa, a condition I consider derived. Examples of taxa having a thin premaxillary are *dayi*, *nox*, *solidus* and species 4. In contrast, the premaxillary of the S.E. Asian ariids *Batrachocephalus* and *Ketengus* are very extensive and strongly ossified. Lundberg (1982) and Stewart and Pavlik (1985) cited similar situations in the ictalurid *Trogloglanis* and the pimelodid *Cheirocerus*. A possibly homoplastic condition exists in the gonorhynchiforms which have very thin and flat premaxillaries (Fink and Fink, 1981).

This character was difficult to qualify.

70. *Lateral ethmoid shape*

The usual and presumed plesiomorphic condition of the lateral ethmoid is short and triangular to rhombic (Fink and Fink, 1981; Howes, 1983; 1983a; other refs; pers. obs.). In ariids there are several forms of the outer, lateral prominence ("wing") of the lateral ethmoid, suggesting trends or synapomorphies in the family. About five different shapes occur in the Australo-Papuan ariids (figs 6-8): triangular and rhombic, or almost square, through sharp and attenuated (*argyropleuron*), curved posteriorly (species 5, *novaeguineae*) to truncate and oblong, posteriorly directed (*crassilabris*).

The influence of ontogeny and intraspecific variation in the shape of the lateral ethmoid could not be assessed in my material because of lack of sufficient material representing different growth stadia. Furthermore, clear qualitative description proved difficult. This character may, once clarified, impart significant phylogenetic information.

The lateral ethmoid of *nella* (and see Character 68) is well-invested with lamellated or cancellous bone. In *thalassinus* and *bilineatus*, *spatula* and *danielsi* it is very extensive posteroventrally.

71. Palatine facet

Arratia (1987) and Grande (1987) discussed the palatine facet and Grande gave an overview of the palatine form in catfishes.

In summarising the different forms of the siluroid palatine, Howes (1985), found that on "grounds of commonality" the bone is rod-shaped and articulating with part of, or the entire, lateral ethmoid margin. This is the situation in the Ariidae, and the articular facet lies 1/2 to 2/3 along the length of the palatine.

The extent of the palatine-lateral ethmoid contact differs among the Australo-Papuan ariids (fig. 24). A long facet is exhibited by *nella*, *argyropleuron*, *polystaphylodon*, *nox*, *solidus* and *dayi* and appears to be the derived character state. Unfortunately, I was unable to reliably quantify facet length in my C&S material.

The relative PALATINE LENGTH is difficult to assess (e.g. *cf.* snout length), although it appears to differ among the Australo-Papuan ariids. A shorter palatine is probably derived.

72. *Supraoccipital shape*

The majority of siluroid taxa possess a triangular, flat supraoccipital bone which is tapered posteriorly to meet the nuchal plate (or preceding supraneural) before the dorsal fin. This apparently plesiomorphic system lends support to the dorsal spine-locking mechanism of some groups (Lundberg, 1982) such as *Pangasius* (Tilak, 1964), +*Hypsidoris* (Grande, 1987), some doradids, mochokids, bagrids (pers. obs.) and most ariids.

The supraoccipital in many catfish families consists of a very broad basal portion thence a short, narrow, tapered portion. Such is the case in diplomystids (Arratia, 1987), ictalurids (pers. obs.; Grande and Lundberg, 1988; Lundberg, 1982), some bagrids (Tilak, 1965a; Skelton, 1981; Bailey and Stewart, 1984), sisorids (Tilak, 1963b), silurids (pers. obs.; Tilak, 1963) and schilbeids (pers. obs.; Tilak, 1964). Extremes are exhibited in the loricariid *Hypostomus*, where the supraoccipital is greatly reduced (Schaefer, 1987) and the pimelodid *Phractocephalus* where it is much enlarged (Lundberg *et al.*, 1988).

The ariids display about three derivations of the primitive supraoccipital form, although the effect of ontogeny appears to be significant (fig. 9). The posterior section may be slender and rectangular (as in *Galeichthys*, *dayi* and species 5); or very broad, often short (as in *froggatti*, *carinatus*, species 6, *mastersi*, *Sciadeichthys*, *Hexanematichthys* and *quadriscutis*). The slender process in *nella* and the American ariid *grandicassis* expands laterally as growth proceeds (fig. 62).

This character could have contributed to the phylogenetic reconstruction. It was omitted because of anticipated high levels of homoplasy and uncertainty whether character states could be accurately recognised in the different taxa (e.g. because of overlapping muscle tissue).

The height and form of the medial longitudinal keel on the supraoccipital in some taxa could not be adequately quantified. It is frequently more dominant in juveniles.

73. Uncinate process, epibranchial 3

As in the Diplomystidae (Arratia, 1987), only the 3rd epibranchial bears an uncinate process in the Ariidae (fig. 32). This apomorphy is shared with the bagrids (pers. obs.; Tilak, 1965a; Skelton, 1981), Chacidae (Brown and Ferraris, 1988), several Asian catfish families (pers. obs.; Tilak, 1963; 1963b; 1964), plotosids and doradids. Mahajan (1966) believed that possession and form of the uncinate process was "significant" in catfishes.

In most ariids, the uncinate process is angular and overlapping the middle of the 4th epibranchial (figs 31,32), a condition I consider plesiomorphic. In *argyropleuron* it is expanded slightly; in species 5 and *novaeguineae* it overlaps the proximal part of the epibranchial; in *nox* and *solidus* the process is slender and articulates with the epibranchial.

Unequivocal recognition of the various character states proved difficult in the C&S material, although synapomorphies were recognised (e.g. the slender process articulating with the epibranchial in *nox* and *solidus*). This character could have contributed to the phylogenetic reconstruction.

74. Chambered fin spines

Internal transverse partitions of the fin spines can be seen in radiographs of *Hemiarius stormii*, *Cephalocassis melanochir* and "*Ariodes*" *dussumieri*, *Arius caelatus* and *A. macronotacanthus* (extralimital ariids); and *nella* (fig. 63). In *thalassinus* and species 1 the spines are partly chambered. Taylor (1986) partly characterised *Ariodes* Müller and Troschel on its chambered spines (his definition however, based on *dussumieri* and not the type of the genus).

This character appears to be very homoplastic. For example, chambered spines do not occur in the phenetically similar *Hemipimelodus borneensis* (*cf. melanochir*), nor *argyropleuron* and *polystaphylodon* (*cf. nella*) (see also Character 53).

75. Barbel form and length

In catfishes and other Otophysi, the barbels enhance the food-searching and habitat-locating ability (see also Character 90).

The ariid barbels exhibit variation in form and length. Whereas in most taxa they are moderately flattened and thick, they may be flattened and strap-like (*mastersi*), rounded in cross-section (*nox*, *solidus*), thick and fleshy (*argyropleuron*), wisp-like (species 4), or have a low basal membrane (*spatula*).

Barbel length varies from always very long (*novaeguineae*, *macrorhynchus*, *armiger*, *berneyi*) or very short (species 7, species 4) (i.e. isometric) to becoming relatively shorter with growth (i.e. negatively allometric). Stewart (1986a) noted this in *Pimelodina*. Furthermore, ariid barbel length can vary with habitat (e.g. in *leptaspis*).

Barbels of inconsistent length and/or various apomorphic morphologies appear to have been independently derived in several catfish lineages, and be directly related to diet and habitat.

Barbel STRUCTURE may contain phylogenetic information. I conducted preliminary investigations into the composition of the barbels using various staining techniques (mainly Mallory's Triple Stain and Haematoxylin). These showed that in most ariids the barbel consists of a central rod of elastin tissue and two lateral rods of collagen fibre. In species 5 however, there are no collagen rods. Unfortunately this investigation was discontinued because I had insufficient sound material. Ghiot and Bouchez (1980) found that the barbel of *Pimelodus clarias* consists largely of elastin and a single rod of collagen fibres. Study of barbel structure, which is largely lacking (Arratia, 1987: review) may reveal important information on siluroid relationships. (See also Characters 30, 31).

The supposed ariid *Ancharius brevibarbus* from Madagascar has fringed barbels (pers. obs.).

76. Snout crescent

Roberts (1978) partly distinguished *Arius cleptolepis* (= *berneyi*) on the presence of a crescentic snout groove. Such a groove occurs in other Australo-Papuan taxa, including *proximus*, *mastersi* and *latirostris* and it is usually more apparent in juveniles. No phylogenetic interpretation can be attached to this labile character in Australo-Papuan ariids and it exhibits intraspecific variation. A possibly homologous feature exists in the Western Hemisphere ariid taxon *Selenaspis*, where each pair of nostrils is separated by a deep transverse groove.

77. *Unculi* ?

Roberts (1982) investigated the distribution in ostariophysan fishes of unicellular horny projections, which he termed *unculi*. These are related morphologically to the multicellular horny tubercles (including nuptial or breeding tubercles) of several groups of fish, among them the Ostariophysi (refer Wiley and Collette, 1970).

Individuals of about half the ariid taxa I examined have tiny elongate processes scattered over the snout and sides of the head in adults at all levels of maturity. Although closer examination using SEM techniques was only partly successful, it confirmed that these regularly-shaped structures are not strands of mucus nor artefacts of their preserved condition. Taxa possessing these structures include *Bagre*, *Galeichthys*, *leptaspis*, *spatula*, *danielsi*, *crassilabris*, *mastersi* and *berneyi*. Although presence or absence of these tiny processes may be phylogenetically informative, I believe it would be premature to evaluate the character in this study. For example, fresh material is required to permit adequate description of the processes. The "cilia" of ictalurids (Lundberg, 1982) may be homologous.

Possible function of these "unculi" in the ariids is unknown and should be investigated. They are not associated with breeding. Roberts (1982) suggested unculi function in mechanical skin protection, rasping, adhesion and hydrodynamics. He recorded unculi in 6 siluroid families (most of them phylogenetically apomorphic) and they are present in all other ostariophysans except gymnotoids.

78. Lateral line

The lateral line in the Ariidae is variable in appearance. For example, in *armiger*, *Cephalocassis*, *truncatus* and species 5 it is highly ramified, especially anteriorly. In most taxa the line is simple with regularly spaced short branches along its length. Diversity in lateral line form is widespread in catfishes and may be correlated with ecological and physical conditions (refer Howes, 1983; Buckup, 1988; Ferraris, 1988).

In some catfish taxa the anterior lateral line sensory tubules are encased in bony plates (e.g. the ariid *froggatti*), a condition thought to be plesiomorphic (Arratia, 1987; Grande, 1987). Lack of suitable material prevented assessment of this character in all Australo-Papuan ariids.

79. Head height and body shape

Ariids usually have a moderately elongate body and moderately depressed head. In species 1, species 5 and *Cochlefelis* the head is comparatively depressed (fig. 47) and it is comparatively elevated in *froggatti*, *carinatus*, *taylori*, *conorhynchus* (Table 3) and the extralimital *Batrachocephalus*. A depressed body (and head) represents an adaptation for a benthic existence (Mahajan, 1966; Alexander, 1965), it and a compressed body (e.g. in *Hypophthalmus*) being derived in catfishes (Howes, 1983).

The CAUDAL PEDUNCLE is moderately slender. It appears to be deeper in *argyropleuron*, *nella* and *polystaphylodon* and more slender and/or depressed in *thalassinus*, *bilineatus*, *mastersi* and *latirostris* (fig. 64).

80. Fin filaments

A character supporting the genus *Nemapteryx* Ogilby (type species, *armiger*) is the presence of filaments on the fin spines. This phenomenon is not rare in juveniles of many taxa however, and persists in *Arius arius*, *armiger*, *Bagre*, *Ailurichthys* and probably some other taxa. It contains no phylogenetic information in Australo-Papuan ariids.

81. Caudal fin shape

Tail shape is variable in siluroids (Lundberg and Baskin, 1969). An emarginate shape is derived in ictalurids (Lundberg, 1982); and a rounded tail is plesiomorphic in trichomycterids (Arratia *et al.*, 1978).

The ariid caudal fin is forked or deeply emarginate. The lobes range from broad and short (e.g. *argyropleuron*, species 4) to narrow and attenuated (e.g. *thalassinus*, *proximus*, *nox*). In an attempt to quantify caudal fin size, I calculated the ratio between medial and longest outer fin ray in the Australo-Papuan ariids. However, on the reduced set of individuals assessed the results are equivocal, the medial ray ranging from 2.2-4.3 shorter than the outer ray. Although not revealed by the ratios, it is plausible that the "more benthic" taxa have a shallower, broader caudal fin whilst the "more active" taxa have a deeply forked and tapered fin.

4.3 MERISTIC AND MORPHOMETRIC CHARACTERS

82. Total number of vertebrae

The total number of vertebrae (including hypural) in Australo-Papuan ariids ranges from 45 (*conorhynchus*) to 61 (*mastersi*). Similar variation is exhibited by extralimital ariids.

Lundberg's (1982) observation that species with similar total number of vertebrae can be very different in sectional counts is borne out in the Australo-Papuan ariids. e.g. carinatus: 17-18 precaudal + 3 haemal + 29-30 caudal - total 49-51 cf. argyropleuron: 15-18 + 6-7 + 26-27 - total 48-51.

Stewart (1986a) concluded that the primitive vertebral count for catfishes is approximately 39-45. Nevertheless, whereas this may be a primitive range for siluroids, the range within individual catfish groups may be higher or lower: e.g. in the Loricarioidea (Schaefer, 1987) where preural vertebral number is less than 26-37; the Ictaluridae (Grande, 1987): 36-55; pimelodids (Stewart, 1986, 1986a): 30-63; clariids (Howes, 1983): 60+; and ariids: 43-67.

Either a reduced and/or a higher number is considered derived by different authors (e.g. Stewart, 1986;1986a; Howes, 1983; Schaefer, 1987; Ferraris and Fernandez, 1987).

Lundberg (1982) and Skelton (1981) considered that lower (Trogloglanis) and higher (Gephyroglanis sclateri) numbers of vertebrae were associated with body size - a phenomenon termed pleomerism, recognised by Lindsey (1975). Essentially, fish vertebral number is correlated with maximum recorded body length. Of the ostariophysan groups investigated, Lindsey found high correlations in the Cyprinidae, Mochokidae and Ictaluridae.

I have compared (Table 4) the range of total vertebrae in Australo-Papuan ariids against maximum recorded SL. Whereas many species appear to exhibit pleomerism, about 30% do not. For example, novaeguineae, solidus and mastersi have more vertebrae than would be expected under Lindsey's rule and nella, midgleyi, species 1, thalassinus and possibly augustus have less. The low total count in *thalassinus* is attributed to the enlarged caudal vertebrae (Kailola, 1986a; Character 41). Species 5, with 60 vertebrae, may attain a much higher SL than 350mm (only 4 specimens known). Other than these, I offer no opinion on the reason(s) for non-correlation nor on the validity of Lindsey's rule.

Although carefully assessed on available information, I perceived no correlation between total or sectional vertebral count in ariids and habitat. Vertebral counts may be useful at the taxonomic level (e.g. between *leptaspis* and *midgleyi* [Kailola and Pierce, 1988], and *thalassinus* and *bilineatus* [Kailola, 1986a]) or in supporting recognised genera or species groups (e.g. *Nedystoma* has fewer vertebrae, *Cochlefelis* and *Hexanematichthys* have more).

Vertebral counts for a range of extralimital ariids is presented in Table 5.

83. Anal fin count

Primitive catfishes have 14-16 anal rays (+*Hypsidoris*: Grande 1987) and 11-15 (*Diplomystes*). Lundberg (1982) suggested that a lower count is relatively more primitive in the ictalurids. Ranges presented in Grande (1987) and Arratia (1987) support this polarity.

The most common anal ray count of the Australo-Papuan ariids lies between 16 and 22 (fig. 65). The taxon *novaeguineae* has an exceptionally high number of anal rays. Comparable numbers are only seen in the Western Hemisphere taxa *Bagre* and *Anemanotus*, among the Ariidae. Higher anal ray counts have been recorded for autapomorphic auchenipterids and pimelodids (Buckup, 1988; Ferraris and Fernandez, 1987) and are characteristic of some families (e.g. see Grande, 1987: Table 2).

84. Gill rakers

Differences in the gill raker number in fishes generally reflects diet (Lagler et al., 1962). Planktivorous fishes have more and slender rakers, whilst predaceous and omnivorous fishes have fewer and stout rakers. Generalised carnivory, assumed to be the more primitive diet, is widespread among primitive ostariophysans (Lundberg and Mago-Leccia, 1986). Roberts (1972) pointed out that most of the survivors of global archaic fish groups are efficient predators: apparently a better "survival" trophic adaptation in times of adverse environmental conditions. In contrast, planktivory has evolved independently several times (Fink and Fink, 1981). Extreme gill raker counts are probably derived (Lundberg, 1982).

Most of the Australo-Papuan ariids have a moderate or low gill raker count (9-22) on the leading edge of the first arch (fig. 66; Table 3). This correlates with the dominance of carnivory and omnivory in their diet (see also Roberts, 1978). In the predaceous species 1, species 5 and species 6, the rakers are stout, strong and well-spaced.

Five taxa (solidus, species 4, dayi, nox and novaeguineae) have more numerous (28-67) rakers. All but the enigmatic novaeguineae consume fine particles, such as suspended plant material and zooplankton, small insect larvae and fine detritus.

85. Pectoral ray count

Stewart (1986) believed that a higher number (11 or more) of pectoral rays is the apomorphic state. Conversely, Lundberg (1982) and Schaefer (1987) considered a lower count is derived. Lower counts of segmented rays (6-10) are found in most pimelodids (Stewart, 1986), diplomystids (Arratia, 1987), +Hypsidoris (Grande, 1987), ictalurids

(Lundberg, 1982; Taylor, 1969), some bagrids (Bailey and Stewart, 1984) and most loricariids (Schaefer, 1987). Tilak (1963) suggested there is a trend in catfishes towards reduction in the number of fin radials and associated rays.

The number of segmented pectoral rays ranges from 8-13 in the Ariidae. Lower counts (8-9) occur (e.g.) in *solidus* and *nox* and higher (12-13) in *argyropleuron*, *nella*, *polystaphylodon* and *spatula*. Rarely, the count differs in each fin and not infrequently, individuals of other taxa have 9 or 12 rays.

4.4 ADAPTIVE CHARACTERS

86. Form of the jaw teeth

In the vast majority of siluroids, the jaw teeth are simple, conical or tapering structures (Schaefer, 1987; pers. obs.). Alexander (1965:102) observed that the broad band of cylindrical jaw teeth (cardiform: *sensu* Lagler *et al.*, 1962) "in most unspecialised catfish" are suited for holding food; and Gosline (1973) believed that "grasping" dentition is ancestral. The teeth in +*Hypsidoris* are simple, sharp-tipped conical structures; those in diplomystids are close-set, elongate and conical with spatulate or pointed tips (Arratia, 1987; Roberts, 1973; pers. obs.). All of my outgroup specimens have slender, conical or sharp-tipped teeth except for *Pangasius* and the callichthyids which have fine, villiform teeth.

The range of premaxillary and dentary tooth type exhibited in the Ariidae is wide indeed: spatulate with short cusps (*Ketengus*), truncate (*Batrachocephalus*), slightly spatulate (*Cochlefelis*), strong and caniniform (*Hemiarius*, others), conical with blunt or sharp tips (several taxa), slender and sharp-tipped (e.g. argyropleuron), low and villiform (several), small and shallowly curved (Brustiarius) and molariform with age ("Cathorops") (fig. 67).

As has been observed by others (e.g. Fryer and Iles, 1972; Gosline, 1973; 1975) the type of dentition in fish is correlated with diet. I surmise therefore, that the more derived ariids possess a dentition other than the plesiomorphic condition, i.e. jaw teeth other than conical and slender have evolved in more than one direction, a phenomenon similar to that in the African Great Lakes cichlids where radial transformation from a common ancestor has occurred rather than a single, linear series (Fryer and Iles, 1972). This view is supported by study of ariid diet and feeding morphologies (Table 3) which range from general to specialised (e.g. molluscivory; lepidophagy). Sazima (1983) investigated lepidophagy, a habit performed by at least three Australo-Papuan ariids (cleptolepis - Roberts, 1978; proximus and utarus - this study) and possibly Arius felis (Hoese, 1966).

87. Number of jaw teeth/width of tooth bands

The presumably plesiomorphic siluroid dentition is of moderately broad bands of grasping, usually depressible teeth that frequently point inwards (Gosline, 1973; 1975). These teeth work the prey back into the mouth (Alexander, 1970) and, for large-mouthed catfishes employing a "sink" ingestion method, appear to be functionally appropriate. Gosline (1973) determined that feeding in catfishes is done primarily by suction, and described the "sink" system mechanism (see also Howes, 1983; Roberts, 1972). Examples of siluroids (including many ariids) having this dentition and feeding method are numerous.

As well as different tooth form, ariids differ in the relative abundance of teeth on the premaxilla and dentary. Of the Australo-Papuan taxa, spatula and danielsi, which have a very broad gape, also have the widest bands of teeth. The next widest band is in midgleyi, species 7 and latirostris, and so on (Table 3). Galeichthys, which feeds mainly on crabs and fish (Coetzee and Pool, 1985) has a broad band of premaxillary teeth. In latirostris, spatula and danielsi, adults have more series of teeth than do juveniles.

Most wide-mouthed ariids have 7 or more series of teeth, fish with small or moderately narrow mouths have from two (dayi) to 6-8 series. Five predaceous, wide-mouthed ariids however, have few (one to six) series of teeth (species 1, augustus, novaeguineae and species 5, and Hemiarius stormii), a condition which appears to contradict Gosline's (1973) and other authors' feeding theories. However, in four of these taxa, the teeth are non-depressible and wedge-shaped (less so in augustus). These fish must seize their prey, the few well-spaced series of powerful teeth being just as or more effective than are numerous series of grasping, slender teeth.

The "sink" feeding method may be adequate in itself for novaeguineae, which has the broadest mouth (50-62% HL) of all the Australo-Papuan ariids yet the smallest teeth (see also Character 88). The very wide-mouthed S.E. Asian ariids Ketengus and Batrachocephalus, with one to 6 series of stout and oblong teeth, do not compare with novaeguineae as in them the gill openings are moderately restricted and the jaws are thick.

Gosline (1973) argued that jaw teeth specialised in various ways for biting, shearing or scraping, rarely form more than a few rows (e.g. in characins). For example, the callichthyid catfishes have a narrow tooth band (pers. obs.) and the greatly modified loricariid teeth are presented as one group (Schaefer, 1987). Lagler *et al*. (1962) noted a higher number of teeth in predaceous fish and few to none in planktivorous fish.

Reduction in the number of series of jaw teeth is apomorphic in catfishes (Lundberg, 1970~~)~~, cited in Lundberg, 1982.. *Hypophthalmus* and *Trogloglanis* (Ictaluridae) lack teeth, an apomorphic condition in the gonorhynchiforms and cypriniforms (Fink and Fink, 1981).

My attempts to compare the number of premaxillary tooth series with length of the tooth band in Australo-Papuan ariids were unsuccessful because band curvature could not be discounted.

88. Mouth size and lip form

I accept Gosline's (1973) and Alexander's (1970) view that the mouth of the more generalised catfishes is relatively large compared to that of characins and cyprinids. Most ictalurids, ariids, diplomystids, +*Hypsidoris*, many pimelodids, silurids, schilbeids and bagrids have wide mouths, compared to the "relatively small mouths" of (e.g.) *Pseudodoras* (Alexander, 1965:102), auchenipterids (Mees, 1974) and callichthyids.

Alexander (1965:102), in believing the wide-mouthed condition in catfishes is advanced because it involves "extreme [head] depression", failed to recognise its independent correlation with diet. Thus *Arius*, *Diplomystes* and *Pimelodus* do not have "relatively small mouths" compared to that of *Pseudodoras*.

As with the gymnotoid *Rhabdolichops* (Lundberg *et al*., 1987) the mouth shape of *nox*, *solidus*, *dayi* and species 4 is almost quadrangular. In *nox* and *solidus*, the mouth is terminal, the lips thin, and there are few series of jaw teeth. These two species actively feed over the floodplain year-round and move in the middle water column (Coates, 1983). The fleshy lips of species 4 and *dayi* suggest a somewhat different feeding ecology (e.g. in the mud film above the substrate) (and see Characters 17 and 84).

Approximately half of the Australo-Papuan ariids have a mouth size 37% or more of HL (fig. 48). All of them are predaceous, some also omnivorous as juveniles. I consider the narrow-mouthed condition derived within the Ariidae and probably within the Siluroidei - where it has arisen independently in several lineages (*cf.* *Chrysichthys*, *Bagrichthys*, *Synodontis* and callichthyids with other bagrids, some pimelodids, doradids and silurids).

The mouth POSITION generally conforms to the phyletic transformation series of mouth size. In nearly all wide-mouthed Australo-Papuan ariids, it is terminal or subterminal (Table 3). (But note: the subterminal mouth of *thalassinus* juveniles is overshadowed by the produced snout of adults; and the longer upper jaw in *danielsi*, *spatula* and *macrorhynchus* makes the mouth inferior.) The jaw symphyses are elevated in some wide-mouthed ariids, e.g. *novaeguineae*, *midgleyi*, *armiger* and species 5.

In *carinatus*, *froggatti*, *crassilabris* and *conorhynchus* the small mouth is distinctly ventral. Such is often a feature of ground-feeding catfishes (Roberts, 1972; Gosline, 1975). The mouth is surrounded by thick, almost plicate, fleshy lips in *crassilabris*. The ictalurid *Trogloglanis*, loricarioids, some sisorids and some mochokids have a similar mouth and thick lips (Howes, 1983a; pers. obs.). Lundberg (1982) and Lagler *et al.* (1962) observed that these structures are well-suited to detritivory or feeding off sediment, the lips forming a "hood" over the food particles so preventing their being washed away.

Biting-type fish have unmodified, relatively thin lips. Lip form in Australo-Papuan ariids ranges from the "*crassilabris*"-type to thin and fleshy, moderately thick and firm, to very thin or reduced (e.g. *conorhynchus*, *macrorhynchus*).

89. Mobility of the jaw teeth

Fink (1981) recognised four types of tooth attachment in actinopterygian fishes. The Type 1 teeth (a primitive attachment mode in which the tooth is ankylosed to the tooth-bearing bone or tooth plate) through Types 2, 3 and 4 (in which collagen lies between the dentine and the bone, sometimes forming a hinge for tooth rotation). Possession of Type 1 attachment was largely correlated with a carnivorous or piscivorous diet (Fink, 1981). Depressible teeth occur in some taxa with Type 2 attachment mode, and always in taxa having Type 4 mode. Fink suggested that the predominant trend within the Actinopterygii has been to evolve depression mechanisms with Type 2 attachment rather than Types 3 and 4, which are ontogenetic modifications.

The Diplomystidae and most other catfishes (including ariids), have depressible jaw teeth. Generally, teeth on the autogenous tooth plates are non-depressible.

Although investigation of tooth attachment mode was beyond the scope of my study, I consider that in the ariids, where paedomorphic expression of tooth attachment predominates, fixed jaw teeth are the derived character state. This state is exhibited by species 1, species 5, *Hemiarius stormii* and *augustus* (Table 3); and is correlated with large mouth, predatory habit and macroscopic diet (see also Character 88).

90. Eye position and size

The usual siluroid eye position is superolateral. This supports the observation of Dullemeijer and Barel (1977) that the eye is a functionally dominant feature.

In many siluroids, there has been a trend for the eyes to shift to a superior position and Howes (1983) noted several unrelated siluroids having a ventrolaterally situated eye: *Hypophthalmus*, *Ageneiosus*, some species of *Auchenipterus* and *Pangasius*; also *Ompok* and *Wallagonia* (Siluridae) (pers. obs.).

A ventrolateral eye is derived in the Ariidae. Examples are *novaeguineae* and *"Cathorops" hypophthalmus*. The apparently low-placed eye in other ariids (e.g. *argyropleuron*, *danielsi*) is directly related to low head height (fig. 47). The eye is usually positioned in the second quarter of the head length. In species 5 it is in the first quarter and in species 3, *bilineatus*, *argyropleuron*, *nella*, *polystaphylodon* and species 4 it is approximately midway between snout tip and gill opening.

Eye SIZE varies both inter- and intraspecifically and there is an overall trend in the Australo-Papuan ariids for negative allometry in eye size. However, in species 5, *augustus*, *spatula*, species 1 and species 7 the eye is consistently small relative to head length at all growth stadia (mean $</=$ 11% HL), suggesting that these taxa inhabit waters with fast currents (Roberts and Stewart, 1976). The taxa *berneyi*, *dayi* and species 3 have the largest eyes (mean $>/=$ 20% HL) (fig. 68).

91. Papillae on rear of the gill arches

Roberts (1978) recorded papillae on the gill arch posterior aspect in two northern New Guinea ariids, velutinus and solidus. Other taxa exhibiting this condition are species 4, crassilabris, conorhynchus, nella and macrorhynchus.

Orobranchial papillae appear to have evolved independently in several catfish lineages. They occur in diplomystids, the Nematogenyidae (Howes, 1983a; Arratia, 1987), some pimelodids (Stewart and Pavlik, 1985; Stewart, 1986) and several extralimital ariids. A distinct arrangement of the papillae and fleshy ridges form a synapomorphy for three pimelodid genera (Stewart and Pavlik, 1985). Higuchi (1988) found that gill arch papillae in some doradid taxa are provided with taste buds. Stewart suggested the papillae aid in sifting food items from sediment sucked into the buccal cavity, a function probably true in the ariids.

Roberts'(1972) observation that planktivorous and carnivorous fishes have smooth palate and gill arches compared to detrital feeders applies to the ariids. However, I suspect that some omnivorous and predaceous taxa possess papillate surfaces at juvenile stadia only, these fleshy, sifting structures being resorbed(?) when individuals move away from the substrate into different feeding regimes (and see Character 17). Dietary changes with growth in catfishes have been noted for Ictalurus, Bagrus (Alexander, 1965) and midgleyi in Lake Argyle, Western Australia (Kailola and Pierce, 1987).

92. Gut shape

The ariid stomach is invariably rectangular-ovate, lying along the body. The intestine originates from the posterior LHS, ascends and loops over the oesophagus-stomach connection before descending along the RHS. I examined the Australo-Papuan taxa with a view to recognising differential gut forms following the lead of Merriman (1940) in two Western Hemisphere ariids. Difference in intestinal convolutions has been used successfully to distinguish other fish groups (e.g. Catostomidae - Berner [1948]; Scombridae - Collette and Russo [1984]).

Presence/absence of food in the gut and quality of specimen fixation affected the appearance of this character however. Nevertheless, both more- and less-convoluted gut forms are exhibited by the Australo-Papuan ariids (fig. 69): very convoluted in *thalassinus* and *bilineatus*; almost straight in *nella*, species 1 and species 5 (examples).

Roberts (1972) discussed the connection between gut form and diet in fishes: thin-walled and straight in planktivores and carnivores, convoluted in detritivores, etc. The intestine is shorter in predaceous fishes, elongate and arranged into many folds in predominantly herbivorous species (Lagler *et al.*, 1962; Fryer and Iles, 1972). It has a large mucosal surface in carnivorous and omnivorous cyprinids (Hofer, 1988).

4.5 SUMMARY OF CHARACTERS, WITH CRITICAL COMMENT ON RELATIVE VALUE

Characters used in phylogenetic analysis

1. Oral incubation-low fecundity
2. Mesocoracoid presence
3. Epioccipital extension
4. Aortic tunnel condition
5. Supraoccipital-nuchal plate articulation
6. Lateral ethmoid-frontal articulation
7. Otolith size and auditory bulla
8. Elastic Spring Apparatus
9. Form of the Mullerian Ramus
10. Subvertebral cone presence

The first 10 characters support family definition.

11. Subvertebral cone shape
12. Development of 4th neural spine-epioccipital flanges
13. Situation of first pharyngobranchial
14. Development of posterior cleithral process
15. Eye covering
16. Extent of gill opening/membrane adhesion
17. Development of buccopharyngeal pads or flaps
18. Mesethmoid shape
19. Shape of the nasal bone
20. Shape of the lachrimal
21. Vomer shape
22. Size of mandibulary pores
23. Epioccipital development
24. Extrascapular development
25. Size of temporal fossa
26. Metapterygoid position
27. Metapterygoid-hyomandibular suture length
28. Skull ornamentation
29. Shape and position of adipose fin
30. Barbel number

This and Character 37 were included with a view to assessing the family overall, as all New Guinea and Australian ariids have (only) 3 pairs of barbels.

31. Position of the barbels
32. Lateral line direction at tail base
33. Shape of the swimbladder. This may be correlated with habitat.
34. Female ventral fin pads
35. Vomer dentition
36. Stability of vomerine tooth patches
37. Infraorbital number
38. Peritoneal colour
39. Buccopharyngeal cavity colour
40. Secondary hypurapophyses
41. Size of the caudal vertebrae
42. Size of the nuchal plate. Autapomorphic within New Guinea and Australian ariids but represents a synapomorphy in the family.
43. Possession of posterior gill rakers

Characters 44, 45 and 56 support family definition.

44. Ventral ray number and musculature
45. Caudal element number
46. Posterior dorsomedian fontanelle length
47. Shape of this fontanelle
48. Size of the frontals
49. Extent of laminar bone over anterior vertebrae
50. Palate dentition
51. Palate tooth plate position
52. Presence of teeth on tooth plates
53. Fin spine thickness
54. Branchiostegal number
55. Length of the abdominal cavity
56. Scaleless body
57. Reduction in gonad size

Characters not employed

58. Pectoral girdle
59. Caudal skeleton
60. Hyomandibular articular facet
61. 5th parapophyses
62. Pelvic girdle shape
63. Urohyal shape
64. Otoliths
65. Weberian Apparatus
66. Axillary pore
67. Parasphenoid alary processes
68. Ossification
69. Premaxillary thickness
70. Lateral ethmoid shape
71. Palatine facet length
72. Supraoccipital shape
73. Uncinate process
74. Chambered fin spines
75. Barbel form and length
76. Snout crescent
77. Unculi?
78. Lateral line form

Characters 63, 68, 70, 72, 73 and 78 may have contributed to a sound phylogenetic reconstruction.

79. Head height and body shape
80. Fin filaments
81. Caudal fin shape
82. Vertebral number
83. Number of anal fin rays
84. Gill raker number
85. Number of pectoral fin rays

In addition to the following characters, numbers 58, 75, 77?, 81 and 84 include ecologically adaptive features.

86. Form of the jaw teeth
87. Number of jaw teeth series, width of tooth band
88. Mouth size and lip thickness
89. Tooth mobility
90. Eye position
91. Papillae on the gill arches
92. Gut shape

5. PHYLOGENETIC RECONSTRUCTION OF AUSTRALO-PAPUAN ARIIDS

5.1 INTRODUCTION

Patterns of evolutionary relationship among the Australo-Papuan ariids were inferred using phylogenetic methods of reconstruction outlined in Chapter 3. Parsimony was invoked. The homology of characters was carefully assessed and 57 were employed in analyses. Polarity was determined largely by comparison with an outgroup comprising other siluroids, ostariophysans and primitive teleosts. This assessment was supplemented by ontogenetic transformation series and character trends including those exhibited by extralimital ariids.

Many of the 57 characters are osteological but general morphological and functional features were also considered. Meristics and correlated characters were generally avoided (Chapter 4).

5.2 METHODS

5.2.1 Analysis

Cladistic analysis was performed using the programme PAUP (Phylogenetic Analysis Using Parsimony), version 2.4.1. This programme was written by D.L. Swofford (Illinois Natural History Survey) and made available for IBM computers (Swofford, 1986). Other packages available included PHYLIP (Phylogeny Inference Package) written by J. Felsenstein (University of Washington). Although it can handle more OTU's than can PAUP, PHYLIP was not immediately useable on my data set. It requires preliminary rearrangement of the data matrix to permit analysis of unordered characters and other than binary characters; and tree construction relies on the order in which OTU's are present in the infile.

PAUP is a programme for inferring phylogenies using numerical methods. Maximum parsimony is used to estimate "Wagner trees" (Kluge and Farris, 1969). There are no *a priori* restrictions on the nature of permissible character state changes. The preferred tree is the shortest, demonstrating the minimum number of "evolutionary steps" (i.e. changes from one character-state to another). In minimizing the total number of steps, the number of "extra" steps (homoplasies) are also minimized. The shortest Wagner tree thus equates with the most parsimonious cladogram or phylogenetic reconstruction.

Because I believe that in evolution homoplasies frequently occur, I have not performed analyses using the Camin-Sokal method (which prohibits reversals from derived to ancestral character-states) or the Dollo method (which permits a character to arise only once) (Camin and Sokal, 1965; Farris, 1977).

Multistate character coding (letters) was performed. Characters were either *ordered* (i.e. based on an hypothesis of transformation from ancestral to derived morphology) or left unordered (i.e. when an hypothesis of character-state transformation could not be made objectively). PAUP is able to handle unordered characters, assuming that all possible character-state changes are equally likely. By leaving characters as *un*ordered, the results are in no way biased; i.e. by deciding *a priori* a possible incorrect transformation series which would influence the final outcome. Its ability to deal with such unordered characters, plus being able to treat missing data either because it is unknown or is inapplicable (e.g. presence or absence of teeth on palatal tooth plates in a species which lacks palatal tooth plates) made PAUP a particularly appropriate programme for my study.

In its compilation, PAUP performs an exhaustive addition sequence whereby each OTU or Operational Taxonomic Unit (Camin and Sokal, 1965) is connected in turn to each branch and the resulting tree optimized. After trying all possible branches and computing the length required for the resulting tree in each case, the OTU is added to the branch which minimizes the tree length at that step. This process is repeated sequentially until all OTU's have been connected. Briefly, in LOCAL branch swapping, each interior branch of the tree is rearranged. In GLOBAL swapping, each possible subtree is removed from a tree and reinserted at all other positions on the tree. After completion of each rearrangement, the tree length is recomputed to find a shorter (i.e. more parsimonious) tree.

The one disadvantage of PAUP is its inability to handle more than 50 OTU's. As my initial matrix comprised 78 taxa (34 ingroup, 20 extralimital ariids, 24 outgroup), this necessitated running series of analyses based on mixes of taxa.

A matrix (Table 6) was input to series of LOCAL and GLOBAL branch swapping routines, with the maximum number of equally parsimonious trees set at the upper limit of 100. After assessing results of different analyses, the character matrix was modified in an attempt to eliminate the more homoplastic characters.

The MULPARS option was invoked to discover multiple equally parsimonious trees via branch swapping (the exhaustive ALLTREES option could not be invoked with such a large number of OTU's). During the MULPARS, all equally short trees are saved and input to the branch swapping procedure in turn until no reduction in tree length is achieved.

Series of analyses were performed using the different rooting methods MIDPOINT, OUTGROUP and LUNDBERG. For root = MIDPOINT, the tree

Table 6. Character matrix used in reconstructing the hypothesised phylogeny of Australo-Papuan ariidae.

		CHARACTERS and CHARACTER STATES
		000000000111111111122222222223333333333444444444455555555
OTU's		123456789012345678901234567890123456789012345678901234567
Ingroup		
1	species 1	BCCCBBBBCAABBBAAADBAAAAAADCBBACBC-AAABBBBBCAABAAAAAABDABB
2	ARMIGER	BCCCBBBBCACBBDAAACBAAAAAABBBBACBAAAAABBBBBCAACACBAAADCBBB
3	PROXIMUS	BCCCBBBBCABABBACABAAABBAABBACABBCAAAABBBBBCAAA-ABAAAACBBB
4	MASTERSI	BCCCBBBBCABABBABABBAABAACBBABABAAAAAAABBBABAAA-ABAAABCABB
5	LATIROSTRIS	BCCCBBBBCAAABBAABBBAABAAABBABABBAAAAABBBBBBAABABBAAAACBBB
6	LEPTASPIS	BCCCBBBBCAAABBAAABBAABAAABBABABBAAAAABBBBBCAAA-ABAAAACABB
7	MIDGLEYI	BCCCBBBBCAAABBAAABBAABAAABBABABBAAAAABBBBBBAABAABAAAACBBB
8	AUGUSTUS	BCCCBBBBCAABBBAAABBAAAAAABBABACBAAAAABBBBBCAABABBAAAADBBB
9	species 2	BCCCBBBBCAAABBABABBAABAAABBABABBAAAAABBBBBBAABAABAAAACBBB
10	GRAEFFEI	BCCCBBBBCAAABBABABAAABAAABBABABBAAABABBBBBAAABAABAAAACABB
11	BERNEYI	BCCCBBBBCAAABBACBBAAABAAABBABABBAAABABBBBBAAABAABAAAACBBB
12	species 3	BCCCBBBBCAAABBABABAAABAAABBABABBAAB-ABBBBBAAABAABAAACCBBB
13	species 4	BCCCBBBBCABABDADCAABABAAADABCAAAAAB-ABBBBBAAACACCAABDCBBB
14	FROGGATTI	BCCCBBBBCACCCAADAAAAACABABBAAAAAABB-ABBBBBAAABABBAAABBBBB
15	CARINATUS	BCCCBBBBCACCCAADAAAAACABACBAAAAAABAAABBBBBAAABABBAAABCBBB
16	CRASSILABRIS	BCCCBBBBCACCBAADAAAAACABACABAAABABB-ABBBBBAAACACBB--ACCBB
17	DANIELSI	BCCCBBBBCAAABBAAACBAACAAABBAAACBA-AAABBBBBCAACAABAAAACBBB
18	SPATULA	BCCCBBBBCAABBBAAACBAACAAABBAAACBAAAAABBBBBCAACAABAAAACBBB
19	DAYI	BCCCBBBBCACBBDADCBAAABAACBACBAAAABB-ABBBBBAAACBCCB--DCCBA
20	NOVAEGUINEAE	BCCCBBBBCACBADBAADCCAAAACBBCBACAABB-DBBBBBAAACBCCAAACCCBA
21	species 5	BCCCBBBBCABAABBAADCBAAAAADBBCACBD-AAABBBBBCAABAAAAAAEDABB
22	THALASSINUS	BCCCBBBBCAABBBABAFBAABAAABBACABCCAAAABBBABCAABAABAAAABABB
23	BILINEATUS	BCCCBBBBCAABBBABABBAABAACBBACABCCAAAABBBBBCAABAABAAAABCBB
24	ARGYROPLEURON	BCCCBBBBCABABBACBAABBBAAADBACAACCAB-ABBAABBAABABCABAACBBB
25	POLYSTAPHYLODON	BCCCBBBBCABABBACBCABBBBAADCABAACB-B-ABBBABBAABABCABAACABB
26	NELLA	BCCCBBBBCAAABBACBCABBBBAADCABAACB-B-ABBBABBAABABCABAACABB
27	species 6	BCCCBBBBCABBBBABABAAABBAABBBAABBA-AAABBBBBCAABABBAAABCABB
28	NOX	BCCCBBBBCABABDAACBBAABAACCCBCABBAAABABABBBCAABABBAAADCCBB
29	SOLIDUS	BCCCBBBBCABABBAAACBAABAACCCBCABBAAABABABBBCAABABBAACACBBB
30	species 7	BCCCBBBBCABBBBABABBAABAAABBABABBA-B-ABBBBBBAACACBAAAACBBB
31	VELUTINUS	BCCCBBBBCABABBABBBBAABAAABBABABBAAB-ABBBBBBAACABBB--ACBBB
32	TAYLORI	BCCCBBBBCABA-BABBB--A-AAA--ABABB-AB-ABBBBBBAACBCBB--ACBBB
33	MACRORHYNCHUS	BCCCBBBBCABABBACAECBABAAACCACACBAAB-ABBBBBBAACAACB--DCBBB
34	CONORHYNCHUS	BCCCBBBBCA-B-AADAAA-----A--BAAAB--B-ABBBBBAAA----B--BCCBB
Extralimitals		
35	ARIUS	BCCCBBBBCABABBABBAAAABAABCBABABBAAAAABBBBBAAABABBAAAACBBB
36	GALEICHTHYS	BCBBABBBCAABBCABABAAAAAAABBABABAA-AAABBBBBAAABBBAAAADCBBB
37	ANCHARIUS	-C-ABAA-AB---BADAACBAC---BCBAABB--B--BBBBBCAAA---B--C-BBB
38	ARIOPSIS	BCCCBBBBCABA-BACBBAAABAABCBABABB-AAAABBBBBCAABABBAAAACBBB
39	BATRACHOCEPHALUS	BCCCBBBBCABABBACADCCABAACDAABC-CA-B-ABBBBBAAAA-BAAAABBBBB
40	OSTEOGENEIOSUS	BCCCBBBBCABABDAAADBCABAABDABBB-CCBB-ABBBBBAAABACBAAADCBBB
41	GENIDENS	BCCCBBBBCAAABDACAAAAABAABCBAAABA--B-ABBBBBBAABABBAAAACBBB
42	BAGRE	BCCCBBBBCAACBDAB-DCCAABAACACCD-C--AA-BBBBBCAAA-ABAAADCCBB
43	HEXANEMATICHTHYS	BCCCBBBBCAAABBABABBAABAACBBABABBAAAAAABBBACAAA-ABAAABCABB
44	HEMIPIMELODUS	BCCCBBBBCACBBDBDCAAAABAACCBBAAACAAB-BBBBBBAAACBCCB--DBCB-
45	CEPHALOCASSIS	BCCCBBBBCACBBDBDCAAAAAAABCCBAAAB--B-BBBBBBCAACBCCAAAACBBB
46	CATHOROPS	BCCCBBBBCACCBDADBCCAAABBCCBBCABB-BB-ABBBBBAAAA-CDAAAACCB-
47	AILURICHTHYS	BCCCBBBBCAABBDA--CBBA-BABBABBD--AAAACBBBBBCAABBABAAADCBBB
48	SCIADEICHTHYS	BCCCBBBBCAA--BABABAAA-BAA--ABABBABAA-BBBBACAAA-BBAAAB-AB-
49	GUIRITINGA	BCCCBBBBCAAABBACABAAAB-ACCBABABB--AAABBBBBAAAA-ABAAAACBBB
50	G. PLANIFRONS	BCCCBBBBCAAABBABABBAAB-ABBBABABB--AAABBBBBAAAB-AAAAAACBBB
51	ARIODES ARENARIUS	BCCCBBBBCAB--BABB----------ABABBAA---BBBBBAAA----AAAACBBB
52	KETENGUS	BCCCBABBCABABDADACBCACAABDABBABCA-B--BBBBBCAAA--BB--ACCBB
53	HEMIARIUS	BCCCBBBBCABBBBAAADAAAAAAACBBAABBA-AAABBBBBCAACBCAAAABCBBB
54	A. TRUNCATUS	BCCCBBBBCABACBADACAABCBABBABBAACC-B-ABBBBBAAABABAAAABCBBB
Outgroup		
55	RITA	ABAAAAAABB-BAAACAAAAAAABCAABBF-A--AACBBBBBCBBA---B--ADCB-
56	PIMELODUS	AAABBAAABB-ABBAAADBB-BAABABBAACA--B-ABBBBBCBBA---B--ACCB-
57	RHAMDIA	AAAAAAAACB-CBBABBBBCAAAABACBAABA--B-ABBBBBCABA---B--AECB-
58	ANADORAS	ACCAAAABBB--AABDAC-DACABCA-ACEBA--B-ABB-B--BBA---B--BE-A-
59	PTERODORAS	ACCAAAABBB---ABDAC-DACABC--AAABA--B-ABB-B--BBA---B--BEAA-
60	NEOSILURUS	AAAAAAAAAB-BADABABBDACABCACB-EAA-BAAEBBBBBCDFCA--B--AECB-
61	MYSTUS	AAAAAAAAAB-C-D-A-BB--A--BBBBBABA--AACBBBBB-ABCA--AAAAEBB-
62	SCHILBE	AAAAAAAACB-B-D---AA-AA--BAAC------AA----BB--BBA--AAADFCB-
63	PANGASIUS	AAAA-BA-AB-A--AA-DA-A-AA-BA-CD----AA-BA--BAAB-------AF-B-
64	CHRYSICHTHYS	AAAAAAAAAB-C-B---A--ABAACACA------AA----BB-ABBB--B--A-BB-
65	BAGROIDES	AAAAAAAACB-C-A---A--A-AACBCBAE-A--AA---BBB-ABBA--B--BDCB-
66	SYNODONTIS	AACAAAABAB-B-A---A--AB--CBCAAA----B----BBA--BA---B--B-C--
67	BAGRUS	AAAAAAAAAB-C-B-A-CA-ABA-CBC-----A-AAC--BBB-ABBA--AAADFCB-
68	ICTALURUS	AAAAAAAABB-C-B---AA-A-A-CBBB-----BAA---BBB-CBCA--B--ADBB-
69	NOTURUS	AAAAAAAABB-A-D---A--ABABCBAC-----BAA---BBB-CFBA--B--ACCB-
70	PYLODICTUS	AAAAAAAABB-B-D---A--ABA-CBAB-----BAA---BBB-EBBA--B--ACAB-
71	PARASILURUS	AAAAAAAABB-B-D-A-ABCAAABBBBC------AAB---BB-DBBA--B--EFCB-
72	OMPOK	AAAAA--A-B---DBAA------------D-A--B--BB--BCBB----AAAEF-B-
73	SILURICHTHYS	AAAAA--A-B---DBAA------------D-A--B--BB--BCBB----B--E--B-
74	WALLAGONIA	AAAAAA-A-B---DBAA------------B-A--B--BB--BCEB----AAAEF-B-
75	DIANEMA	AAA----A-B---CAD-----------CBB-A-BB--BB---AAC----B--CA-A-
76	BROCHIS	AAA----A-B---CBD-----------CBB-A-BB--BB---AAC----B--DA-A-
77	DIPLOMYSTES	AAAAAAAAAB-AAAABAAAD--BACBABAB-AABAAEBBBBBAAEBA--B--AEABB
78	HYPOSTOMUS	AAAA-AAA-B----A--C-C-CABCCB-CB---BB-C--BBB-FDA---B--BACA-

was rooted midway on the longest path connecting any pair of OTU's; for root = OUTGROUP, the outgroup members form a sister group to the ingroup members; at root = LUNDBERG, the shortest unrooted ingroup tree is subsequently rooted at the position in which an hypothesised ancestor or an outgroup would join the tree.

Use of the APOLIST option (in preference to CSPOSS as my data set was very large) gave a list of the apomorphies for each node of cladograms. This option, helpful in detecting incongruence, was not invoked for all analyses.

In most analyses, all characters were equally weighted. A weight of 10 for one character (number 1, oral incubation) all other characters unity, was applied in one series of analyses. In two series of analyses, an HTU or Hypothetical Taxonomic Unit (Farris, 1970) was defined.

Adams' and strict consensus trees (Swofford's CONTREE programme) were calculated on equally parsimonious trees generated by each analysis as a means of determining congruence between the computed classifications.

In seeking to reconstruct the most parsimonious hypothesised phylogeny of the Australo-Papuan ariids, several intermediate objectives presented themselves before final analyses could be performed. These particularly emanated from the number of OTU's involved (PAUP's upper limit is 50), and included identifying sister groups of taxa, establishing best "mixes" of outgroup taxa and recognising the more labile (homoplastic) characters. The steps and their outcomes, are explained in 5.5.

5.2.2 Format

Letters A, B, C etc. code the states of the 57 characters used. The complete data matrix for 78 OTU's (ingroup, outgroup, extralimital ariids and all characters) is presented as Table 6. The letter "A" is reserved for the supposed plesiomorphic character state except when it is "B" in Characters 9, 10, 22, 31, 34, 38, 39, 40, 55, 56 and 57; and "C" in Character 46. Characters 9, 22, 43, 44, 45 and 54 are phenetically coded.

The two subspecies of the ingroup taxon midgleyi are represented in the analyses as a single OTU, as they do not differ in any infile character.

I have used Chernoff's (1986) format to depict the cladograms and state their construction. Nodes of each tree are numbered so that branches can be defined; and the derived character states in each cladogram are listed for each branch. Autapomorphies defining a branch (e.g. node number, OTU) are noted in the systematic account (Chapter 6).

5.3 COMPARATIVE MATERIAL

Specimens are listed by family, species, catalogue number (if applied) and locality. Skeletal preparations are either alizarin-stained or dry.

5.3.1 Ingroup ariids

Material referred to are those listed in Chapter 2 (Osteology) and the wider set upon which the systematic accounts are based (Chapter 6).

5.3.2 Extralimital ariids

A complete list of extralimital ariids examined during the whole study is given as Appendix A. Only those directly utilised during phylogenetic analysis are listed here. Abbreviations and collection acronyms are stated in Chapters 1 and 6.

Ailurichthys marinus: 2, C&S, Biloxi Bay, Mississippi, 79 and 122 mm SL (type species of *Ailurichthys* Baird and Girard);

Ancharius fuscus: 1, C&S, MNHN 1966-897, Madagascar, 131 mm SL (type species of *Ancharius* Steindachner);

Ariodes arenarius: 1, ZMB 3001, China, type specimen of *Ariodes* Müller and Troschel, 254 mm SL;

Ariopsis felis: 1, dry skeleton, unreg., off South Carolina, USA, 260 mm SL; 1, dry skeleton, UMMZ 179147, Gulf of Mexico, 192 mm SL (type species of *Ariopsis* Gill);

Arius arius: 2, C&S, LACM 38129-95, Sind, Pakistan (type species of *Arius* Valenciennes and *Pseudarius* Bleeker);

Arius truncatus: 1, C&S, unreg., CAS 32710, Perak, Malaysia. 224 mm SL;

Bagre bagre: 1, C&S, unreg., Sao Paulo, Brazil, 111 mm SL (type species of *Bagre* Cloquet);

Batrachocephalus mino: 1, C&S, ex LACM 38132-62, Sind, Pakistan, 225 mm SL (type species of *Batrachocephalus* Bleeker);

"*Cathorops*" species: 1, C&S, unreg., Sao Paulo, Brazil, 131 mm SL;

Cephalocassis melanochir: 1, C&S, ex CAS 49426, Kapuas River, Borneo, 166 mm SL (type species of *Cephalocassis* Bleeker);

Galeichthys feliceps: 1, C&S, unreg., southern Africa, 280 mm SL (type species of *Galeichthys* Valenciennes);

Genidens genidens: 1, C&S, unreg., Sao Paulo, Brazil, 123 mm SL (type species of *Genidens* Castelnau);

Guiritinga barba: 1, C&S, unreg., Brazil, 179 mm SL (type species of *Guiritinga* Bleeker);

Guiritinga planifrons: 1, C&S, unreg., Sao Paulo, Brazil, 138 mm SL;

Hemiarius stormii: 2, C&S ex ANSP 60720, Thailand, 81 and 83 mm SL (type species of *Hemiarius* Bleeker);

Hemipimelodus borneensis: 1, C&S, ANSP 60710, Bangkok, Thailand, 106 mm SL; 2, C&S, ex UMMZ 181175, Mekong River, Cambodia, 122 and 123 mm SL (type species of *Hemipimelodus* Bleeker);

Hexanematichthys sagor: 2, C&S, ex CAS SU27734, north Borneo, 143 and 233 mm SL (type species of *Hexanematichthys* Bleeker);

Ketengus typus: 2, C&S, ex ANSP 60704, Thailand, 88 and 113 mm SL (type species of *Ketengus* Bleeker);

Osteogeneiosus militaris: 1, C&S, unreg., Surabaya, Java, 285 mm SL (type species of *Osteogeneiosus* Bleeker).

Sciadeichthys emphysetus: 1, ZMB 2990, type species (?) of *Sciadeichthys* Bleeker, 320 mm SL.

5.3.3 Outgroup taxa

BAGRIDAE - *Bagroides macropterus*, 1, dry skeleton, UMMZ 201686-S, Thailand, 227 mm SL; *Bagrus docmac*, 1, dry skeleton, UMMZ 187332-S, Paraguay, SL not stated; *Chrysichthys auratus*, 1, dry skeleton, UMMZ 210275-S, Egypt, 176 mm SL; *Mystus aor*, 1, dry skeleton, Bangladesh, 293 mm SL; *Mystus* species, 1, C&S, unreg., Surabaya, Java, 130 mm SL; *Rita chrysea*, 6, of which 121 mm SL spec. C&S, ex CAS 54540, Orissa Province, India; *Rita hastata*, 2, CAS 34868, Maharastra Province, India; *Rita kuturnee*, 2, CAS 48798, Andrha Pradesh, India; *Rita parvimentata*, 1, CAS SU41044, Andrha Pradesh, India; *Rita rita*, 11, of which 85 mm SL spec. C&S, CAS 34866, Hugli River, India.

CALLICHTHYIDAE - *Brochis splendens*, 1 specimen; *Dianema urostriata*, 1 specimen; *Dianema longibarbis*, 1 specimen.

DIPLOMYSTIDAE - *Diplomystes chilensis*, 1, CAS 45718, Chile; 1, CAS SU23963, Chile.

DORADIDAE - *Anadoras grypus*, 1, C&S, ex USNM 284601, Brazil, 80 mm SL; *Pterodoras* species, 1, C&S, ex USNM 257988, Venezuela, 82 mm SL.

ICTALURIDAE - *Ictalurus punctatus*, 1, dry skeleton, UMMZ 169030-S, Missouri, 265 mm SL; *Noturus flavus*, 1, dry skeleton, UMMZ 189178-S, Michigan, 232 mm SL; 1, dry skeleton, UMMZ 194599-S, Michigan, 148 mm SL; *Pylodictus olivaris*, 1, dry skeleton, UMMZ 169029-S, Missouri, 434 mm SL.

MOCHOKIDAE - *Synodontis macrostigma*, 1, dry skeleton, UMMZ 200089-S, Kafue River, Zambia, 125 mm SL.

PANGASIIDAE - *Pangasius sutchi*, 1 specimen.

PIMELODIDAE - *Pimelodus clarias*, 1, C&S, ex USNM 258185, Venezuela, 79 mm SL; *Rhamdia cabrerae*, 1, C&S, ex USNM 114359, Guatemala, 101 mm SL; *Rhamdia quelen*, 1, dry skeleton, UMMZ 207348-S, Paraguay, SL not stated.

PLOTOSIDAE - *Neosilurus* species, 2, C&S, unreg., Kimberley area, NW Australia, 81 & 93 mm SL.

SCHILBEIDAE - *Schilbe mystus*, 1, dry skeleton, UMMZ 200154-S, Kafue River, Zambia, 170 mm SL.

SILURIDAE - *Ompok leiacanthus*, 1 specimen; *Parasilurus asotus*, 1, dry skeleton, UMMZ 187595-S, Lake Biwa, Japan, 145 mm SL; *Silurichthys phaiosoma*, 1 specimen; *Wallagonia miostoma*, 1 specimen.

5.4 STATEMENT OF CHARACTER POLARITIES

1. Oral incubation - low fecundity

A = oral incubation not practised;

B = oral incubation practised.

2. Mesocoracoid

A = mesocoracoid present;

B = mesocoracoid incomplete;

C = mesocoracoid absent.

3. Epioccipital extension

A = epioccipital reduced (i.e., not produced posteriorly);

B = epioccipital moderately produced;

C = epioccipital much produced.

4. Aortic tunnel

A = open aortic canal at all stadia (fig. 45);

B = aortic canal partially closed in adult;

C = aortic canal completely covered to form a tunnel in all stadia beyond mouth juveniles.

5. Supraoccipital - nuchal plate articulation

A = supraoccipital - nuchal plate connection interrupted by a supraneural;

B = supraoccipital articulates directly with nuchal plate.

6. Lateral ethmoid - frontal articulation

A = single lateral ethmoid - frontal articulation;

B = at least dual articulation.

7. Otolith size and auditory bulla

A = moderate to small otolith and bulla;

B = enlarged otolith and bulla.

8. Elastic Spring Apparatus (ESA)

A = ESA absent or independently derived;

B = ESA present, homologous structure.

9. The Müllerian Ramus

A = ramus tip expanded (fig. 45);

B = tip truncate to moderately attenuated, slightly curved;

C = tip very attenuated, well curved.

10. Subvertebral cone

A = subvertebral cone present;

B = cone absent.

11. Subvertebral cone shape

A = low subvertebral cone (fig. 17A);

B = moderately elevated (fig. 17B);

C = well elevated, strong (fig. 17C).

12. 4th neural spine - epioccipital flange

A = low ridges or laminae (fig. 38A);

B = moderately elevated ridges (fig. 38D);

C = well-elevated to high laminae or flanges (figs 19B; 46).

13. First pharyngobranchial

A = first pharyngobranchial situated close to distal end of epibranchial, usually slender (fig. 33A);

B = first pharyngobranchial situated along shaft of epibranchial or near its angle (fig. 32A,B);

C = first pharyngobranchial united with epibranchial at its angle, or missing (figs 32C, 33C).

14. Posterior cleithral process

A = process long (fig. 83);

B = process moderately long (fig. 185);

C = process fan-shaped;

D = process short (fig. 80).

15. Eye covering

A = naked eye - free (or almost) orbital rim;

B = subcutaneous eye.

16. Extent of gill opening

A = wide gill openings, branchiostegal membranes meeting well forward, overlapping (fig. 134B);

B = moderately wide gill openings, membranes not overlapping but meeting at a definite angle;

C = less wide gill openings, membranes meeting obtusely or concave;

D = restricted gill openings (fig. 84B).

Due to difficulty in determining states, B and C of the original matrix were combined in the 3rd through 5th series of analyses (section 5.5). Hence B and C became B, D became C.

17. Buccopharyngeal pads or flaps

A = gill arch pads and buccopharyngeal flaps low or poorly developed at adult stadia;

B = pads and flaps of moderate size in adults;

C = pads and flaps large and fleshy in adults (fig. 49).

18. Mesethmoid shape

A = divergent cornua with median, deep notch (fig. 4A);

B = divergent broader cornua with medium or shallow notch (fig. 4B);

C = broad cornua; mesethmoid anterior margin slightly convex to truncate with only remnant of a notch (fig. 4C);

D = convex, broad mesethmoid (fig. 4D);

E = prominent and blunt apex, cornua reduced; bone creased transversely (fig. 4E).

F = prominent and rounded apex, cornua broad; margin of bone fluted (fig. 4F);

19. Shape of nasal bone

A = simple and straight longitudinal tube, slightly expanded anteriorly (figs 5A,B,D);

B = curved tube, tending to parallel the curve of the mesethmoid neck and/or slightly bifurcate anteriorly (figs 5H,C);

C = irregularly shaped or very broad anteriorly or strongly bifurcate (figs 5E–G).

20. Shape of first infraorbital (lachrimal)

A = rhombic, with well-produced angles (fig. 22B);

B = flattened, angles extremely produced (fig. 22C);

C = rectangular with few obtuse angles (figs 22D,F);

D = other forms (e.g. *Diplomystes*: ref. Arratia, 1987).

21. Shape of the vomer

A = 'T'-shaped + variations (figs 12A,D);

B = conical, arms much reduced (figs 12B,C).

22. Mandibulary pores

A = (very) large openings (figs 23D,E);

B = moderate-sized openings (fig. 23A);

C = very small or concealed openings (fig. 23C).

23. Epioccipital

A = epioccipital not in skull roof (figs 10; 38C);

B = epioccipital invading skull roof (figs 19A; 38A,B).

24. Extrascapular

A = extrascapular apparent (fig. 38C);

B = extrascapular amalgamated with epioccipital (figs 11A; 19B).

25. <u>Temporal fossa</u>

A = fossa large and (moderately) prominent at all growth stadia (figs 38B,C);

B = fossa smaller or tending to reduce (fig. 10);

C = fossa much reduced or absent (especially in adults) (fig. 11B,C).

Because determination of states B and C were equivocal in material representing different growth stadia, they were combined as "B" in the 3rd through 5th series of analyses (section 5.5).

26. <u>Position of metapterygoid</u>

A = well before middle of quadrate (outgroup - e.g. pimelodid);

B = metapterygoid hind margin above middle of quadrate (fig. 26C);

C = metapterygoid hind margin in line with hind margin of quadrate (figs 26A,B);

D = metapterygoid hind margin well beyond hind margin of quadrate (fig. 26D).

27. <u>Metapterygoid - hyomandibular suture</u>

A = broad suture (fig. 26B);

B = moderately wide suture (figs 26A,C);

C = short suture (fig. 26D).

28. <u>Skull ornamentation</u>

A = granular - tuberculated - rugose skull surface (figs 100, 140);

B = smooth to striate (fig. 123A);

C = smooth (fig. 81E).

29. Shape and position of adipose fin

A = long-based adipose over all of anal fin, or base subequal to anal fin base length (7-22 [mean 15]% SL)(fig. 91);

B = moderately long-based adipose, over middle or anterior third of anal fin (6-16 [mean 10]% SL);

C = short-based adipose, over (middle), posterior half or third of anal (3-12 [mean 6.5]% SL)(fig. 118).

30. Barbel number

A = 3 pair (maxillary, mandibulary, mental);

B = 1 pair (maxillary only);

C = 1 pair (mandibulary only);

D = 2 pair (maxillary and mandibulary);

E = 4 pair;

F = 3 pair (nasal, maxillary, mandibulary).

31. Barbels - position

A = bases close together, aligned (or almost), near symphysis (fig. 107B);

B = bases moderately separated, slightly staggered;

C = bases widely separated, laterally on mandible, well staggered (fig. 130B).

32. Lateral line at tail base

A = lateral line slightly curved one way at tail base;

B = lateral line sharply turned up at tail base;

C = lateral line bifurcate at tail base.

Bleeker (1858) partly based his genus Hemipimelodus on the bifurcate nature of the lateral line.

33. Shape of the swimbladder

A = swimbladder ovate or rounded; or heart-shaped; or triangular; edges always smooth (figs 51; 52);

B = heart-shaped swimbladder, edges internally creased (fig. 53);

C = heart-shaped swimbladder, moderately to deeply scalloped (fig. 54);

D = long, oval-oblong, board-like swimbladder (fig. 55).

34. Pads on the ventral fins

A = pads present in some form;

B = pads absent.

35. Vomer dentition

A = vomerine teeth present (figs 20B,E);

B = vomerine teeth absent (figs 20A,D).

36. Vomer dentition - stability

A = vomer tooth patch shape stable;

B = vomer tooth patch shape unstable (fig. 57).

37. Infraorbitals

A = 4 infraorbitals (fig. 21A);

B = 5;

C = 6;

D = 7 (fig. 21B);

E = more than 7.

38. Peritoneal colour

A = dark peritoneum;

B = pale or slightly dusky peritoneum.

39. Buccopharyngeal cavity colour

A = dark buccopharyngeal cavity;

B = pale buccopharyngeal cavity.

40. Secondary hypurapophysis

A = secondary hypurapophyses flattened and 'teardrop'-shaped (fig. 40D);

B = not as above (figs 40A-C,E).

41. Size of caudal vertebrae

A = posterior or anterior caudal centra 50% or more smaller or larger than remaining centra.

B = no great disparity in size of vertebral centra, penultimate 10th centrum up to 40% wider than remaining centra;

Recognising that two character states were involved under "A", in the 3rd through 5th series of analyses it was subdivided to read:

A = last caudal centra much narrower than other centra (fig. 39F);

C = anterior caudal centra twice wider than remaining centra (fig. 39D).

42. Size of predorsal [= nuchal] plate

A = size of nuchal plate increasing with growth (fig. 140A).

B = nuchal plate not changing with growth;

43. Rakers on posterior or trailing edge of gill arches

A = rakers present on posterior face of all arches;

B = rakers absent from posterior face of first arch;

C = rakers absent from posterior face of first and second arches.

44. Ventral fin elements and pelvic musculature

A = 6 elements + specialised pelvic musculature;

B = 7 elements, no homologous musculature;

C = 8, ditto;

D = 11-13, ditto;

E = 9, ditto;

F = 5, ditto.

45. Caudal elements

C = 7+7;

A = 7+8;

D = 8+8;

B = 8+9;

E = 9+9;

F = variable (e.g. *Neosilurus*).

46. Posterior dorsomedian fontanelle length

A = fontanelle very small or absent (even in juveniles) (figs 7A, C);

B = fontanelle reducing during ontogeny (fig. 7B);

C = extensive fontanelle, always open (fig. 8).

47. Shape of posterior dorsomedian fontanelle

A = elongate-rectangular fontanelle (fig. 8C);

B = rounded or ovate-triangular fontanelle (figs 8A,B).

48. Size of the frontals

A = frontal tapered to moderately narrow posteriorly, anterior space reduced (adults) (fig. 7A);

B = frontal moderately broad posteriorly, anterior space moderately enlarged (fig. 2);

C = frontal broad posteriorly, anterior arms narrow, space enlarged (figs 8B,C).

49. Laminar bone on anterior vertebrae

A = deeply excavated medially, 4th-6th transverse process bases largely exposed or expanded (fig. 36A);

B = moderately excavated medially, 4th-6th process bases moderately-well covered (fig. 36B);

C = shallow excavation medially, 4th-6th process bases concealed (fig. 36E);

D = convex or truncate posterior margin (as in "*Cathorops*").

50. Additional palate dentition

A = tooth plates always present (fig. 20);

B = tooth plates absent (fig. 24C).

51. Position of palatal tooth plates

A = tooth plates at front of palate or anterolaterally (figs 20B-E);

B = tooth plates longitudinally arranged: small anterior patch, elongate posterior patch (fig. 20A).

52. Dentition on palate tooth plates in females

A = plates always toothed;

B = plates always untoothed (fig. 60D);

C = plates occasionally lacking (most) teeth.

53. Fin spine thickness

A = spines robust, moderately thick and strong; well-serrated; spine thickness increases with growth;

B = spines very thick, may be very rugose; sometimes internally chambered and/or flattened or broad;

C = spines moderately thin, but with strong serrae;

D = spines moderately thin with fine serrae;

E = very thin with few low serrae and somewhat flexible.

54. Branchiostegal number

A = 4 branchiostegals;

B = 5 branchiostegals;

C = 6 branchiostegals;

D = 7 branchiostegals;

E = 8-9 branchiostegals;

F = |9 branchiostegals.

55. Abdominal cavity length

A = precaudal vertebrae 39% or more of total vertebral number;

B = precaudal vertebrae 33-38% of total vertebral number;

C = precaudal vertebrae 32% or less of total vertebral number.

56. Naked body

A = some catfishes (doradids, loricarioids) possess bony plates or frequently toothed scutes on the body;

B = all ariids have a naked body.

57. Gonad reduction

A = reduced gonad size (fig. 61);

B = gonad "normal", bilobed.

5.5 RESULTS

Recapitulation: 57 characters; 34 ingroup, 20 extralimital and 24 outgroup OTU's.

Examples of infiles and results of series of analyses are listed. Throughout, consensus trees were based on between 100 and 200 equally parsimonious trees.

5.5.1 First series

Aim: to identify sister taxa within the ingroup and from there to reduce the number of ingroup plus extralimital taxa to less than or equal to 50.

1. 57 characters + ingroup + 16 outgroup OTU's; Lundberg rooted: shortest tree length 328.00 steps;
2. 48 characters + ingroup + 16 outgroup (different mix) OTU's; outgroup rooted: tree length 219.00 steps;
3. 57 characters + ingroup + 4 outgroup + 12 extralimital ariids: shortest tree length 357.00 steps;
4. Ditto + the 5 outgroup OTU's with least missing data;
5. 57 characters + ingroup only; midpoint rooted.

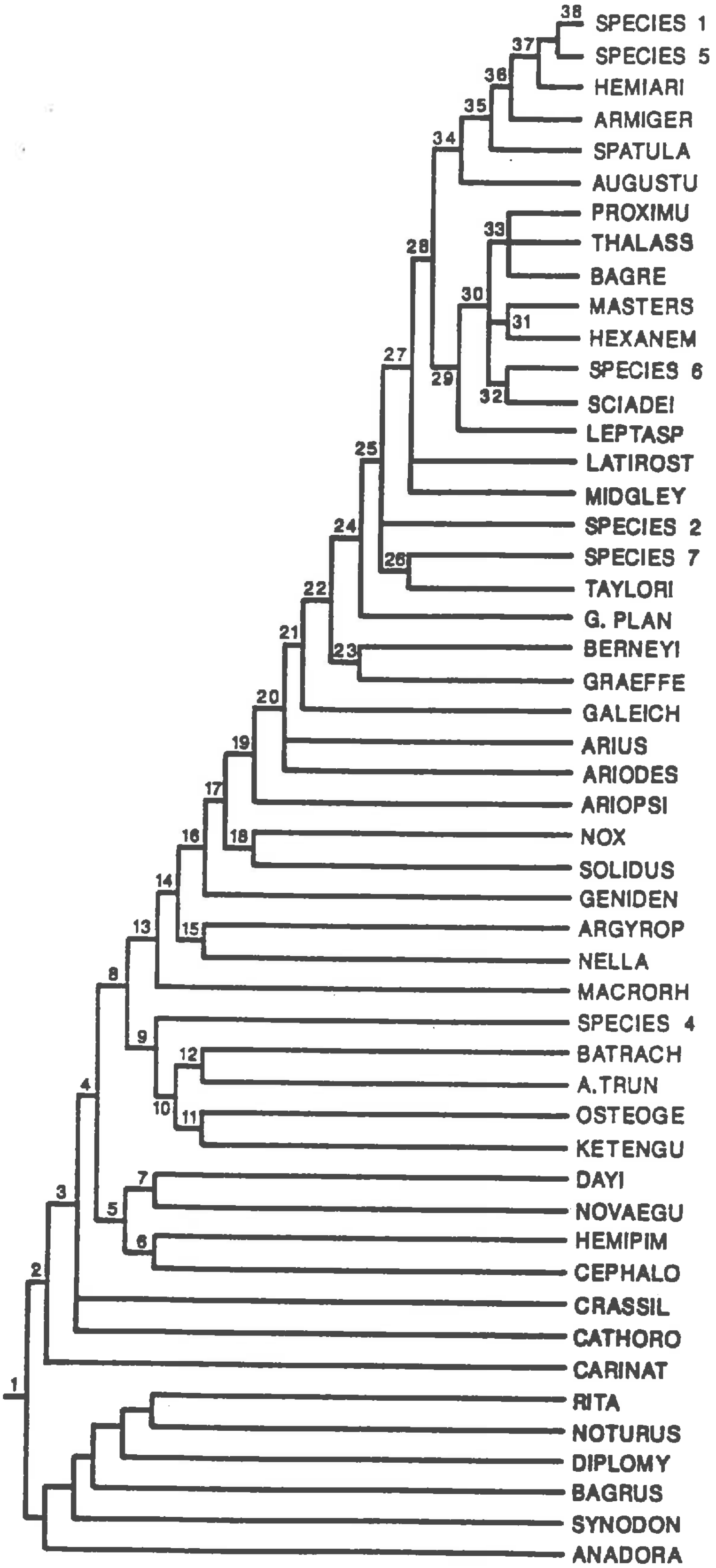

Figure CAT6. Strict consensus tree from 200 equally parsimonious trees formed by 357.00 steps. Fifty seven characters, 27 ingroup OTU's, 17 extralimital ariids and 6 outgroup OTU's were used. The seven taxa omitted (yet "represented" by a member of its species group) are: danielsi, bilineatus, froggatti, conorhynchus, velutinus, polystaphylodon and species 3. The three extralimital ariids omitted are: Ailurichthys, Guiritinga and Ancharius. The six outgroup OTU's represent 5 families. Names of the OTU's are abbreviated to 7 letters, where appropriate.

Result: a. the following seven clusters consistently formed: *danielsi* + *spatula*; species 1 + species 5; *froggatti* + *carinatus*; *crassilabris* + *conorhynchus*; *velutinus* + *taylori*; *argyropleuron* + *polystaphylodon* + *nella*; *nox* + *solidus*.

b. and almost always: *bilineatus* + *thalassinus*; *graeffei* + species 3 + *berneyi*; *dayi* + *novaeguineae*.

c. and associations were: *armiger* and *augustus* with species 1 + species 5; *macrorhynchus* with *argyropleuron* + *polystaphylodon* + *nella*; *coatesi* with *velutinus* + *taylori*.

5.5.2 Second series

Aim: to determine the effect on tree topology of different mixes of outgroups and extralimital taxa and alternative ingroup sister taxa.

Ten analyses, giving more than 100 equally short trees.

1. 57 characters + ingroup + 16 outgoup OTU's: shortest tree length 320.00 steps;
2. Ditto + different mix of outgroup OTU's: tree length 293.00 steps;
3. 57 characters + 27 ingroup* + 17 extralimital ariids + 6 outgroup OTU's: shortest tree length 358.00 steps (*7 sister taxa omitted - see results of First Series);
4. Ditto but different outgroup OTU mix, different extralimital mix: tree length 353.00 steps;
5. 43 characters + same OTU's: tree length 195.00 steps;
6. As for 3. above, but with alternative sister taxa*: shortest tree length 357.00 steps (fig. CAT6);
7. As for 3. above but with the "best" outgroup set (i.e. least missing data): tree length 355.00 steps;
8. 54 characters + ingroup + 1 extralimital ariid (*Hemiarius*) + 15 outgroup OTU's: tree length 328.00 steps;

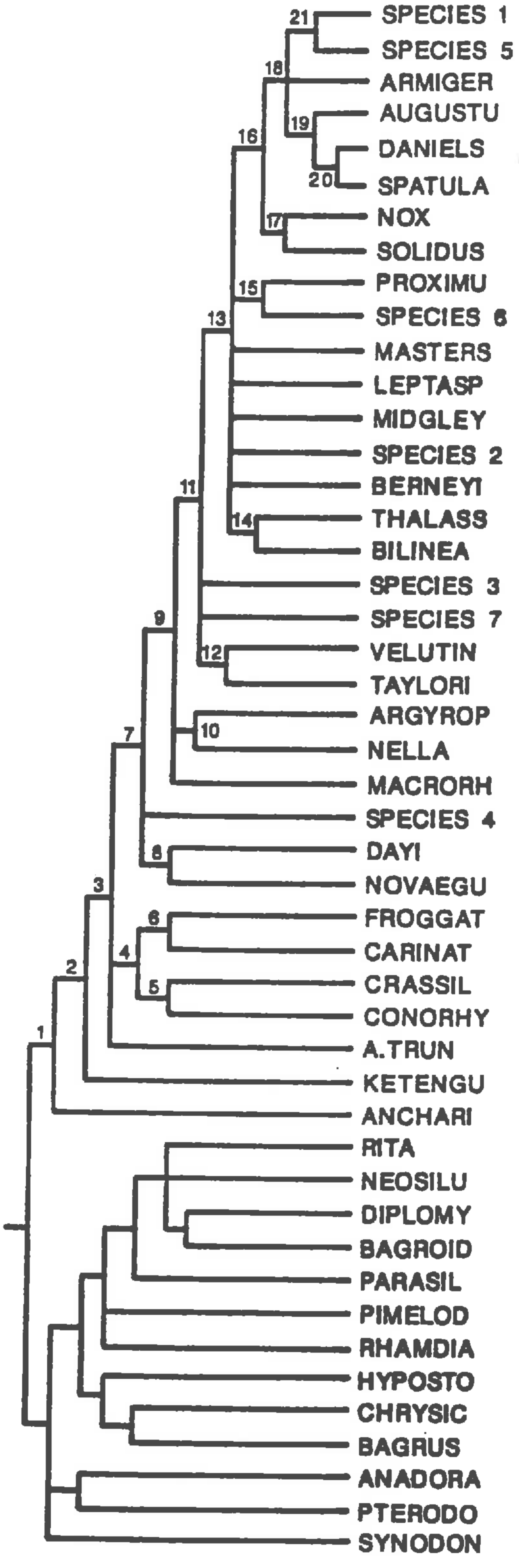

Figure DOG1. Strict consensus tree from up to 200 equally parsimonious trees based on 160.00 steps. 42 characters, 31 ingroup OTU's, 3 extralimital ariids and 13 outgroup OTU's were employed. After reduction of the character set, 3 lots of ingroup OTU's became identical: graeffei with berneyi, polystaphylodon with nella, latirostris with midgleyi. Hence, the 1st taxon of each couplet was dropped from the analysis. A. truncatus, Ketengus and Ancharius were selected from the extralimital ariids, as in earlier reconstructions they were most removed from the ingroup ariids. The outgroups represent 7 families.

The dropped characters, which exhibited different states within consistently recognised sister groups, are numbers 11, 12, 17, 18, 19, 26, 27, 29, 33, 46, 47, 48, 53, 54 and 55.

Names of OTU's were abbreviated to 7 letters, where appropriate.

9. 54 characters + 26 ingroup (8 "sister" taxa omitted) + all extralimital ariids (not Ancharius) + 5 outgroup OTU's: tree length 366.00 steps;

10. Ditto but with alternative sister taxa: tree length 374.00 steps.

Result: a. Seven sister groups confirmed;

b. Whereas analyses 3, 6 and 7 gave equally parsimonious trees and were computed on almost identical infiles (sister taxa rotated, outgroup improved) tree topology was not identical. i.e. PAUP had trouble finding equally parsimonious trees of consistent topology. This is indicative of a high level of homoplasy.

5.5.3 Third series

Aim: to reduce the effect of equivocal and highly homoplastic characters (recognised from earlier analyses) on tree topology.

Three analyses on a new data set of 42 characters were performed. The 15 deleted characters displayed irregular states within the consistently-recognised sister groups. Equivocal states of characters 16, 25 and 41 were clarified and all identical OTU's were omitted.

1. 42 characters + 31 ingroup + 3 extralimital ariids + 13 outgroup: shortest tree length 160.00 steps (fig. DOG1);

2. 42 characters, 24 ingroup (7 sister taxa omitted) + 19 extralimital ariids + 7 outgroup OTU's: tree length 175.00 steps;

3. Ditto but with 17 extralimital ariids: tree length 176.00 steps.

Result: a. Homoplasy still high - tree topology inconsistent;

b. Guiritinga and Ariodes not different to Arius.

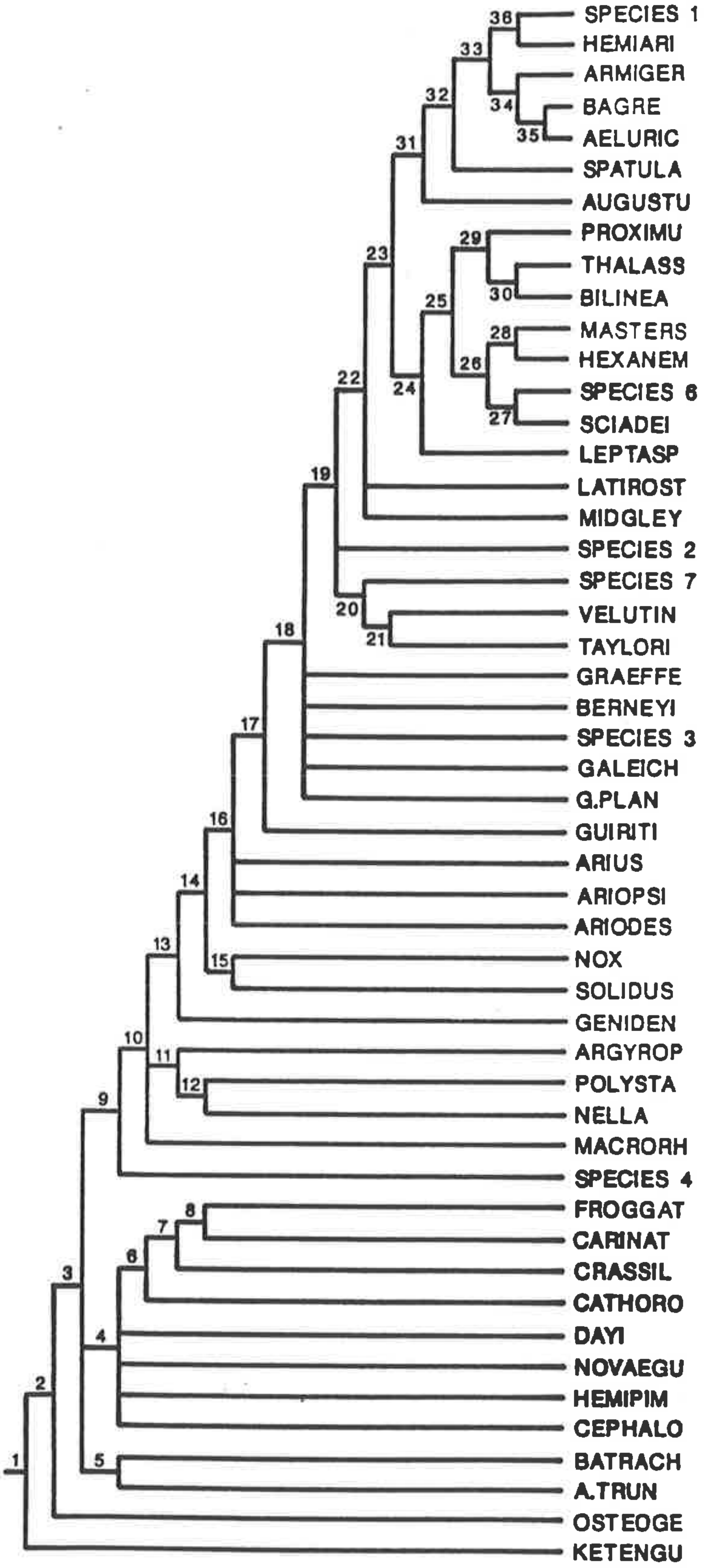

Figure DOG5. Strict consensus tree from up to 200 equally parsimonious trees with a length of 272.00 steps. 31 ingroup taxa (not *conorhynchus*, *danielsi* and species 5) and 19 extralimital ariid taxa were employed with 48 characters (9 "family" characters were omitted: numbers 1, 2, 7, 8, 9, 10, 44, 45, 56). *Ketengus*, being the OTU consistently positioned at the most proximal part of the dendograms, was designated HTU. Names of the taxa are abbreviated to the first 7 letters, were appropriate.

5.5.4 Fourth series

Aim: to determine the effect on the cladogram form of no designated outgroup and alternative rooting methods.

Two analyses, all characters and no outgroup specified; 31 ingroup + 19 extralimital ariids (not *Ancharius*).

1. Root = midpoint, *Ketengus* as HTU: shortest tree length 272.00 steps;

2. Root = outgroup, *Ketengus* as HTU, "family" characters 1-2, 7-10, 44-45, 56 omitted: shortest tree length 272.00 steps (fig. DOG5).

Result: Topology of consensus trees identical for two-thirds of left hand side, remainder rotated; branch lengths variable.

5.5.5 Fifth series

Aim: to reduce homoplasy due to PAUP recognising the family Ariidae.

Three analyses of the new data set wherein monophyly character 1 was weighted, remaining "family" characters omitted with the 19 remaining characters in the data set being the least equivocal of the original 57.

1. 20 characters + ingroup (without *conorhynchus*, *graeffei*, *berneyi*, species 2) + 17 outgroup OTU's: shortest tree length of 106.00 steps (fig. FIN1);

2. Ditto + 29 ingroup + 19 extralimital ariids (not *Ancharius*) + one outgroup OTU (*Diplomystes*): tree length 121.00 steps;

3. Ditto, without *Diplomystes*, *Ketengus* as HTU: shortest tree length 108.00 steps (fig. FIN3).

Result: Tree topology differs from those of previous analyses. PAUP is unable to resolve many taxa (e.g. in distal half of cladogram) as a high level of homoplasy is still in evidence.

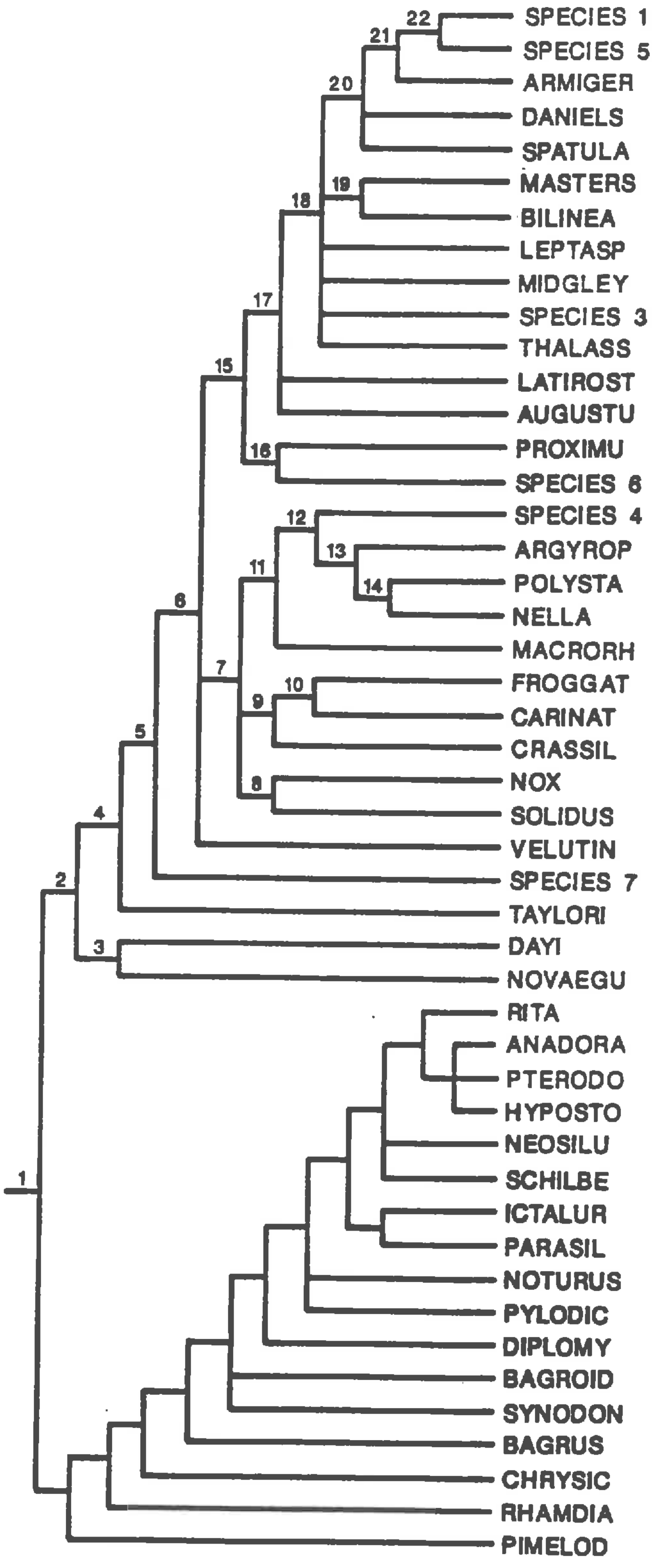

Figure FIN1. Strict consensus tree from 200 equally parsimonious trees, with a length of 106.00 steps. 20 characters, 30 ingroup taxa (not species 2, berneyi, graeffei and conorhynchus) and 17 outgroup OTU's were employed. Character 1 (oral brooding) was weighted. The character sets of OTU's graeffei, berneyi and species 2 became identical to that of midgleyi after reformation of the matrix subsequent to reducing the number of characters. Ten catfish families are represented in the outgroup. Names of the taxa are abbreviated to the first 7 letters, where appropriate.

5.6 TREE ANALYSIS

Where no outgroup was specified, the cladograms produced by PAUP involve more homoplasy (Tables 8,10,14,16, cf. Table 12). Furthermore, the effect of using extralimital taxa (where homoplasy remained high) to determine the extent of convergence within the family Ariidae was indicated; i.e. the convergence revealed in cladograms constructed on the ingroup only is a real example of convergence within the whole family.

PAUP had to manipulate both ordered and unordered character states in every analysis. This necessitated making parsimonious assumptions of convergences. The trees in which homoplasy is higher are those constructed from more ariid (both ingroup + extralimital) OTU's than from outgroup + ingroup OTU's. This situation reveals that convergences and parallelisms of character states are common to all members of the family, not just to Australo-Papuan members. The amount of homoplasy required in tree construction was not improved by using fewer, presumably "more stable", characters (e.g. figs FIN1, FIN3).

No change was effected in tree topology when Ketengus was used as HTU (fig. FIN3). More importantly, its employment confirmed the seven clusters and other associations of OTU's arrived at in earlier analyses (e.g. fig. CAT6).

For ingroup (Australo-Papuan) taxa only, the most parsimonious trees generated using all 57 characters ranged in length from 293 to 328 steps. The tree topologies were never identical because of the high level of homoplasy: parallelisms, convergences and reversals. A certain degree of congruence was established however, in that sets of taxa consistently grouped at approximately comparable positions on the consensus trees. For example, dayi + novaeguineae; crassilabris +

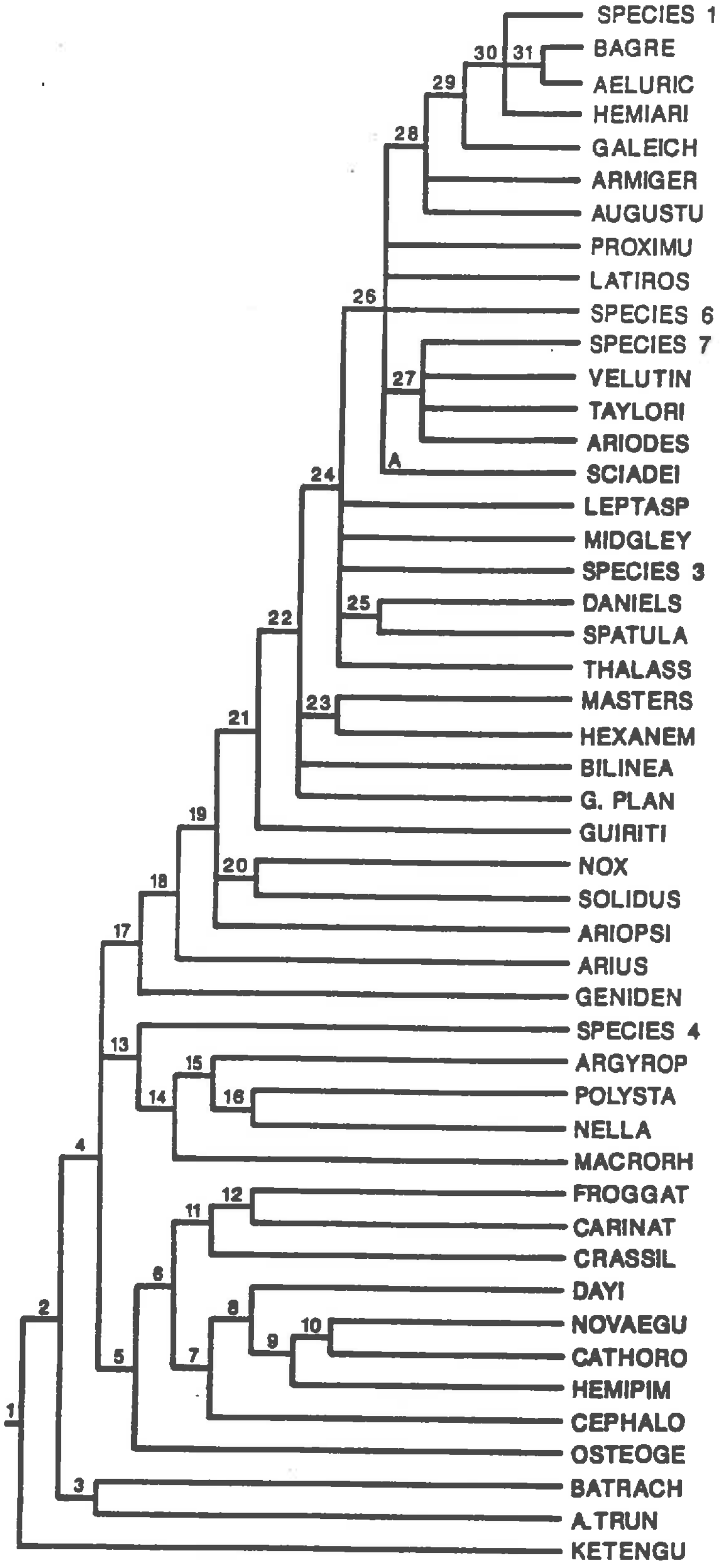

Figure FIN3. Strict consensus tree from up to 200 equally parsimonious trees with a length of 108.00 steps. 20 characters, 29 ingroup OTU's (less species 5, *graeffei*, *berneyi*, species 2 and *conorhynchus*) and all extralimital ariids (not *Ancharius*) were employed. *Ketengus* was designated the HTU. Names of taxa are abbreviated to the first 7 letters, where appropriate.

froggatti + *carinatus* always established proximally and species 1 + species 5 established distally.

However, the most parsimonious position of several individual taxa was inconsistent in all analyses. These OTU's include *armiger*, *proximus*, species 2 and species 4.

Two dendograms of largely ingroup taxa are figures DOG1 and FIN1. The derived character states that define the branches of fig. DOG1 (15 characters from original matrix of 57 omitted) and fig. FIN1 (based on the 20 most reliable characters) were traced on the consensus trees and are listed by branch (or nodes) in Tables 9 and 13. Although the level of incongruence is very high in both analyses, synapomorphies are present. They support several groups of OTU's and these are discussed below:

The *froggatti* + *carinatus* + *crassilabris* + *conorhynchus* branch is supported by the uniquely derived characters of extrascapular fusion with the epioccipital (Character 24B) and a long posterior cleithral process (Character 14A). The synapomorphy of the loss(?) of the first pharyngobranchial (Character 13C) further distinguishes *froggatti* + *carinatus*.

The synapomorphies of smooth neurocranium (28C) and reduced gonad (57A) unite *dayi* and *novaeguineae*.

The taxa *argyropleuron*, *nella* and *polystaphylodon* are distinguished by the uniquely derived states of narrowed caudal vertebrae (41A) and longitudinally-arranged palatal tooth plate (Character 51B).

The grouping of *proximus* with species 6 is supported by the convergent character of epioccipital in the skull roof (23B).

The synapomorphy of a dark buccopharyngeal cavity (39A) supports the *nox* + *solidus* clade.

Only two homoplastic characters - bifurcate lateral line (32C) and reduced posterior gill raker set (43C) - support the pairing of thalassinus and bilineatus in fig. DOG1. The taxa are not paired in fig. FIN1.

Well-staggered chin barbel bases (31C) support the terminal split of five or six taxa. Possession of tiny mandibulary pores (22C) and a slightly convex mesethmoid (18C) link danielsi with spatula; while large mandibulary pores (22A) and a deeply excavated laminar bone (49A) are common to species 1 and species 5.

Clades are largely supported by homoplastic characters. For example, in fig. DOG1: a) of the seven derived character state changes between nodes 7 and 9, four are reversals, 2 are parallelisms and only one (43B - a character probably correlated with dietary preference) is unique; b) four homoplasies only distinguish taxa at the next major branch (nodes 9 to 11); and c) the homoplastic character, presence of vomer teeth (35A) alone supports the 17 most distal taxa (branch 11,13: bilineatus to species 1).

The second analysis (as fig. FIN1) gave a tree topology for ingroup taxa very similar to the previous tree (fig. DOG1) with a substantial amount of homoplasy. Presence of vomer teeth (35A) is again the sole (homoplastic) character state distinguishing 15 distal taxa from others (branch 6,15); and only frontal size (character 48A) and reduced temporal fossa (25B) support the 7 more distal taxa.

An alternative homoplasy representation is given in Tables 10 and 14 in which the number of changes each (non-family) character underwent during tree reconstruction is stated (remember: the most parsimonious tree PAUP can achieve). The more labile characters (Table 10) are the posterior cleithral process (Character 14), first pharyngobranchial position (Character 13), lachrimal shape (20), skull ornamentation (28), terminal direction of lateral line (32) and posterior gill raker possession (43). In Table 14, the more inconsistent characters are subvertebral cone size (Character 11), mesethmoid shape (18), metapterygoid-hyomandibular suture length (27) and frontal size (48).

These analyses were performed on reduced data sets (42 in DOG1 analysis, 20 in FIN1 analysis) of "tighter" characters; i.e., in light of earlier analyses, the soundest characters were sought. Nevertheless, there is *still* much incongruence, such that species groups are usually based only on homoplastic characters.

Apart from the consistent grouping of certain taxa, the number of changes necessary for PAUP to reconstruct a phylogeny resulted in consensus trees in which OTU's could not be resolved. For example in fig. DOG1, nine OTU's (*bilineatus* to *proximus*) are sited in an almost uniform string, itself supported by one homoplastic character (35A). (See also fig. FIN1, *thalassinus* to *mastersi*.)

The groups defined in the analyses of almost entirely ingroup OTU's are largely confirmed in reconstructions incorporating extralimital ariid taxa (CAT6, DOG5, FIN3): *dayi* with *novaeguineae*; *froggatti* + *carinatus* with *crassilabris* (+ *conorhynchus*); *argyropleuron* with *nella* + *polystaphylodon*; *nox* with *solidus*; species 1 with species 5; *danielsi* with *spatula*. However, *proximus* does not group closely with species 6 and *thalassinus* and *bilineatus* do not closely approximate in fig. FIN3 (reduced character matrix). In analyses DOG5 and CAT6, where 57 characters (CAT6) or 49 characters (DOG5) were employed, *proximus*, *thalassinus* and *bilineatus* (this taxon not in CAT6) form a species group. [Additional support for this comes from synapomorphies of swimbladder shape (Character 33C), adipose fin shape (29C) and posterior gill raker situation (43C).]

Two other species groups based only on homoplasies, were consistently revealed in analyses, *viz*: *velutinus* + *taylori* + species 7; and *graeffei* + *berneyi* + species 3. The first group of taxa have in common: a moderately large subvertebral cone (character 11B), an untoothed vomer (35B), apomorphic frontal size (48C - not *velutinus*), the posterior dorsomedian fontanelle always open (46C), no toothed plates on the palate (50B - not species 7) and gill rakers present on the trailing edge of the 2nd through 4th gill arches (43B). The second group of taxa share: a moderately wide gill opening (Character 16B; recoded), either no or unstable patches of vomerine teeth (Characters 35B and 36B), rakers present on the trailing edge of all gill arches (Character 43A) as well as some individually derived character states (e.g. moderate buccopharyngeal pads [17B] in *berneyi*).

Of the remainder, the taxa *macrorhynchus* and species 4 should be discussed. In all analyses, these taxa do not affiliate with any others although they are consistently nearest the *argyropleuron* + *polystaphylodon* + *nella* clade. The mesethmoid shape (18E), unique nasal shape (19C) and short hyomandibular-metapterygoid suture (27C) are apomorphies for *macrorhynchus*. The autapomorphy of toothless autogenous tooth plates (Character 52B) and the derived characters of restricted gill opening (16D), extensive metapterygoid (26D) and frontal size (48C) characterise species 4. Both taxa are apomorphic for fin spine thickness (53D) and adipose fin size and position (29C).

As with the analyses of ingroup taxa, groupings of both a) extralimital taxa and b) extralimital plus ingroup taxa consistently formed in the dendograms, based on different mixes of OTU's incorporating extralimital ariids (analyses CAT6, DOG5 and FIN3). (Remember that the coding and co-analysis of the extralimitals is intended only to clarify nominal generic groupings and to provide information on the level of homoplasy in the family.) The clusters are:

(a) *Bagre* + *Ailurichthys*;
Arius + *Ariopsis*; usually + *Ariodes*;
Batrachocephalus + *truncatus*;
Hemipimelodus + *Cephalocassis*.

(b) *Hemiarius* + species 1 + species 5;
Hexanematichthys + *mastersi*;
Sciadeichthys + species 6;
"*Cathorops*" + *Hemipimelodus* + *Cephalocassis* + *novaeguineae* + *dayi*.

The synapomorphies supporting the clustering of the extralimital ariids are given in Tables 7, 11 and 15 and record of the number of changes in Tables 8, 12 and 16. Of them, five groups of OTU's deserve some discussion, *viz*.:

(1) *Arius*, *Ariopsis*, *Ariodes* usually form a clade (information is lacking for *Ariodes* in several character states). Different states in six characters isolate this cluster from *Genidens* and *Guiritinga* (two taxa): subvertebral cone size (11A v. B), posterior cleithral process size (14D v. B), development of buccopharyngeal pads (17A v. B), adipose fin size (29A v. B), curvature of lateral line at tail base (32A v. B) and frontal size (48A v. B). As revealed in Tables 8, 12 and 16 as well as from earlier discussion, all of these characters are highly homoplastic at the A-B states in ariids. For PAUP to reconstruct the most parsimonious cladograms here, it had to switch character states at from 7 to 15 nodes. No more constant characters differentiate these OTU's.

(2) Hemiarius, species 1 and species 5 form a clade supported by several derived states including a convex mesethmoid (18D), thickened fin spines (53B) (not species 5), enlarged mandibulary pores (22A), an extensive metapterygoid (26D/C) and well-staggered chin barbels (31C/B).

(3) The Hexanematichthys + mastersi pairing is supported by a derived character (reduction of the temporal fossa, 25B; recoded) and the unique synapomorphy of dark peritoneum (38A).

(4) Sciadeichthys and species 6 share two reversals (frontal size [48B], nasal shape [19A]) and two parallelisms (epioccipital in skull roof [23B], gill rakers absent from trailing edge of first and second arches [43C]).

(5) The cluster of "Cathorops" + novaeguineae + dayi + Hemipimelodus + Cephalocassis + crassilabris is supported by many convergences. They share an elevated subvertebral cone (11C); all but novaeguineae have a restricted gill opening (16D); all but crassilabris have a small posterior cleithral process (14D). Other synapomorphies of this clade (but not possessed by all) are high 4th neural spine-epioccipital flanges (12C), pad-less female ventral fins (34B), an open posterior dorsomedian fontanelle (46C), an apomorphic frontal size (48C) and extensive laminar bone (49C and D). Hemipimelodus, Cephalocassis and novaeguineae have a skin-covered eye (15B) and a rounded open posterior dorsomedian fontanelle (47B) (also dayi). Only "Cathorops", froggatti, crassilabris and carinatus possess a united extrascapular and epioccipital (24B). The epioccipital invades the neurocranium roof (23B) in "Cathorops", nella and polystaphylodon as well as in several disparate OTU's.

5.7 DISCUSSION

More extensive discussion cannot bring further clarity to the relationships between Australo-Papuan ariids as established with the chosen characters.

Despite modifications to the matrix, use of different OTU mixes, rooting and options, the tree topology was generally similar. That some other ariid characters (Chapter 4) would have contributed to a tighter phylogenetic reconstruction is debatable.

In all reconstructions, both ordered and unordered characters infrequently supported the more distal OTU's; e.g. vomer tooth presence (35A - ordered); lachrimal shape (20B - unordered) and gill opening size (16A, 16B). In the Ariidae, these may either reflect character state reversals or the level of convergence required for reconstruction of the distal part of the tree. Nevertheless, in all trees (figs CAT6 to FIN3) the seemingly more derived taxa are located proximally.

Comparison of extralimital and ingroup ariids has revealed real groupings of genera. However, this is counteracted by the shortfall in taxa compared. Because my aim was to study only Australo-Papuan ariids, a somewhat limited sample of extralimital ariids were analysed with the ingroup - albeit *most* nominal genera were represented (I had insufficient information on the remainder, such as the central American taxon *Potamarius*). Be that as it may, the two last-mentioned groupings (*Sciadeichthys* + species 6; "*Cathorops*" with *novaeguineae* + *dayi*) illustrate the "reliance" of ariid classification on homoplastic characters; and the hitherto unsuspected close relationship of taxa from widely separated geographic regions.

Although *Batrachocephalus* and *truncatus* consistently cluster in these analyses, the former is uniquely characterised among ariids by its extensive, heavy jaws, reduced anterior suspensorial elements, reduced barbels, metapterygoid shape and tooth type. The further relationship of *truncatus*, which possesses a number of homoplastic characters, cannot presently be clarified.

Bagre and *Ailurichthys* share a number of uniquely derived features, such as distally-situated first pharyngobranchial, a flattened subvertebral cone and 3 anterior processes on the frontal, itself expanding with age. Additional characteristics are the tasselated fin spines, very long maxillary barbel and matching pectoral (I,13) and gill raker (9, first arch) counts.

Hemipimelodus and *Cephalocassis* are very similar taxa. Character states only differ in nine of the 57 characters assessed and most of these are the more homoplastic (e.g. fin spine thickness, temporal fossa size). Possession by these taxa of two distinct ovaries and the sexually mature females with padded ventral fins currently support no closer relationship to *novaeguineae* and *dayi* than that of sister species. Several other (more labile) characters concur with this decision.

Despite the synapomorphies mentioned earlier (5.6), several autapomorphies of "*Cathorops*" preclude its synonymy with *Hemipimelodus* and *Cephalocassis*, *novaeguineae* and *dayi*. In "*Cathorops*", the inner jaw teeth are molariform; the laminar bone is convex and raised distally; and the ventral aorta and jugular veins lie together, ventral to the vertebral centra (in all other ariids each jugular lies lateral to the centra); and the united 2nd and 3rd transverse parapophyses are angled forward. However, the highly-developed flanges at the back of the neurocranium and the well-developed and intrusive epioccipital tend to support a closer relationship between "*Cathorops*" and *crassilabris* (refer also the five cladograms, 5.6). *Potamarius* (*q.v.*) also exhibits "*Cathorops*"-*crassilabris*-like features.

Unfortunately, I have no information on some character states in *Sciadeichthys* and therefore its association with species 6 cannot be clarified. *Sciadeichthys* is a taxon having tooth patches fixed to the parasphenoid or orbitosphenoid (possibly only in females) and a swimbladder consisting of two complete, articulated sections.

5.7.1 *Monophyly*

The monophyly of the Ariidae is established by the habit of oral incubation (Character 1). The several supporting, derived morphological features such as the following: the absence of a mesocoracoid (Character 2), possession of an extended epioccipital (Character 3) and homologous ESA (Character 8) are shared with some outgroup taxa (doradids, mochokid). The frontal and mesethmoid meet at a minimum of two sites in all ariids except *Ketengus* (one site) (Character 6). All ariids have strong pelvic musculature (Character 44), a naked body (Character 56) and large otolith (Character 7). The formation of an aortic tunnel (Character 4) and absence of a supraneural (except in *Galeichthys*) (Character 5) largely distinguish the Ariidae from other catfishes, although these character states are frequently present in the Pimelodidae.

Five additional characters lend support to the recognition of the ariids as a monophyletic group within the Siluroidei. These characters were unscored because they are based on incompletely investigated studies, trends or autapomorphies. They are:

(1) the epidermal viscous mucus secretions. These secretions are unaffected by thiols, have heat labile protease (sensitive red blood

cell lytic factor) and a protein factor that accelerates clotting of plasma. Such features are not present in the secretions of other catfishes (Al-Hassan *et al.*, 1985; Di Conza, 1970). The mucus from *Arius* is a unique secretion of physiological importance and appears to be a novel anti-predatory adaptation (Al-Hassan *et al.*, 1985). This secretion may be a modified fright substance (refer Pfeiffer, 1977; Fink and Fink, 1981; Nelson, 1984).

(2) maximal consolidation of the anterior vertebrae. Up to 3 and 4 subsequent vertebrae are firmly articulated with the complex vertebra in ariids, on average more than in any other siluroid family (Bhimachar, 1933; Howes, 1983a; Roberts, 1973; Tilak, 1965; pers. obs.). The number of rigidly-united vertebrae is largely associated with the SL of the specimen, the investing (laminar) bone gradually extending backward with age (and see Regan, 1911a). This feature is illustrated in the small and larger specimens of *armiger*, *leptaspis* and *bilineatus* (refer material examined; also Character 49). Although Taylor (1986) used the extent of laminar bone to partly diagnose *Galeichthys*, in general this is not a sound character. In all ariids I have examined, the first pleural rib is attached to the 6th vertebra, whether or not it is covered by laminar bone.

(3) exceptionally firm articulation of the vertebral column (and therefore the trunk) with the skull (Tilak, 1965; Bhimachar, 1933). In addition to the normal attachment of the first vertebra centrum with the skull, the ariids exhibit firm unification at the subvertebral cone (Character 11), the epioccipital flange and the transverse process of the fourth vertebra (Character 3), the neural process of the fourth vertebra with the supraoccipital and the exoccipital above the foramen magnum (Bhimachar, 1933). Mahajan (1966) concluded that a solid

connection of the vertebral column with the skull led to a more efficient functioning of the sound-producing apparatus in the Sisoridae; an apomorphy which may well hold true for the Ariidae.

(4) precocial larvae. Among catfishes, only ariids and the Loricariidae produce such larvae, the large young resembling the adult in every aspect of external morphology yet retaining a large yolk sac (refer Character 57). Such a developmental feature is a significant specialisation over many catfish families whose larvae are atricial (Fuiman, 1984).

(5) meristics, viz: in all taxa the dorsal fin consists of a spinelet, a spine and seven branched rays; the caudal of 15 (7+8) branched and two unbranched principle rays (Character 45); the ventral of 6 branched rays.

Studies on the DNA complement (LeGrande, 1980) and karyotype of several ariid taxa (Fitzsimons et al., 1988) have revealed features suggesting monophyletic grouping; e.g. high DNA complement per cell, chromosome number and arm length.

5.8 CONCLUSIONS FROM ANALYSES

(a) Sets of Australo-Papuan sister taxa were revealed. These groupings largely contradict previous generic associations.

(b) A remarkably high level of convergence and reversal exists in the taxa as illustrated by their distinguishing character states. Characters in which the states were frequently switched in the most parsimonious tree reconstructions include: fin spine thickness, size of adipose fin, palatal flap development, posterior cleithral process size, mesethmoid shape, nasal shape, gill opening width, abdominal cavity length, first infraorbital shape, posterior gill raker disposition and lateral line direction. All of the states of these characters are unordered. Given that errors may have been perpetuated through either comparison of structures across different growth stadia or by non-recognition of intraspecific variation, most characters chosen for analysis appeared to be the most stable, least equivocal and with higher information content than were other recognised characters (refer 4.1; Chapter 3). What is even more remarkable, is that homologues of a number of these characters have been used "successfully" in phylogenetic reconstructions of other siluroid families (e.g. the Ictaluridae, Chacidae, Loricariidae, Diplomystidae) where they have rarely exhibited *any* homoplasy!

(c) Although homoplastic characters do not actually contribute to phylogenetic reconstruction (3.1), in this family - where most character variation is the result of convergences and reversals - their positive contribution to the definition of taxonomically informal *subgroups* cannot be ignored.

(d) Modern taxonomic tools (such as ultrastructure [e.g. SEM] and molecular techniques [e.g. DNA sequencing; further work along the lines of LeGrande, 1980 and Fitzsimons *et al*., 1988]) and other characters (such as musculature, mucus properties, barbel composition and optic fibre patterns in the retina [Frank and Goldberg, 1983]) should be employed in future studies to further reveal the evolutionary history of this widespread family.

(e) Three sets of grouped extralimital taxa should be recognised as synonyms of each other. Thus *Ailurichthys* Baird and Girard, 1854 is a synonym of *Bagre* Cloquet, 1816; *Hemipimelodus* Bleeker, 1858 is a synonym of *Cephalocassis* Bleeker, 1858; *Arius* Valenciennes, 1840 is the senior synonym of Ariodes Müller and Troschel, 1849, Genidens Castelnau, 1855, Guiritinga Bleeker, 1858, Ariopsis Gill, 1861 and Pseudarius Bleeker, 1862.

(f) Within the New Guinea and Australian region, synonyms of these and other nominal genera are confirmed. Hence Netuma Bleeker, 1858, Neoarius Castelnau, 1878, Pararius Whitley, 1940 and possibly Nemapteryx Ogilby, 1908 are synonyms of Arius Valenciennes; Septobranchus Hardenberg, 1941 remains a synonym of Cinetodus Ogilby, 1908; and Doiichthys Weber, 1913 is a synonym of Nedystoma Ogilby, 1898. Hemiarius Bleeker, Hexanematichthys Bleeker, Brustiarius Herre and Cochlefelis Whitley are subgenera within Arius. Tetranesodon Weber, 1913 is a synonym of Pachyula Ogilby, which is itself a subgenus within Cinetodus Ogilby.

(g) PAUP was unable to resolve the appropriate position for Galeichthys. This taxon exhibits certain character states not possessed by other ariids. It has a reduced epioccipital extension, the aortic tunnel is incomplete at all growth stadia and there is a supraneural between the supraoccipital and the nuchal plate - states which prevail in non-ariid siluroids. The laminar bone of the anterior vertebral region is less extensive and the lapillus otolith appears to be smaller, compared to that in other ariids; the supraoccipital is narrow, and the neurocranium is covered by thick tissue. The possession of oral incubation in this taxon has masked these plesiomorphic characters in phylogenetic recontructions (cf. Ancharius for which reproductive habit is unknown).

(h) The phylogenetic analysis performed here casts doubt on the reputation of the Madagascan taxon Ancharius as an ariid. This taxon possesses an open aortic canal, low auditory bulla and reduced otolith, an unproduced epioccipital, the vestige of a nasal barbel, a supraneural before the nuchal plate and an expanded Müllerian Ramus. Presently unavailable information on its reproductive habits will determine its merit as an ariid. Meanwhile, I deem it prudent to remove Ancharius from the Ariidae.

(i) The shared possession of a structurally homologous ESA (Character 8) with some other monophyletic groups may be an important indication of the wider phylogenetic relationships of the family Ariidae.

6. SYSTEMATICS

6.1 INTRODUCTION

6.1.1 Reclassification of Ariidae in New Guinea and Australia

The series of analyses performed (Chapter 5) clearly reveal that previous classification schemes are inappropriate. They largely masked ariid relationships and contributed to regional naming of higher level taxa.

The 34 (ingroup) + 19 extralimital (less Ancharius) taxa represented, form a somewhat homogeneous phylogenetic tree, despite the amount of homoplasy. The type species of many nominal genera do not exhibit unique characteristics which could unequivocally differentiate each from the other. Rather, because only homoplasies frequently distinguish species groups, these type species exhibit a closer affinity with each other than suggested in the earlier classifications.

The purpose of a classification is to facilitate statements about similar organisms; i.e. similar organisms are grouped so that generalisations can be made about them (Mayr, 1981). A negative approach to reclassifying the Ariidae would be to refer all taxa to one genus OR, to erect numerous monotypic genera for unresolved taxa and species groups. By such means, information on relationships and character states would be lost, and the resulting classification would be ill-defined and far too cumbersome: no improvement over previous schemes (refer Table 2).

The difficulty in producing a phylogenetic classification when diagnostic characters of particular groups overlap each other was mentioned by Arratia (1987), using the Siluroidei as her example. She found that this "unsatisfactory situation is repeated [in the suborder, in families], subfamilies and genera" (p. 82). Similarly, in her study of piscivorous East African cichlids (where there is low morphological variation between the several species groups and genera), Stiassny (1981) found very few apomorphies (one of them a meristic character) to define the cichlid *Rhamphochromis* Regan. This taxon exhibits a unique morphotype which, she concluded, was defined by characters linked through a gradal series to those found in less-modified piscivores.

A similar situation, where low morphological differentiation is present in combination with a high level of speciation, exists in the Ariidae (especially in the genus "*Arius*").

Phylogenetic reconstruction reflecting true relationships, and their subsequent revised classifications, will only be achieved in such groups when morphological characters are compared in conjunction with a thorough knowledge of the species' ecology, behaviour, biology, inter- and intraspecific variation in morphological and meristic characters (refer Stiassny, 1981; Lynch, 1971). Some of these issues were addressed in Chapters 3 and 4.

The concept of the "lowest" supraspecific taxon - the genus - is pivotal to the revised classification of the Australo-Papuan ariids based on my study. Mayr's (1969; 1981) view, that a genus is separated from other genera by a decided gap, relies on the definition of the "decided gap" (Lynch, 1971). However, I could recognise a "decided gap" between only a few ariid taxa. ~~Yet between a relatively few taxa, have I recognised the disjunction reflecting synapomorphies.~~ However, for the majority of the family I have examined, the genera I recognise conform to Lynch's (1971: 19) definition as being "morphologically discrete units characterised by a relatively high degree of homogeneity, in terms of both morphology and ecology".

My revised classification cannot avoid using the paraphyletic genus "*Arius*" (or "genus group", following the rationale of Ax, 1987).

Since Hennig (1966), paraphyly has been redefined and extensively discussed by authors such as Farris (1974), Wiley (1981), Patterson (1982), Ax (1987) and Oosterbroek (1987). These authors' conclusion, that paraphyletic groups are uncharacterisable; are based on plesiomorphies; have no real existence, is borne out in "Arius".

Paraphyletic groups are extensively represented in conventional classifications; and are often mistaken for natural (= monophyletic) groups. Such classifications are the expression of a dilemma: on the one hand, traditional (or Linnaean) classifications are formal mechanisms which order taxa into fixed categories, and are not designed to accommodate the products of phylogenetic development; on the other hand, "phylogenetic systematization" (Ax, 1987) ranks taxa at particular hierarchical levels of the phylogenetic system. In other words, classifications basically incline to rejecting supraspecific units based on convergent agreements (as for example, in paraphyly); yet are obliged to include them in a formal classification.

The inconstant position of the included species of "Arius" on the cladograms (Chapter 5) measured against the tighter groupings of species in Cinetodus, Nedystoma and Genus 1 has, therefore, not facilitated the categorization of these species. Following this study, I have firm belief in Ax's truism that "All categorical terms applied to taxa above species taxa are nothing but arbitrary labels. The assignation of categories to supraspecific taxa of the phylogenetic system can, in principle, never be made objective" (1987: 237).

My approach to a new classification of the Ariidae is one of caution, for the following reasons:

(1) I did not study all known representatives of the family;

(2) application of alternative techniques (section 3.5.3c) may reveal finer relationships than have my techniques;

(3) the family's world-wide distribution, variety of habitat preferences and the high homoplasy of character states coupled with a conservative basic morphotype, suggests a recent radiation from a general adaptive genotype;

(4) no meaningful phylogenetic classification can be achieved by recognising formal groups based almost entirely on reversed and convergent character states.

I will define well-corroborated monophyletic groups of species as genera and subgenera within them, unresolved taxa as species groups or "incertae sedae". By this means, I hope to initiate stability in the classification of the family. I accept, as Chernoff (1986) did, that my estimate of relationships could change with future data collection because of the overall lack of uniquely derived character states shared by few lineages.

6.1.2 Generic and subgeneric relationships

Within the New Guinea and Australian ariids, I recognise three genera and one genus group. Six subgenera are distributed within these (Table 17). This classification is supported both by synapomorphies revealed from phylogenetic reconstruction, by associated meristic and morphological information and by limited sets of homoplastic characters.

(A) the genus *Nedystoma* Ogilby.

(B) the genus *Cinetodus* Ogilby including:

  (1) the subgenus *Cinetodus* Ogilby;

  (2) the subgenus *Pachyula* Ogilby.

(C) a new genus (#1).

(D) the genus group "*Arius*" Valenciennes, which consists of:

(1) the subgenus Brustiarius Herre;

(2) the subgenus Cochlefelis Whitley;

(3) the subgenus Hemiarius Bleeker;

(4) the subgenus Hexanematichthys Bleeker;

A number of individual species and species groups also belong in "Arius" (Table 17).

6.1.3 Key to genera and genus group of Australo-Papuan ariids

A. Sexually mature females without ventral fin pads; subvertebral cone well-elevated and strong .... B

AA. Sexually mature females with ventral fin pads; subvertebral cone low to well-elevated C

B. Gonad not clearly bilobate; posterior cleithral process reduced .... Nedystoma (section 6.3)

BB. Gonad bilobate; posterior cleithral process well-developed, horizontal and oblong .... Cinetodus (section 6.4)

C. Palatal tooth plates arranged longitudinally, 2 on each side; distal caudal vertebral centra vertically extended ... Genus 1 (section 6.5)

CC. Palatal tooth plates (if present) at front of palate or anterolateral; no distal caudal vertebral centra vertically extended (anterior ones may be enlarged) .... "Arius" (section 6.6)

6.2 METHODS AND MATERIALS

Fresh material was collected by trawling and market surveys which, however, yielded a limited variety of taxa. This shortfall was made up through access to preserved material in various institutional collections or from those of colleagues.

Type material of all nominal genera from the Indo-Australian region was examined. Representatives of most other taxa recorded from this region, as well as some taxa from other parts of the family's known distribution, was also examined.

Information on individual specimens was recorded on a standardised form (fig. 70).

6.2.1 Counts and measurements

Measurements of structures and length less than 250 mm were made with dial calipers recorded to the nearest 0.1 millimetre. The standard length of larger specimens was measured using a mm-graduated board (a folding carpenter's rule) which had a vertical metal bar fitted to its proximal end. For these specimens the measurements were rounded off to the nearest millimetre. Twisted specimens were pressed along this board and temporarily straightened enabling a more precise measurement. Such specimens and all loaned types, were measured twice, and a mean value recorded for each character; all other specimens were measured once. Measurements were made from the left (sinistral) side of the body with the exception of asymmetrical paired structures (e.g. maxillary barbels, pectoral spines), or if the particular sinistral structure was evidently damaged.

The terminology and methods follow that of Hubbs and Lagler (1958), but several modifications relative to the morphology of these fishes, have been made (Kailola, 1983).

In view of the apparently imprecise ratios and usually unexplained measurements recorded in earlier ariid literature, it is appropriate to describe the measurements performed in this study (some measurements were described in Chapter 1.8) (refer figs 71-75).

Total length (TL) - from the snout tip to the tip of the longest caudal fin lobe;

Fork length (FL) - from the snout tip to the tip of the shortest caudal fin ray;

Head height (Hd ht) - the vertical distance from the occipital region to the breast across the operculum;

Head width (Hd w) - the distance between the normally-positioned operculae at the same position at which the head height is measured;

Eye diameter (eye) - the greatest horizontal distance between the orbit rim (called "length of orbit" in Hubbs and Lagler);

Pectoral and Dorsal spine lengths (D sp.; P sp.) - the distance from the structural base of the spine to its tip excluding the membranous filament tipping the spine. Where part of the spine was obviously lost (towards the tip), the length was not recorded unless the impression of the spine was clear in the fin. Consistent measurement was occasionally made difficult by the spine being "locked" at an angle to the body. The dorsal spinelet was not measured;

Snout length (Sn) - is measured from the snout tip to the front margin of the orbit;

Internostril distance (Intn. dist) - a straight-line measurement of the space between the anterior nostril openings;

Mouth width (Mth w) - the straight-line distance across the mouth opening, measured from each rictus;

Width of the "maxillary" (= premaxillary) tooth band (w.mxt.b) - the broadest straight-line distance measured across the curve of the tooth band;

Length of the "maxillary" tooth band (l.mxt.b) - the longest (= anteriad-caudad) distance of the tooth band, usually measured across the lateral arm;

Barbel length (Bbl) - measured with the barbel taught, from its insertion to its tip. Barbels which lacked their tip were not measured;

Occipital process (= supraoccipital) length (OPl) - the straight-line distance between the anterior-most point of the bone dorsomedially and its most posterior point where it meets the predorsal (= nuchal) plate;

Occipital process breadth (OPb) - widest distance measured in a straight line, at the base of the process where it meets the remainder of the bony head shield. In thick-skinned specimens some difficulty was experienced in discerning the limits of the process;

Bony interorbital width (b.Io.w.) - the narrowest expanse of the bony head shield between the eyes obtained by holding the caliper points firmly against the edges of the bone;

Length of the dorsal fin base (l.D base) - the greatest overall basal length, between the outer aspects of the first spine and the last ray;

Length of the anal fin base (l.A base) - the straight-line basal distance between the outer aspect of the first ray and the last ray;

Predorsal length (Pred.) - the distance between the snout tip or upper lip and the anterior base of the first dorsal spine;

Length of fin rays - measured from the structural base of the ray to its tip;

Interdorsal fin space (i-d.space) - the distance between the base of the last dorsal ray and the anterior of the adipose fin;

Adipose fin base length (ad.f.b.l) - the basal distance between the anteriormost elevation of the fin and its posterior contact with, the body;

Caudal peduncle depth (cpd) - the shallowest vertical distance between the upper and the lower profile of the peduncle;

Caudal peduncle length (cpl) - the straight-line distance between the base of the last anal ray and the centre of the caudal fin base.

Counts were made with one or two needle-like probes. Some structures (e.g. the anal fin rays, lateral line tubules) were often difficult to discern because of the thickened body skin or mucous around or over them. Consequently, osteological material was examined.

Only the total count is given for the anal and ventral (or pelvic) fins (encompassing both branched and unbranched rays). In the anal fin, the anterior, unsegmented rays grade into the branched rays. The short, broad spinelet (buckler) of the dorsal fin is not included in the fin formula. The gill rakers (GR) were counted along the first arch, recorded both as the total number and as the number on the upper and lower limbs of the arch, the raker in the arch angle being included in the lower limb count. The total raker count on the front of the fourth arch was also counted as were rakers along the posterior aspect of all complete arches, when present. Usually only the left-hand set of gill arches were checked. When the operculum and associated branchiostegals had to be severed so that counts could be made, the right-hand side was examined. In this study, a raker is recognised as a firm structure with its base narrower than its length.

The vertebral count is in four parts (fig. 76): (a) the anterior fused vertebrae concealed by the laminar bone; (b) the trunk vertebrae with open haemal arches (these two sections constitute the precaudal vertebrae); (c) the haemal vertebrae of closed haemal arches and bifurcate spine tips; (d) the remaining vertebrae up to and including the terminal (hypural) vertebra (these two sections are termed the caudal vertebrae). Counts were obtained both from radiographs and osteological preparations (Chapter 2). (Roberts [1978] did not include the terminal [hypural] vertebra when stating vertebral counts of New Guinea ariids.)

6.2.2 Synonymies

An abbreviated synonymy is presented wherein references to original descriptions, misapplied names, new combinations and incorrect spellings are listed. The complete references for abbreviated synonymies appear in the bibliography. The type locality of each nominal taxon is stated, with information on the condition and museum number of types representing Australo-Papuan species.

No names are proposed here for new taxa.

6.2.3 Material examined

Relevant collection information and SL are given. A Gazeteer of all Australo-Papuan localities from where material was collected, is presented as Appendix B. Distribution data was frequently supplemented with correctly identified material from museums and/or noted in recent literature. Specimens utilised in statistical analyses are asterisked.

6.2.4 Description

A definition and taxonomic description of each species is given. Characters which define the family or genus may not be repeated here, except for a meristic summary. Morphometric data are presented in selected ratios and as percent of HL and SL. Comparison of species within a genus is made where appropriate, sometimes facilitated by scatter diagrams and frequency histograms (Sokal and Rohlf, 1973) of counts of structures and morphometric ratios. The definition of each taxon is largely morphological.

Description of colouration is based on fresh material, colour transparencies and field notes.

Illustrations of small specimens were prepared either with the aid of a WILD M5 stereo-dissecting microscope with Camera Lucida attachment or for larger specimens, by transferring actual measurements to graph paper and reducing the sketch so obtained before overdrawing. Outline drawings of the whole or parts of specimens are presented supplemented with colour and black & white photographs where appropriate.

Institutional abbreviations are stated in Chapter 1.8.1

6.2.5 *Statistical analyses*

Each taxon was arbitrarily allocated a number and specimens were ordered under the species' number. The layout and explanation of characters is presented in Appendix C. The analyses were performed on a VAX 780 computer using relevant BMDP packages (Dixon, 1985).

To ascertain which factors contributed most to an explanation of the total variability, all variables were initially evaluated using *Principal Component Analysis* (BMDP subprogramme 4R in Dixon, 1985). Principal component analysis provides a low-dimensional representation of the data. New independent variables are created, which are linear combinations of the original variables. Successive linear combinations defined by eigenvalues, maximise the variance of the resulting scores (see Reyment *et al.*, 1984). Means, standard deviations, standard error of the mean, variation coefficient and range were computed for all data using the BMDP subprogramme 1D (Dixon, 1985).

Clear distinction could not be made easily between several sympatric ariid taxa classified *a priori* on the basis of literature descriptions and a combination of certain qualitative characteristics. These nominal taxa were: *latirostris*, *acrocephalus* and *taylori*; *leptaspis*, species 2, *midgleyi*; *graeffei*, *australis*, *curtisii* and certain unidentifiable specimens; *berneyi* and *cleptolepis*; *argyropleuron*, *macrocephalus*, *crossocheilus*, *polystaphylodon*, *leiotetocephalus*, *tonggol*; *microstomus*, *kanganamanensis*, *solidus*, *bernhardi*; and *papillifer*, *velutinus*, *taylori*. The statistically significant variables from relevant pairs or groups of these were "submitted to" *cluster analysis* (BMDP subprogramme KM in Dixon, 1985) to substantiate the presence or absence of distinct groups. The suspected number of clusters was specified and variables were allocated into the cluster whose centre (mean of cases in the cluster) was closest (Thorpe, 1976; Dixon, 1985).

The correlation coefficients between pairs of actual variables and of ratios calculated from them, were presented as *scattergrams* (Sokal, 1965) using BMDP subprogramme 6D for Bivariate Scatterplots in Dixon (1985). In each case, the simple regression delineating the change in the dependent variable Y in relation to the change in the independent variable X, was calculated.

The cluster groupings and scattergrams were subjectively evaluated (e.g. on cluster overlap, biological significance) and interpretation of these results favoured acceptance of a reduction in the number of taxa (see Chapter 6).

Stepwise discriminant function analysis (BMDP subprogramme 7M in Dixon, 1985) was performed on several pairs of ariid taxa where any one or two variables would not discriminate between the taxa such that only a very small percentage remained misclassified. Taxa compared were: *latirostris* - *leptaspis*; *latirostris* - *taylori*; *leptaspis* - species 2; *leptaspis* - *midgleyi*; *graeffei* - *berneyi*; *velutinus* - *taylori*. The discriminant function is chosen to maximise the separation between two groups, relative to the variation within each group (Reyment *et al.*, 1984). In the analysis, variables which discriminate between the groups are linearly combined so that the groups are forced to be as statistically distinct as possible. By the stepwise method, an optimal set of discriminating variables is selected. Independent variables are entered into the analysis on the basis of their discriminating power: the highest value variable (on the selection criteria) is paired in turn with each of the remaining available variables to select the second variable to "enter the equation" to maximise intergroup differentiation, and so on. The procedure continues until differentiation between groups cannot be improved. The programme classifies each specimen initially assigned to a group using the discriminant function Z and gives the percent of correct classifications (Klecka, 1975; Dixon, 1985). To produce less bias in the classification, a jackknife classification is performed wherein a classification function is computed for each case without the actual case, thence used to classify the omitted case. Z functions for most of the compared taxa are stated in Appendix C.

6.2.6 Biological information

In an attempt to form a picture of the co-related environmental influences on and trophic modifications of the Ariidae, biological information was gathered for each taxon:

Habitat information was extracted from survey reports, some papers and general texts on the geography of the area from which specimens were obtained.

Maximum size was noted from either specimens examined or literature records of accurately determined material.

Dietary preference was ascertained from examination of gut content and food remaining in the mouth and from literature accounts of accurately determined material (e.g. Roberts, 1978; Haines, 1979; 1983).

Breeding. The gonads of adult specimens were examined and their maturity stage noted, following the criteria of Pollard (1972). Approximate spawning times were estimated by observation of the development of ariid secondary sex characteristics (e.g. reduction of palate tooth patches and swelling of the oro-branchial cavity in males; thickening of the inner rays of the ventral fin and development of a thick, fleshy "pad" on the 6th ray in females), suffusion of blood in the fins, reduced gut (females, brooding males) and large abdominal fat deposits (prebrooding males) (see also Rimmer, 1985, 1985a). Interspecific variation in the form or development of these characteristics was also noted.

The number of mature or maturing ova were counted as a measure of *fecundity*.

Analysis of the collecting locality, readiness to spawn and time of year gave an indication of any *migration* tendency in ariids.

6.3 NEDYSTOMA

6.3.1 *Definition and content*

Nedystoma Ogilby, 1898

Nedystoma Ogilby, 1898: 32 [type species *Hemipimelodus dayi* Ramsay and Ogilby, 1886, by original designation and monotypy]
Doiichthys Weber, 1913: 532 [type species *Doiichthys novaeguineae* Weber, 1913, by monotypy]
~~Type: *Hemipimelodus dayi* Ramsay & Ogilby, 1886~~

This taxon is distinguished by possession of a *reduced gonad* (character 57A) and *smooth neurocranium* (character 28C); in combination with several homoplastic characters not widely distributed in the family: absence of ventral fin pads in sexually mature females; enlarged, rounded posterior dorsomedian fontanelle; well elevated and strong subvertebral cone; small or reduced temporal fossa; narrow anterior frontal arms + frontal posteriorly broad + enlarged lateral ethmoid-frontal space; extensive laminar bone on anterior vertebrae; reduced posterior cleithral process; reduced abdominal cavity - precaudal vertebrae </= 32% total vertebral number. *Nedystoma* also has

more gill rakers on the first arch than all other taxa except *Brustiarius* Herre, *Cathorops* Jordan and Gilbert and species 4; and a narrow band of very small teeth in each jaw.

Known content of the genus:

dayi Ramsay & Ogilby (freshwater of southern New Guinea);
novaeguineae Weber (estuarine to freshwater of southern New Guinea)

6.3.2 Key to the known species of *Nedystoma*

A. Gill opening restricted; short barbels, chin barbel bases almost transversely aligned; 19-24 anal rays .... *dayi* (p.95)
AA. Gill opening wide; long barbels, chin barbel bases well-staggered; 29-33 anal rays .... *novaeguineae* (p.202)

DISCUSSION

The taxa included in this genus are very diverse for a number of character states, e.g. gill opening width; eye position, size and freedom; mouth width; buccopharyngeal flap development.

As well as naming the genus, Weber (1913) erected a new family to accommodate *novaeguineae*. He was followed by Weber and de Beaufort (1913) and Munro (1958, 1964, 1967). Chardon (1968) was the first to formally recognise that Doiichthyidae is a synonym of Ariidae. The characters which influenced Weber however (e.g. covered and low-set eye, fine teeth, numerous gill rakers and anal rays) are not autapomorphic in a phylogenetic reconstruction.

ETYMOLOGY

Greek, *nedys* = womb, pouch; *stoma* = mouth. In reference to the habit of oral incubation practised by members of this family (the type of *dayi* is incubating).

6.3.3

Nedystoma dayi (Ramsay & Ogilby)

(Figures 77, 78, 79; Tables 18, 19)

Hemipimelodus dayi Ramsay & Ogilby, 1886: 16 (Strickland River, New Guinea)

Nedystoma dayi Ogilby, 1898: 33

DEFINITION

Palate naked; premaxillary tooth band horizontal, short and narrow; mouth horizontal, gape quadrangular; lips fleshy and thin; 2-3 pairs of large flaps of epithelium posteriorly on palate. Dorsomedian head groove rounded posteriorly; barbels thin and wispy, 14-22 %SL, bases close together on chin. Gill opening restricted, membranes continuous with isthmus medially; gill rakers posteriorly on all arches; total rakers on first arch 29-43. Eye diameter 16-38 %HL; eye free from head skin. Anal base 18-23 %SL. Fin spines long and slender, dorsal spine 20-27 %SL. Lateral line much branched anteriorly. Fresh colouration bluish above, iridescent; lower 2/3 of body white or cream.

DESCRIPTION

D I,7. P I,10-11. A 19-24. GR (first arch) 29-43 of which 7-13 on upper limb. GR (last arch) 33-44. Number of vertebrae 47-49 (40-42 free).

Body rotund, compressed posteriorly. Predorsal profile anteriorly convex, flat at interorbital, posteriorly straight and steep. Snout blunt, almost truncate; upper lip and snout moderately thick and fleshy, lower lip thin; inner lip margins finely crenulate. Mouth subinferior, slightly curved; jaw teeth not exposed when mouth closed. Nostrils ovate, anterior one slightly median to posterior one. Eye oval, mostly free of head skin. Eye situated dorsolaterally and just before mid-head length. Lateral ethmoid prominent. Gill opening restricted, membrane continuous with isthmus medianly and no free skin fold.

Teeth slender, conical, pointed and depressible; embedded in tissue: as narrow transverse band of 3-4 series in upper jaw; in 2-3 series in lower jaw, band broken by naked space at symphysis. No teeth on palate, which is covered anteriorly with many fine, low papillae. Two or 3 pairs of very large folds of epithelial tissue hanging down from back of palate before branchial chamber.

Head shield prominent through thin head skin: of four diverging ridges extending anteriorly to eye and nostrils; and very finely and closely granulated posterior section over nape. Dorsomedian head groove flat, beginning level with nostrils, expanding posteriorly to form a rounded or elliptical space well short of supraoccipital process base. Supraoccipital process narrow and oblong posteriorly, sides concave, and low, rounded keel. Naked space present above operculum; sides of head venulose. Humeral process smooth, of a long-based triangle with short, acute shaft; very heavily ossified anteroventrally. Small axillary pore rounded.

Barbels thin and wisp-like. Maxillary barbel rarely reaches head margin, usually to 1/2 eye diameter before it. Mandibulary barbel reaches to head margin ventrally. Mental barbel reaches opposite middle or hind margin of eye. Chin barbel bases close together, almost aligned.

Gill rakers numerous, subequal in length to opposing filaments. Short rakers present on back of all arches: 34-50 along back of first arch; 38-51 on second; 34-44 on third. No fleshy pads present on gill arches per se, but palate folds or valves and a third or fourth in pharynx, are closely associated with gill arches.

Spines of dorsal and pectoral fins long and sharp, slender and compressed, with pattern of very fine, longitudinal striae. Pectoral spine slightly curved. Anterior margin of spines usually smooth but tip with 4-6 low, antrorse serrae: about 20 low serrae on posterior margin of dorsal; 20-30 antrorse or perpendicular serrae on hind pectoral margin. Short filament at tip of spines. Longest dorsal ray 2.2-3.9 times last ray. Pectoral extends to below middle of dorsal. Ventral fin slender in both sexes, reaching to anal origin in males, to 5th-7th ray in females. Sexually mature females exhibit the very minimum of thickening on inner ventral ray. Adipose fin above posterior half of anal fin. Anal margin slightly concave, longest ray 2.2-3.9 times last ray. Caudal lobes broad basally, slender and tapered.

Lateral line straight, curved dorsad at tail base. Extensive system of branched lines extend from anterior third of lateral line, lines short and regularly spaced over remainder. 20-24 vertical series of papillae ascend from line along body length. Caudal peduncle moderately deep.

Fresh colouration: Bluish or charcoal grey above, sides and trunk iridescent dark blue, lower 2/3 of head and abdomen white or cream. Fins dusky olive or grey, ventral and pectoral fins yellowish or cream.

Colour in preservative: Upper 2/3 of head and front of body bluish brown, charcoal or tan, back above remainder of lateral line brown or tan; snout, rest of head and sides cream or pale dusky. All fins pale brown, upper aspect of pectoral dark brown. Barbels dark brown. Peritoneum pale.

DISTRIBUTION

NEW GUINEA: south-draining rivers. Lorentz River, Digoel River at Tanah Merah, upper, middle and lower Fly River, Lake Murray, Strickland River, Kikori River, Baimuru, Beara, Wame River, Purari River and delta area from the upper estuarine zone including Ivo River and Pawria, to Bevan Rapids, Wabo and Kibi Creek, and Matupe River at Murua. Maunsell and partners (1982) caught *N. dayi* between 350 and 850km from the Fly River mouth.

BIOLOGY

Habitat: Haines (1979) found *N. dayi* in fast-flowing and still freshwater, main river channels and side-branches but rarely in the upper estuarine zone (around Kikori); very rarely in the predominantly fresh and fluctuating salinity tidal waters of the *Pandanus*-*Sonneratia* zone and the *Nypa* zone of the Purari delta. Roberts (1978) collected *N. dayi* from a deep, swiftly flowing side-channel of the Strickland River; Boyden *et al*. (1975) reported *N. dayi* as very common at Kiunga, where the river is very wide, turbid and with widely fluctuating levels, and it occurs in similar habitat in the upper Strickland River (D. Gwyther, 1984).

Maximum size: to 350 mm FL (Haines, 1979).

Diet: Based on examination of stomach contents of my material, it appears that *N. dayi* is predominantly a detritophage, feeding on mud, algae and decaying animal and plant matter. However, it also consumes small invertebrates such as insects and crustacea In 21 stomachs containing food, Haines (1979) found prawn remains in one, crabs in one, insects in 3, plant material other than fruit in one, and algae and detritus in 15. All of the stomachs Roberts (1978) examined were filled with aquatic dipteran larvae - mostly *Culicoides* spp. but also fair numbers of much smaller Chironomidae. Maunsell and partners (1982) found that stomachs contained mainly chironomids and terrestrial insects, with some snails and organic detritus.

Breeding: Spawning probably occurs early in the late dry/early wet season. Haines (1979) observed breeding individuals in the freshwater delta, the lower Purari River and the main river and side-branches around Wabo; and ripe females were present in the Purari system in January (Haines, 1979). Roberts (1978) collected incubating males in late 1975, and the incubating male holotype and paratype (QM I.879) were probably collected towards the end of the year. Maunsell and partners (1982) caught mature females in the upper and lower Fly, early and mid-July. Haines (1979) found a minimum size at sexual maturity of 140 mm FL. The fecundity is as low as 10-20 (Haines, 1979). Roberts (1978: 12) counted "about 20" 10 mm diameter eggs in the mouth of a 183 mm SL male; Maunsell and partners recorded 15-17 ripe ova, 5 mm diameter, in one individual. In one gonad of each of two females I examined, were 16 eggs (diameter 7.5-11 mm) and 6 eggs (diameter 9-11.4 mm), respectively. The mouth of the incubating holotype (AMS B.9938) (illustrated by Whitley, 1941a) contains 14 small fish with SL range from 28.4-30.7 mm. Their yolk sacs are attached and all face forward.

DISCUSSION

Haines (1979) believed that N. dayi is replaced ecologically in the Purari delta and estuaries by "Nedystoma sp." (= "Arius" species 4).

Tortonese's (1964) H. dayi specimens are referable to "Arius" species 4.

Of all Australo-Papuan ariids, N. dayi is most similar to "Arius" species 4. The taxa can be distinguished by "generic" characters (e.g.

shape of the dorsomedian head groove; absence/presence and shape of ventral fin thickening in mature females) and other characters including: number of palatal flaps (2-3 pairs in *dayi*, one pair in species 4), snout length (30-36 %HL in *dayi*, 37-43 %HL in species 4), length of the premaxillary tooth band, and maxillary barbel length (46-76 %HL in *dayi*, 29-56 %HL in species 4).

TYPES

Ramsay and Ogilby did not state the number of their types and referred to only three. At the Australian Museum, B.9938 (162 mm SL) is the stated holotype ("9½inches"), with paratypes B.9939 (111.5 mm SL, number not attached to specimen), B.9940 (166 mm SL) and a fourth specimen. The AMS register book records B.9941 as a "Type, Strickland River, Roy. Geogr. Soc. Exped." with "destination: National Museum, Vic., letter 140/1887", and B.9942 as a Type with remark "Ex Harvard Univ., Mass., ex 14/90". M. Gomon (NMV) says there are 4 "cotypes" of *N. dayi* in the collection at NMV, numbers 51616-51619, SL's 89.3, 95.8, 98.2 and 148 mm. None ~~are~~ is an incubating male~~s~~. The actual whereabouts of B.9941 therefore is uncertain. The third AMS paratype appears to be AMS B.9942: it is an incubating male, 162 mm SL.

However, Fowler (1931) stated that the holotype and 4 paratypes are in the Queensland Museum, all as QM I.879. I have examined this lot: 3 specimens belong to *N. dayi* (75, 124 and 161 mm SL) and the other to *Cinetodus crassilabris* (80 mm SL, now reregistered as QM I.26087). The status of most of the supposed paratypes is therefore unclear.

Condition of "types": QM specimens sound, although shrunken and caudal fins tattered. The 161 mm specimen is incubating. The AMS holotype is in sound condition although bent and with cuts along the belly, at the lower jaw symphysis and across the RHS gill membrane. The tip of the dorsal spine, half of the RHS pectoral spine and a fair portion of the caudal fin, are lost. One paratype (B.9939) has the jaws cut through at each corner. I have not examined the NMV "types".

ETYMOLOGY

Named after Mr Francis Day FLS, FZS in recognition of his work on the fishes of India.

MATERIAL EXAMINED

SOUTHERN IRIAN JAYA - 5*, RMNH 28820, Digoel River near Tanah Merah, 14-17 April 1955, coll. M. Boeseman, 134-174 mm SL.

SOUTHERN P.N.G. - 1*, AMS B.9938, Strickland River, 07°35'S, 141°35'E, reg. Jan. 1886, coll. Froggatt, 162 mm SL (= HOLOTYPE); 1*, AMS B.9939, same data, 111.5 mm SL (= PARATYPE); 1*, AMS B.9940, same data, 166 mm SL (= PARATYPE); 1*, AMS B.9942, 07°17'S, 141°25'E, 162 mm SL (= PARATYPE); 3*, QM I.879, same data, 75, 124 & 161 mm SL (= PARATYPES); 2*, AMNH 13987, east bank of Fly River, opposite Sturt Island, Oct. 1936, coll. R. Archbold, A.L. Rand & G.H. Tate, 75 & 83 mm SL; 1*+1, AMS I.25992-001, Kibi Creek at Wabo damsite, 18 Jan. 1977, coll. A.K. Haines, 187.5 & 253 mm SL; 1*, AMS I.25992-002, same data, 200 mm SL; 1*, unreg. same data, 192 mm SL; 1*, AMS I.26976-001, billabong, mid-Purari River, 27 Nov. 1974, coll. A.K. Haines, 225 mm SL; 1, ZMA 119.486, same locality, May 1975, 205 mm SL; 1, QM I.22655, Arehava area, Purari delta, Jan. 1975, 187 mm SL; 1, UMMZ 215077, Wame River, March 1975, coll. A.K. Haines, 129 mm SL; 2, QM I.26081, same data, 158 & 225 mm SL; 2*, NTM S.12353-001, without data except from Purari River area, 1974-75, 214 & 220 mm SL; 3, AMS I.25993-001, same data, 196-201.5 mm SL.

6.3.4

Nedystoma novaeguineae (Weber)

New combination

(Figures 80, 81, 82; Tables 18, 19)

Doiichthys novae-guineae Weber 1913: 534, 608, fig. 12 (Varen River - tributary of the Lorentz River)

Doiichthys novae guineae: Tortonese, 1964: 24

Doiichthys novaeguineaea: Munro, 1967: 86, pl. 8, fig. 123

DEFINITION

Head broad and depressed; mouth wide, 50-62 %HL; snout spatulate. Eyes lowset, covered by head skin. Teeth very small, in one row in both jaws; palatal teeth in four patches: teeth few, patches small. Gill opening very wide; gill rakers numerous, 45-51 on first arch; rakers present on back of arches. Dorsomedian head groove rounded posteriorly. Barbels very long, maxillary barbel 51-57 %SL; bases well-separated on chin. Fin spines strong, very large serrae along pectoral spine inner margin; 29-33 anal rays. Caudal vertebrae 36-38, including 2-3 haemal vertebrae. ~~Matures at small maximum SL.~~ It is adult at a small size.

DESCRIPTION

D I,7. P I,9-10. A 29-33. GR (first arch) 45-51, of which 16-19 on upper limb. GR (last arch) 40-45. Number of vertebrae 50-52 (44-45 free).

Body slender, compressed; head depressed. Predorsal profile steep and straight, concave at interorbital. Snout well-rounded, broad and spatulate; lips much reduced along jaws, but fleshy at mouth corners. Mouth terminal (almost superior), very wide and curved; jaws slightly elevated at symphysis, particularly the lower. Nostrils small, ovate, anterior one slightly lateral to posterior one. Eye margin not free of head skin. Eye lateral, adjacent mouth corner and in line with or slightly below mouth gape; situated at mid-head length. Gill opening wide, membranes meeting anteriorly at an acute angle, leaving broad, free margin.

Teeth very small, conical, blunt tipped; very slightly depressible. Teeth in single row on both jaws, row interrupted on lower jaw by naked space at symphysis. Two small, separate patches of teeth on lateral extremities of palate: outer one of 7-10 teeth, vomerine patch of 2-3 teeth. Palate smooth anteriorly, finely creased posteriorly; no evidence of epithelial ridges.

Head shield very finely rugose, striate; prominent through thin skin. Dorsomedian head groove elongate, wider posteriorly; almost flat. Groove begins just behind jaw symphysis; distal end rounded, not reaching supraoccipital process base. Supraoccipital process oblong, sides slightly convex, and with low, angular median keel. Head laterally venulose; naked space in head shield above gill opening. Humeral process triangular above, heavily ossified below, a flange projecting over pectoral base. Shaft of process short, extending 1/5-1/4 distance along pectoral spine. Axillary pore large and slit-like.

Barbels very long, thin and flattened. Maxillary barbel reaches anal fin origin. Mandibulary barbel reaches anus or beyond to about 9th anal ray. Mental barbel extends to ventral base and up to 10-12th anal ray. Chin barbel bases strongly staggered.

Gill rakers slender, noticeably longer than opposing filaments. Shorter rakers present along posterior face of all gill arches: 46-54 (mean 49.6) on first arch, 46-58 (mean 50) on second, 30-46 (mean 39.2) on third. Arches posteriorly smooth, not padded.

Spines pungent and strong. Dorsal rounded, with pattern of fine, lengthwise striae and distal 2/3 of posterior margin finely serrated. Pectoral spine flattened, 7-10 large retrorse serrae along posterior border. Dorsal fin high, longest ray 3.1 longer than last ray. Pectoral low on sides, extending beyond dorsal fin. Ventral fin slender, reaching anal origin (both sexes); sexually mature females lacking any epithelial thickening on inner rays. Adipose fin oblong and moderately large, situated over posterior 2/3 anal fin. Anal long-based, margin truncate; longest ray 2.4-3 longer than last ray. Caudal lobes narrow and pointed.

Caudal peduncle compressed. Lateral line curved dorsad anteriorly and at tail base, and vertical series of pores ascend from line along its length.

Fresh colouration: Unknown.

Colour in preservative: Fawn or yellowish brown, brown over back and top of head, silvery on belly and sides. Fins yellowish or tan, darker brown on margin of dorsal and caudal lobes. Barbels brown or fawn. Peritoneum pale.

DISTRIBUTION

NEW GUINEA: tidal reaches and estuaries of south-draining rivers. Varen River, Katau, lower Fly River, Balimo (Aramia River), Era River and Wame River (Purari River delta).

BIOLOGY

Habitat: Predominantly estuarine (Liem and Haines, 1977); or fresh and brackish water (Weber, 1913). Haines (1979) found *N. novaeguineae* only in the *Pandanus*-*Sonneratia* zone of river systems, and rare in the Purari, common in the Era. Tidal influence in the Aramia River extends hundreds of kilometres from its mouth, and possibly a similar situation exists along the Lorentz River into the Varen River.

Maximum size: 150 mm SL.

Diet: Haines (1979) recorded the species as a prawn-eater. The stomachs of two specimens I examined contained bristles (polychaete), small crustacean fragments and plant detritus.

Breeding: The two female specimens from the Era River, collected in December, have developed ovaries at about maturity stage IV-V. This indicates that spawning occurs during the early wet season. One female bears 33 large ova, ova diameter 1.4-2.0 mm. The 150 mm SL fully mature fish has a total of 11 large, yolked ova in the gonad (diameter 3.4-6.8 mm; mean 4.9 mm) and more numerous smaller, yoked ova (diameter 2.0-2.7 mm).

DISCUSSION

N. novaeguineae is apparently rare. It was not collected by Roberts (1978) and Boeseman Allen and Boeseman, 1982). ~~(pers. comm.; 1954 Dutch New Guinea Expedition).~~ Its small size may, however, render it inconspicuous.

Among Australo-Papuan ariids, this small species has a very distinct external morphology. The unique shape of the mesethmoid, lachrimal and nasal bones and possession of 7 infraorbitals, further characterise it.

TYPES

This species is based on 6 syntypes, 108-137 mm TL. Five are registered in the ZMA as ZMA 104.122 (Nijssen et al., 1982); and one is in the AMNH, number 9482, 93 mm SL.

Condition of types (on two syntypes examined, 84.5 & 103 mm SL): fair. Body rigid and somewhat shrunken; all barbels intact, although most fins are tattered, notably the caudal.

ETYMOLOGY

Named for the type locality.

MATERIAL EXAMINED

SOUTHERN IRIAN JAYA - 2*, ZMA 104.22 (in part), Varen River, trib. of the Lorentz River, 3 May 1907, coll. H.A. Lorentz, 84.5 & 103 mm SL (= SYNTYPES).

SOUTHERN P.N.G. - 1*, AMS I.27416-001, Era River, 9 Dec. 1974, coll. A.K. Haines, 145; 1*, AMS I.27416-002, same data, 150 mm SL; 1*, USNM 288554, Wame River near Kapuna, 6 May 1975, coll. A.K. Haines, 112 mm SL; 1*, KFRS F02671, Balimo area, near Aramia River, July 1968, 93 mm SL; 1*, QM I.22656, 8-mile Passage, Fly River delta, 15-16 July 1981, coll. J. Watson, 56 mm SL.

6.4 CINETODUS

6.4.1 Definition and content

Genus *Cinetodus* Ogilby

Cinetodus Ogilby, 1898: 32 [type species *Arius froggatti* Ramsay and Ogilby, 1886, by original designation and monotypy]
Pachyula Ogilby, 1898: 33 [type species *Hemipimelodus crassilabris* Ramsay and Ogilby, 1886, by original designation and monotypy]
Tetranesodon Weber, 1913: 545 [type species *Tetranesodon conorhynchus* Weber, 1913, by monotypy]
Septobranchus Hardenberg, 1941: 223 [type species *Septobranchus johannae* Hardenberg, 1941, by monotypy]
~~Type: *Arius froggatti* Ramsay & Ogilby, 1886~~

This taxon is distinguished by the amalgamation of the extrascapular and epioccipital (character 24B) and possession of a long, horizontal and oblong posterior cleithral process (character 14A); in combination with several homoplastic characters: absence of ventral fin pads in sexually mature females; well-elevated and strong subvertebral cone; a restricted gill opening; broad-based triangular supraoccipital process; well-elevated and extensive laminae of the 4th neural spine and the ventral aspect of the supraoccipital; large pectoral axillary pore; strong, compact pectoral girdle and coracoid keel; dark blue or black colour on the proximal dorsal aspect of the pectoral fins; chin barbel bases almost transversely aligned, close together; heavily ossified skull; distinctly ventral mouth; low number (3-5) of haemal vertebrae. Gonads bilobate.

Known content of the genus:

froggatti Ramsay and Ogilby (estuarine to freshwater of southern New Guinea and northern Australia);
carinatus Weber (fresh to brackish water of southern New Guinea);
crassilabris Ramsay and Ogilby (freshwater of southern New Guinea);
conorhynchus Weber (freshwater of southern new Guinea)

6.4.2 Key to the known species and subgenera of *Cinetodus*

A. First pharyngobranchial lost or fused with epibranchial; teeth present on autogenous plates on palate; posterior dorsomedian fontanelle reducing with age; posterior aspect of gill arches smooth .... (*Cinetodus*) .... B (p. 208)

AA. First pharyngobranchial present, free from epibranchial; no tooth-bearing autogenous plates on palate; posterior dorsomedian fontanelle open at all growth stadia; numerous papillae along posterior aspect of gill arches .... (*Pachyula*) .... C (p. 222)

B. Inner margin of pectoral spines with many large, flattened serrae; both vomerine and outer palatal tooth patches present (i.e. 4 patches across front of palate); Br.6 .... *carinatus*

BB. Inner margin of pectoral spine moderately serrated; vomerine teeth absent (i.e. 2 patches); Br.5 .... *froggatti*

C. Total vertebral number 51-54; lips very thick and fleshy .... *crassilabris*

CC. Total vertebral number +/- 45; lips reduced .... *conorhynchus*

DISCUSSION

Whitley (1956) placed *Pachyula* as a subgenus of *Hemipimelodus* Bleeker, both taxa characterised by an edentate palate. He recognised the thick lips and large adipose fin of the type, *crassilabris*, as worthy of ranking. Hardenberg (1941) made no reference to Ogilby's genera.

ETYMOLOGY

Greek, *kineo* = move, moveable; *odontos* = tooth. In reference to Ogilby's (1898: 32) interpretation that the palatal teeth were "implanted on a movable cushion".

Subgenus *Cinetodus* Ogilby

Type: *Arius froggatti* Ramsay and Ogilby, 1886: 14

6.4.3

Cinetodus (*Cinetodus*) *froggatti* (Ramsay & Ogilby)

(Figures 83, 84, 85, 86; Tables 20, 21)

Arius froggatti Ramsay & Ogilby, 1886: 14 (Strickland River)

Cinetodus froggatti: Ogilby, 1898: 32

Tachysurus froggatti: Fowler, 1928: 62

Septobranchus johannae Hardenberg, 1941: 223, fig. 3 (Merauke)

DEFINITION

Elevated body at dorsal fin; steep predorsal. Mouth small (27-31 %HL); snout blunt. Head shield finely striate; supraoccipital very broad, triangular. Premaxillary teeth in oblong patches; no vomerine teeth; palatal tooth patches oblong, well separated. Chin barbel bases close together; gill opening restricted, membranes continuous with isthmus; club-shaped rakers along back of all arches. Adipose fin large and oblong. Fresh colouration dark blue or reddish above; upper pectoral fin dark bluish brown.

DESCRIPTION

D I,7. P I,10-11. A 17-19. GR (first arch) 11-16, of which 5 on upper limb. GR (last arch) 10-16. Number of vertebrae 49-52 (42-46 free).

Heavy-bodied fish, well elevated at nape, moderately tapered anteriorly and posteriorly. Predorsal profile steep; rounded before eye, slightly concave at interorbital, strongly convex at nape. Head narrowed anteriorly; snout blunt; lips well-developed but thin and fleshy, almost continuous with palate epithelium medially, thicker laterally. Mouth subinferior, gape small, almost horizontal; no premaxillary teeth exposed when mouth closed. Nostrils ovate, posterior one directly behind anterior one. Fine, papilla-like structures scattered over anterior of head in large individuals. Eye ovate, moderately large, dorsolateral, free from head skin; eye situated 1/2 to all its diameter before mid-head length. Lateral ethmoid slightly prominent before eye. Gill opening restricted, terminating short distance ventral to pectoral base; gill membranes continuous with isthmus.

Teeth small and conical, slightly depressible, their tips blunt or spatulate; usually embedded in thick, spongy tissue. Premaxillary teeth in 8-10 irregular series forming two broad, oblong, contiguous patches. Crescentic bands of teeth on lower jaw separated at symphysis by edentulous space. Vomer edentate; two oblong and oblique palatal tooth patches, well-separated. Palate smooth with two long, oblique ridges of epithelial tissue just before branchial chambers.

Head shield consisting of close-set, anastomosing fine striae and granular rugae; shield usually exposed through thin skin. Dorsomedian head groove lanceolate, bounded by strong, striate ridges, extending from between nostrils to about 1/2 eye diameter before base of supraoccipital process. Process very broad and convex at base; sides straight, slightly converging posteriorly; no median longitudinal keel. Side of head noticeably venulose; small, smooth triangular space in head shield posterodorsal to gill opening. Humeral process prominent, almost horizontal, blunt tipped; finely granular like head shield. Process oblong above, expanded and ossified anteroventrally; extending 1/3-1/2 along pectoral spine. Axillary pore ovate and moderately large.

Barbels flattened and thin. Maxillary barbel extends from head edge to below dorsal spine; mandibulary barbel from preopercular ridge to base of pectoral; mental barbel from short distance beyond eye to level with gill membrane ridge ventrally. Chin barbel bases almost transversely aligned.

Gill rakers short, 1/4-1/3 length of opposing filaments. Gill arches smooth, stout rakers with expanded tips present along posterior of all gill arches: 14-18 along first arch; 13-17 along second; 11-16 along third. Low, fleshy epithelial fold posterodorsally on second (and third) arches.

Fin spines robust, moderately compressed. Anterior spine margin finely granular with 3-6 antrorse serrae towards tip; sides finely striate; posterior margin with antrorse, sharp serrae: 8-15 along dorsal, 18-30 along pectoral. Spines approximately equal in length. Last dorsal ray 2.4-3.1 shorter than longest ray. Pectoral extends to below posterior dorsal rays. Ventral fin narrow in males, reaching well short of anal origin; broad-based in females, reaching opposite 2nd to 4th anal ray. Sexually mature females lack or have minimum thickening on inner (6th) ventral ray. Adipose fin large and oblong, originating before or opposite anal origin and terminating opposite or beyond base of last anal ray. Anal high, outer margin almost truncate, longest ray 2.6-3.8 longer than last ray. Caudal lobes broad basally, moderately slender distally; upper lobe longer.

Caudal peduncle stout. Lateral line almost straight, sloped dorsad below dorsal fin and at tail base. Many short oblique, branching lines diverge from line above and below, very extensive anteriorly; few vertical series of pores extend over back and lower sides.

Fresh colouration: Blackish blue or dark reddish brown above, tan on sides, grey, cream or white below. Sometimes bronze or golden sheen over back and upper sides. Barbels dark brown. Pectoral fin dark bluish brown above; other fins dark or light brown.

Colour in preservative: Dusky fawn to dark or bluish tan above, cream, white or pinkish below. Barbels brown. Pectoral fin charcoal above, margin and undersides pale; other fins brown or orangey, stippled dark brown, adipose fin dark basally. Peritoneum pale or greyish.

DISTRIBUTION

NEW GUINEA: south-draining rivers and associated coast: Digoel River, Merauke, Katau, Fly River (from mouth to Kiunga), Lake Murray, Strickland River, Kikori River and delta, Pie River, Wame River, Purari River and delta; estuaries and shallow coastal waters of the Gulf of Papua, Kerema Bay.

AUSTRALIA: north-draining river(s?): Roper River system (including Waterhouse River, Roper River and Wilton River).

BIOLOGY

Habitat: *C. froggatti* is common in the lower mangrove to *Pandanus*-*Sonneratia* zones of the Purari River delta, sometimes present in the freshwater delta (Haines, 1979). Haines never caught it in pure fresh water. In contrast with the Purari system, *C. froggatti* is moderately common in fresh water in the Fly River system (Roberts, 1978; R. Moore, pers. comm.). The Digoel River specimen I examined probably also came from fresh water. The species inhabits slow, moderately fast and fast-flowing water, grey and turbid or clear reddish brown (Roberts, 1978). *C. froggatti* is also found in muddy, moderately saline waters.

Maximum size: 423 mm SL (Roberts, 1978).

Diet: Exclusively molluscivorous (Haines, 1979; Roberts, 1978; pers. obs.). Both bivalve and gastropod molluscs are swallowed whole by *C. froggatti*. Roberts (1978) listed the taxa ingested by the specimens he obtained. Gastropods only were in the stomachs of my specimens. Maunsell and partners (1982) recorded gut contents from small (to 100 mm SL) specimens as: crustacean fragments, insects and a blind goby (Pisces: Trypauchenidae). However, their findings are not reliable: a sample of six small ariids labelled "*C. froggatti*" and sent to me by Maunsell and partners after publication of their report, actually consisted of: *Nedystoma novaeguineaea* (Weber) (1 specimen), *C. carinatus* (Weber) (2 specimens) and "*Arius*" species 6 (3 specimens). I did not examine these authors' figured specimen (p. 182) from the Fly River delta.

Breeding: Haines (1979) caught 39 female and 14 juvenile *C. froggatti*, but no males. The breeding season extends from October to February in the coastal areas of the Gulf rivers surveyed by Haines, and females with gonad stages of V and VI were caught in the Roper River system (Australia) in September (H. Midgley, pers. comm.). The 370 mm SL specimen from the Wilton River I examined was fully mature. One gonad (cut open) contained 20-25 ova of 10.5-11 mm diameter. Smallest size at first maturity noted by Haines (1979) is 21 cm FL.

DISCUSSION

Hardenberg (1941) described this species as *Septobranchus johannae*. His figure and description agree with similar-sized *C. froggatti*, and although I have not located the type, I support Munro's (1964) placement of *S. johannae* in the synonymy of *C. froggatti*.

Roberts (1978) remarked on the close outward similarity of *Cinetodus froggatti* and *C. carinatus* (Weber). The features shared by these taxa include the convex nape and broad supraoccipital process, elevated body and dark upper pectoral base; as well as characters of the genus. Palatal dentition and pectoral spine serrature distinguish between the taxa, as well as mouth width (27-31 %HL in *froggatti*, 30-43 %HL in *carinatus*), adipose base length (12-16 %SL in *froggatti*, 14-22 %SL in *carinatus*) and gill raker count on first arch (11-16 in *froggatti*, 15-19 in *carinatus*). No other Australo-Papuan ariids could be confused for these taxa.

This species was represented solely by the holotype for more than 70 years, both Tortonese and Munro recording additional specimens in 1964 (my specimens CSIRO A.3023 and CSIRO A.2983 are not the same specimens that Munro reported).

I do not consider that the palatal tooth patches in *C. froggatti* are more "movable" than those in other ariids (*contra* Ogilby, 1898, Weber and de Beaufort, 1913 and Munro, 1967).

TYPES

Arius froggatti: Based on one specimen, AMS B.9936, 244 mm SL ("11 3/4 inches" length).

Septobranchus johannae: The whereabouts of the single type (30 cm SL) is unknown.

Condition of type: fair. Body shrunken anteriorly, creased across interdorsal space, bent behind adipose fin. Jaws cut at LHS corner, lower jaw sagging. Belly slit, skin pocked. Fins mostly intact although dorsal membrane split, tips of caudal lobes and margin of anal lost. No body pigmentation remains.

ETYMOLOGY

Named for W. Froggatt, who collected all of the Royal Geographical Society of Australasia's specimens on its visit to New Guinea.

MATERIAL EXAMINED

SOUTHERN IRIAN JAYA - 1*, RMNH 28816, Digoel River north of Tanah Merah, 13 April 1955, coll. M. Boeseman, 365 mm SL; 1, WAM P.29965-005, Manimeri River, 27 March 1989, coll. G.R. Allen, 86 mm SL.

SOUTHERN P.N.G. - 1*, AMS B.9936, Strickland River at 07°17'S, 141°35'E, reg. 1886, coll. W. Froggatt, 244 mm SL (= HOLOTYPE); 1, KFRS F.4648-02 (ex USNM 217079), middle Fly River, Nov. 1975, 391 mm SL; 1, KFRS F03772, Lake Murray, Oct, 1973, 233 mm SL; 1, KFRS F.4679-01 (ex USNM 217080), lower Fly River, Dec. 1975, SL not noted; 1, KFRS F.5626-01, Sagero, N bank of Daru Island, Sept. 1988, 230 mm SL; 1, unreg., same data, 215 mm SL; 3, KFRS F0036, Kikori River, Dec. 1956, 103.5-148 mm SL; 1, KFRS F.5401-02, Ravikoupara, Oct. 1975, SL not noted; 1*, CSIRO A.3023, mouth of Panaroa River, 1955, coll. A.M. Rapson, 185 mm SL; 1*, CSIRO A.2983, Purari River, 4 April 1955, coll. A.M. Rapson, 172 mm SL; 1*, RMNH 30315, Purari River delta, 1974-75, coll. A. Haines, 105 mm SL; 1*, AMS I.26971-001, Arehava, 19 Jan. 1975, coll. A.K. Haines, 206 mm SL; 1*, MNHN 1988-803, Wame River, 5 May 1975, coll. A.K. Haines, 241 mm SL; 1*, QM I.22653, Gulf of Papua, May 1975, coll. A.K. Haines, 147 mm SL; 1*, ZMA 119.485, same data, 167 mm SL; 1*, AMS I.27417-001, Gulf of Papua, no date, 215 mm SL; 1*, USNM 288552, same data, 103 mm SL; 1*, WAM P.30031-001, Moinamu, 7 Aug. 1976, coll. A.K. Haines, 172 mm SL; 1*, unreg., same data, 169 mm SL; 1*, NTM S.12357-001 off Kerema, trawled, June 1978, coll. S. Frusher, 208 mm SL; 1*, KFRS F.5522-01, Aird Hills, 10 Dec. 1974, coll. A.K. Haines, 315 mm SL.

NORTHERN TERRITORY - 1*, QM I.16729, Roper River, 14-16 Sept. 1979, coll. H. & M. Midgley, head only, SL not stated; 85 mm HL; 1*, unreg., same data, head only, SL not stated: 109 mm HL; 1*, NTM S.12080-001, Waterhouse River, 21-22 Sept. 1979, coll. H. & M. Midgley, 370 mm SL.

6.4.4

Cinetodus (*Cinetodus*) *carinatus* (Weber)

New combination

(Figures 87, 88, 89, 90; Tables 20, 21)

Arius (*Hemiarius*) *carinatus* Weber, 1913: 537, 608, figs 13 & 14

(Lorentz River; Sande River)

Arius carinatus: Weber & de Beaufort, 1913: 292, figs 118, 119

Tachysurus carinatus: Fowler, 1928: 62

Hexanematichthys carinatus: Munro, 1958: 123

Arius (*Hexanematichthys*) *carinatus*: Kailola, 1974: 61.

DEFINITION

Elevated body at dorsal fin; predorsal steep. Snout tapered, prominent. Nostrils and axillary pore large. Supraoccipital very broad, triangular. Four tooth patches arranged across front of palate: vomerine patches rounded, others larger and oval. Rakers on posterior of all gill arches; gill opening restricted and membranes forming fold across isthmus. Fin spines stout, dorsal shorter than pectoral; posterior margin of pectoral with 18-30 large, flattened serrae at right angles to spine. Adipose fin rectangular, its base longer than anal. Fresh colouration reddish brown above; upper aspect of pectoral fin dark bluish brown.

DESCRIPTION

D I,7. P I,9-11. A 15-18. GR (first arch) 15-19, of which 6-7 on upper limb. GR (last arch) 15-20. Number of vertebrae 49-51 (42-44 free).

Body robust, tapered from nape to prominent snout; posteriorly well-compressed. Predorsal profile steep and straight thence convex at nape. Snout blunt, moderately rounded in young, more acute in larger individuals; projects beyond almost truncate lower jaw. Mouth moderately narrow, subinferior. Snout tip and lips thick and fleshy, inner margin crenulate or entire, lip thickness increasing with age. Nostrils large and rounded; anterior nostril slightly median. Eye large, dorsolateral, margin free from head skin, 1/2 to 2/3 its diameter before mid-head length. Gill opening restricted, membranes attached to and forming a fold across front of breast.

Depressible, pointed teeth arranged in 9-11 series in broad band in upper jaw; 1/2-2/3 band exposed when mouth closed. Narrow tooth band in lower jaw with 4-6 series of teeth, divided by naked space at jaw symphysis. Teeth on palate slightly stout and pointed, grouped into 4 patches across palate, long axes diverging: inner (vomerine) patch rounded, well-separated medially but adjacent to ovate and much larger outer patches. Both jaw and palate teeth embedded in thick tissue. Palate villose anteriorly, with a pair of long, curved ridges of epithelial tissue just anterior to branchial chamber.

Exposed head shield slightly rugose in young, granular and striate in older fish. Predorsal plate and humeral process similarly rugose or granular. Dorsomedian head groove begins on snout and extends to supraoccipital process base: shallow, lanceolate; widest behind eye. Supraoccipital process very broad, triangular, with slightly concave sides and dominant, smooth, median keel. Smooth space on each side of head shield above gill opening. Humeral process conspicuous, well-ossified especially anteroventrally, its triangular, blunt shaft horizontal, extending nearly halfway along pectoral spine. Large and oval axillary pore.

Maxillary barbel reaches beyond pectoral base in young, past preopercular edge in adults; mandibulary barbel reaches hindborder of gill membrane or beyond; mental barbel to opposite hind eye border. Chin barbel bases moderately staggered.

Gill rakers about half as long as filaments. Rakers present along posterior face of all arches: 17-23 (mean 20.1) on first arch; 15-21 (mean 18.5) on second; 14-19 (mean 16.7) on third. Thin, elongate pads (or epithelial folds) with crenulate margin on upper posterior limb of first and second arches.

Fin spines rounded to moderately flattened; anterior margins rough and serrated towards tip. Dorsal spine robust, about equal to postorbital head length, its distal posterior margin with 6-10 low serrae. Last dorsal ray 2-2.5 times shorter than longest ray. Pectoral spine slender, longer than dorsal, its hind margin armed with 18-30 large dentae (or serrae), projecting at right angles to spine. Pectoral fin extends to approximately opposite last dorsal ray. Ventral ends well before anal origin in males, to anal origin in females; inner rays thickened in mature females. Anal outer margin slightly concave; last ray 2.5-3.2 in longest ray. Adipose fin moderately high and long-based, longer than dorsal base length; originating short distance before anal origin. Caudal moderately forked, its lobes tapered and pointed.

Lateral line straight, curved dorsad before dorsal fin and at tail base. Short lines and venules diverge from line (conspicuous anteriorly) and vertical series of pores extend over back. Caudal peduncle moderately deep.

Fresh colouration: Reddish olive-brown to pale greyish brown above with golden or bronze reflections; white below. Pectoral fin black or dark bluish brown on dorsal aspect, other fins dusky olive. White margin on paired fins.

Colour in preservative: Fawn to dark brown above, greyish fawn to dusky cream below. Fins brown, fawn or tan; dorsal, anal and caudal stippled darker brown; dorsal aspect of upper pectoral dark brown or black. Peritoneum pale fawn.

DISTRIBUTION

NEW GUINEA: south-draining rivers. The Sande and Lorentz Rivers to the Digoel River (Hardenberg, 1936), upper (KFRS material), middle and lower Fly River, Purari River system (Haines, 1979) and the Lakekamu River (Kailola, 1974). *C. carinatus* may be rare in lower river reaches as Maunsell and partners (1982) only collected it above 550 km from the river mouth; and Haines (1979) did not collect it in the Kikori, Era (western Gulf) and Vailala Rivers (eastern Gulf).

BIOLOGY

Habitat: In the Purari and associated rivers, Haines (1979) found that *C. carinatus* is common in the main river and side branches, very abundant in the freshwater delta area, present in the main freshwater river channels and rare or uncommon in the lower mangrove to *Pandanus-Sonnertia* zones (where there is tidal influence). *C. carinatus* is also rarer well upstream. It is a predominantly freshwater species, attaining high population densities in rivers and the still water of billabongs and side creeks (Haines, 1979; Maunsell and partners, 1982). Roberts (1978) caught four adult *C. carinatus* in the mainstream of the middle and lower Fly and Hardenberg's (1936) 38 cm TL specimen came from the middle Digoel River.

Maximum size: 560 mm FL (Haines, 1979); 520 mm SL.

Diet: *C. carinatus* is both an insectivore and detritophage. Food was present in 77 of the 108 stomachs examined by Haines (1979): prawn remains in 4, mud, algae and detritus in 68, fish scales in one. Gut contents identified by Roberts (1978) were aquatic Hemiptera, prawns, aquatic dipteran larvae (*Culicoides*) and debris. In nine individuals 240-540 mm TL, Maunsell and partners (1982) identified gut contents as: 78% aquatic insects, 13% terrestrial insects, remainder plant, macrocrustacea and detritus. The difference in recorded diet between Fly River and Gulf river *C. carinatus* individuals could be size-related.

Breeding: Haines (1979) caught mature and maturing fish in the freshwater delta and lower reaches of the Purari and Pie River systems and suggested that this species breeds in freshwater. Juveniles shared this habitat - although the smallest fish Haines recorded was 100 mm FL. Two large adults caught in October were fully mature; and Maunsell and partners (1982) obtained mature females in the middle Fly River in July. I have no information on fecundity. Haines (1979) found no significant difference in sex ratio among 102 individuals; and the smallest size at first maturity he recorded was 23 cm FL.

DISCUSSION

Cinetodus carinatus is most similar to *C. froggatti*. The major differences between them have been stated under *C. froggatti*.

TYPES

Weber (1913:538) defined six* syntypes and "numerous examples" (transl.) (also syntypes) (*the third listing contains a misprint of "3" instead of "2"). There are actually 20 specimens in the "numerous examples" (H. Nijssen, pers. comm., 1985), of which 18 are in ZMA 111.109 (all about 65 mm TL) and two are in AMNH 9265 (50.1 and 50.3 mm SL, about 63 mm TL). ZMA 111.110 (155 mm SL, 190 mm TL) is Weber's drawn specimen from Van Weelskamp. The three syntypes collected 5, 16 and 20 September 1909 from the Lorentz River are at ZMA (numbers 109.295, 111.111 and 111.112; 260-425 mm TL). The two from the Sande (= Bibis) River (10 Sept. 09) are at the MZB, register number 143 (est. 80 and 90 mm SL, 105 and 110 mm TL). I have examined 5 syntypes.

Condition of types: (ZMA 111.110): good; rigid, tail curved to RHS. Two slits in LHS of body - one below dorsal, other above anal. Long gash in belly from pectoral girdle to between ventral bases. RHS gill membranes slit ventrally. All barbels and fins intact, although dorsal twisted; fin tips frayed or lost. (AMNH 9265): good; all fins intact although caudal, dorsal and pectoral rays bent. These fish appear to be newly-liberated juveniles.

ETYMOLOGY

Latin, carina = keel, ridge (comb). Refers to the strong, numerous serrae along the inner pectoral spine.

MATERIAL EXAMINED

SOUTHERN IRIAN JAYA - 1*, ZMA 111.110, Lorentz River by Van Weelskamp, 29 May 1907, coll. H.A. Lorentz, 155 mm SL (190 mm TL) (= SYNTYPE); 2*, AMNH 9265, Lorentz River, 17 May 1907, coll. H.A. Lorentz, 50.1 & 50.3 mm SL (approx. 63 mm TL)(= SYNTYPES); 1*, RMNH 28007, Digoel River at Tanah Merah, 14-17 April 1955, coll. M. Boeseman, 212 mm SL;
2, MZB 143, Sande River, New Guinea, 10 Sept. 1909, coll. M. Weber, 80 & 90 mm SL (= SYNTYPES).

SOUTHERN P.N.G. - 1, KFRS F.4686-01 (ex USNM 217063), lower Fly River near Elangowan Island, Dec. 1975, 325 mm SL; 2*, unreg., Fly River (exact location unknown), mid-July 1981, coll. J. Watson & R. Humphries, 64 & 85 mm SL; 1*, unreg., Kuku Creek, Bevan Rapids, 11 May 1975, coll. A.K. Haines, 338 mm SL; 1*+1, AMS I.25999-001, billabong, mid Purari River, 27 Nov. 1974, coll. A.K. Haines, 118 & 119 mm SL; 1*, USNM 288556, same data, 156.5 mm SL; 3*, QM I.22654, same locality, 5 May 1975, coll. A.K. Haines, 225-320 mm SL; 1*, UMMZ 215079, same data, 122 mm SL; 1*, RMNH 30313, same data, 160 mm SL; 1*, CAS 60484, Mapaio, 11 Sept. 1974, coll. A.K. Haines, 99 mm SL; 1, KFRS F03996, Lakekamu River, Malalaua area, Oct. 1971, 240 mm SL.

Subgenus *Pachyula* Ogilby

Type: *Hemipimelodus crassilabris* Ramsay & Ogilby, 1886: 18

6.4.5

Cinetodus (*Pachyula*) *crassilabris* (Ramsay & Ogilby)

New combination

(Figures 91, 92, 93, 94; Tables 20, 21)

Hemipimelodus crassilabris Ramsay & Ogilby, 1886: 18 (Strickland River)

Pachyula crassilabris: Ogilby, 1898: 33

DEFINITION

Moderately deep-bodied yet elongate; head tapered and rounded from side-to-side. Eye dorsolateral; mouth subinferior; gape small (16-35 %HL), surrounded by very thick, fleshy lips. Jaw teeth long, sharp-tipped; premaxillary teeth form oblong, short band at symphysis; no teeth on papillose palate. Back of all gill arches papillose and lined with rakers; gill opening restricted and membranes forming broad fold across isthmus. Fin spines robust, rugose; dorsal spine longer than pectoral; adipose fin base longer than anal base. Fresh colouration of upper pectoral fin dark blue.

DESCRIPTION

D I,7. P I,10-11. A 17-19. GR (first arch) 14-18, of which 6 on upper limb. GR (last arch) 16-21. Number of vertebrae 51-54 (44-47 free).

Body robust, rotund anteriorly, elevated at mid-length and well-compressed posteriorly. Predorsal profile steep and straight, slightly convex at nape; snout to interorbital region rounded from side to side. Snout prominent and fleshy; scattered with fine papillae in larger individuals. Nostrils large and rounded, anterior one directly in front of posterior one. Mouth subinferior, gape small and surrounded by extremely thick, fleshy lips. Eye small, free of head skin, situated dorsally and just before mid head length. Gill opening restricted: membranes attached to isthmus short distance below pectoral base and forming a broad truncate fold across breast.

Teeth sharp-tipped, long, slender and depressible; embedded in thick, spongy tissue. Premaxillary band with 11-13 irregular series of teeth; tooth band partly visible when mouth closed. Lower jaw band narrower, divided at symphysis by edentulous space. Autogenous tooth plates absent; palate with many low, scattered papillae anteriorly. Broad ridge of epithelial tissue on each side of palate just before branchial chamber.

Head shield moderately smooth anteriorly, partly concealed by thick skin. Dorsomedian head groove oblong and flat, lanceolate, beginning before eyes and terminating short distance before base of supraoccipital process. Head shield rugose to granular around groove and posterolaterally. Naked patch in shield above gill opening; sides of head smooth. Supraoccipital process triangular with rounded keel, sides straight. Series of granules extend along process and over predorsal plate. Humeral process smooth and thickened anteroventrally, its triangular shaft slightly oblique, 1/3 as long as pectoral spine. Axillary pore moderately large.

Barbels thin and flattened. Maxillary barbel extends to preoperculum or as far as pectoral spine base; mandibulary barbel reaches to 1-2 eye diameters before gill membrane ventrally; mental barbel ends below middle or hind border of eye. Bases of chin barbels slightly staggered.

Gill rakers 1/3 length of gill filaments. Short rakers along finely papillose posterior face of all arches: 17-22 (mean 20.3) on first arch; 19-23 (mean 21.3) on second; 18-20 (mean 19.3) on third. Upper posterior limb of first two arches thickened, as broad fold on second arch.

Fin spines robust, slightly compressed; granular and roughened anteriorly, sides finely ridged longitudinally. Short, triangular serrae extend halfway down posterior margin of dorsal spine, many (30-45) larger serrae along posterior margin of pectoral. Dorsal spine noticeably longer than pectoral spine; dorsal fin high, last ray 2.3-3.2 shorter than longest ray. Pectoral fin extends to below 5th-6th dorsal ray. Ventral fin long, either failing to reach anal origin (males), to about 2nd anal ray (females). Anal margin slightly concave, last ray 2.5-3.5 shorter than longest ray. Adipose fin large, rather high, beginning short distance before anal fin, its base longer than dorsal base. Caudal lobes broad, upper lobe slightly longer.

Caudal peduncle deep and compressed. Lateral line directed dorsad before dorsal fin and at caudal base, with fine, short lines branching off diagonally along its length and vertical series of pores extending over back.

Fresh colouration: Dull grey or pale bluish brown above, pinkish white or cream below; clear division between colours. Barbels and fins pale or dusky. According to Ramsay and Ogilby (1886), inner pectoral surface is basally blue.

Colour in preservative: Dark brown or reddish fawn above, pale tan or fawn below. Barbels brown; upper aspect of pectoral and ventral fins dark brown. Peritoneum grey or dusky.

DISTRIBUTION

NEW GUINEA: South-draining rivers. The Digoel River (Lake Toeba), upper Fly River (Palmer River), Strickland River and upper Purari River. Haines (pers. comm.) did not collect *C. crassilabris* in other Gulf rivers he surveyed.

BIOLOGY

Habitat: Found only in freshwater, more commonly in flowing than still. *C. crassilabris* is present in the main river and branches of the upper Fly, upper Strickland and Purari Rivers (common above Wabo). It also extends downstream to the fringe of the freshwater sections of the river delta (Haines, pers. comm.).

Maximum size: 560 mm FL (Haines, 1979). Roberts' (1978) largest specimen was 500 mm SL.

Diet: A detritophage, feeding on detrital mud, allochthonous vegetable matter and prawns. Eight of the 9 stomachs examined by Haines

(1979) contained food: prawn remains in 5, plant material (not fruit) in 4, mud, algae and detritus in 5. Roberts' (1978) three large specimens had empty stomachs. Stomachs of specimens I examined contained plant material, detritus and crab remains.

Breeding: Spawning probably takes place during the early wet season as a 330 mm specimen caught in November has mature gonads. Fecundity is low, the 308 mm specimen I examined having 16 larger ova in one gonad, 13 in the other. Size at first maturity noted by Haines (1979) was 40 cm FL.

DISCUSSION

One of Ramsay and Ogilby's supposed paratypes of *Hemipimelodus dayi* is a specimen of *C. crassilabris* (QM I.26087).

Although I have not examined it, a specimen of *crassilabris* in the NMV, collected by Ramsay and Ogilby on the Royal Geographical Society Expedition to New Guinea, is probably a second "paratype" of *C. crassilabris*. It was registered at NMV, number 51615, in July 1887.

Desoutter (1977) based her description of this taxon on three specimens: the holotype, one from Lake Toeba and one from the Jimi River. I have examined the last specimen (AMS IB.3354, 380 mm SL; not 467 mm as stated by Desoutter) which is referable to *Arius velutinus* (Weber).

Desoutter had no clear concept of *C. crassilabris*. Elsewhere in her report, she concluded that the specimens Herre (1926) collected in the Philippines and described as *H. manillensis* (Valenciennes) were probably referable to *C. crassilabris*; and (1977: 31) that a specimen in the AMS from Bombay (India) probably also belongs to *C. crassilabris*. However, this specimen (AMS B.7954, 350 mm TL) is a specimen of

A. argyropleuron Valenciennes (my determination). Desoutter did not locate the autogenous palatal toothed plates on both the *A. velutinus* and *A. argyropleuron* specimens.

It is *possible* that Liem and Haines' (1977) and Haines' (1979) "Fleshy-lipped catfish" from the estuarine zone of the Purari delta is referable to *C. crassilabris*, although this species is not found in saline waters. Unfortunately, they retained no specimens.

C. crassilabris and *C. conorhynchus* are easily distinguished from other *Cinetodus* species by the small mouth, shape of the premaxillary tooth band, tooth shape, absence of palatal teeth and presence of papillae on palate and gill arches. *C. crassilabris* differs from *conorhynchus* in having thick, fleshy lips (practically absent in *conorhynchus*), total of 51-54 vertebrae (45 in *conorhynchus*), longer maxillary barbels (43-76 %HL, *cf.* 41 %HL in *conorhynchus*), slightly shorter pectoral spine (15-20 %SL, *cf.* 24 %SL in *conorhynchus*) and "V"-posterior shaped dorsomedian head groove (*cf.* rounded in *conorhynchus*).

TYPES

Ramsay and Ogilby (1886: 18) refer to only one specimen, 7 3/4" long. This specimen is AMS B.9961, 161 mm SL. The supposed paratype is QM I.857, 127 mm SL (see also Discussion).

Condition of types: Holotype: fair. Snout pushed in slightly; jaw cut through on LHS from rictus to below eye; first gill arch on RHS removed; gill membranes torn ventrally. Abdomen slightly shrunken. Colour faded. Fins intact but tips of anal rays and both caudal lobes lost.

ETYMOLOGY

Latin, crassus = thick, stout, fat; and labrum = lip, brim. Refers to this species' very thick lips.

MATERIAL EXAMINED

SOUTHERN P.N.G. - 1*, AMS B.9961, Strickland River (07°17'S, 141°35'E), no date, reg. 1886, coll. E.P. Ramsay & J.D. Ogilby, 161 mm SL (= HOLOTYPE); 1*, QM I.857, Strickland River, coll. E.P. Ramsay & J.D. Ogilby, 127 mm SL (= PARATYPE); 1*, QM I.26087, Strickland River, coll. E.P. Ramsay & J.D. Ogilby, 80 mm SL (ex QM I.879); 1, KFRS F.4684-01 (ex USNM 217074), Palmer River, Nov. 1975, 484 mm SL; 1*, unreg., Kone, 23 Nov. 1974, coll. A.K. Haines, 330 mm SL; 1*, AMS I.27411-001, Kubipara, Oct. 1975, coll. A.K. Haines, 308 mm SL; 1*, AMS I.25994-001, Wame River, 6 May 1975, coll. A.K. Haines, 340 mm SL; 1*, KFRS F.5525-01, Wabo, Jan. 1977, coll. A.K. Haines, 305 mm SL; 3, unreg., Gwaimasi village, upper Strickland River, Aug. 1986-Nov. 1987, coll. P. Dwyer & M. Minnegal (dried skulls only), 80-175 mm length (ex specimens to 485 mm SL).

6.4.6

Cinetodus (Pachyula) conorhynchus (Weber)

New combination

(Figures 94, 95, 96; Table 22)

Tetranesodon conorhynchus Weber, 1913: 546, fig. 24 (Lorentz River near Van Weelskamp)

DEFINITION

No palatal teeth; jaw teeth conical and depressible; premaxillary teeth form short, oblong patch. Head tapered, rounded from side-to-side; snout prominent. Mouth inferior and small; lips almost absent. Eye dorsolateral; barbels short. Palate with scattered papillae. Rakers and papillae on back of all arches; gill opening restricted and membranes form shallow fold across isthmus. Dorsomedian head groove ovate posteriorly. Pectoral spine inner margin with 19-20 broad, strong serrae; adipose fin long-based.

DESCRIPTION

D I,7. P I,10. A 18. GR (first arch) 14, of which 6 on upper limb. GR (last arch) 18. Number of vertebrae - (44-45 free).

Body moderately robust, tapered anteriorly, slender posteriorly. Head almost triangular in cross-section (or rounded from side to side). Predorsal profile straight or slightly convex, somewhat elevated at nape; interorbital convex. Snout elevated and prominent, tip blunt and thick; lips absent on exterior of jaws except at corners of mouth, very "rubbery" and thick on interior of jaw margin. Nostrils situated laterally on head; anterior nostril ventral and slightly median to, posterior one. Eye ovate, with free margin, its hind border § eye diameter before mid head-length. Eye dorsolateral, visible when viewed from above, not from below. Gill opening restricted, membranes attached to and forming a shallow fold across breast for distance about equal to snout length.

Teeth brown-tipped, present on jaws but absent from palate. Teeth conical and slender, peg-like; depressible and well-spaced; embedded in thick tissue; arranged in 4-5 irregular series on upper jaw, 3-4 on lower jaw. Premaxillary band broad; each lateral section almost rounded, contiguous at midline; lower jaw band interrupted by edentulous space at symphysis. Palate thickened, papillose and creased, a narrow oblique ridge posteriorly before each branchial chamber.

Head smooth anteriorly, head shield exposed posteriorly, smooth to rugose or finely striate. Dorsomedian head groove narrow anteriorly and ovate posteriorly, its rounded hind margin bordered by crescent of striae. Supraoccipital process moderately triangular with straight sides and moderately high keel. Sides of head smooth, venules radiating over postorbital and opercular regions. Conspicuous humeral process heavily ossified anteroventrally, its oblong shaft horizontal, blunt-tipped and weakly striate; extends about 1/4 along pectoral spine. Axillary pore moderately large, angular.

Barbels thin, rounded in cross-section. Maxillary barbel extends halfway between eye and pectoral base. Mandibulary barbel reaches about one eye diameter beyond eye. Mental barbel attains posterior eye border. Chin barbel bases almost transversely aligned.

Gill rakers short, half as long as opposing filaments. Rakers present along posterior aspect of all arches: 18 or 19 along first, 21 along second, 18 along third. A moderately thick pad of epithelial tissue on second arch posterodorsally, and all arches with many low papillae.

Fin spines strong, thick and compressed; sides with very fine, longitudinal striae. Anterior (leading) margin smooth or slightly roughened with few low, antrorse serrae distally; posterior (trailing) margin serrate: 8-10 moderate serrae on dorsal, 19-20 very strong, broad serrae on pectoral, projecting somewhat obliquely from spine. Pectoral spine slightly longer than dorsal. Longest dorsal ray 2.5 longer than last ray. Pectoral reaches to below last dorsal rays. Ventral slender, reaching anal origin (information on sexual differences not available). Adipose oblong, with slightly convex outer margin, situated directly above and subequal to, anal fin basal length. Anal elevated anteriorly, longest ray 2.9 longer than last ray. Caudal lobes moderately broad.

Caudal peduncle slender and compressed. Lateral line straight, oblique below dorsal fin and turned dorsad at tail base. Many short lines diverge from lateral line, especially numerous near its origin; and vertical series of pores extend from line across back and flanks.

Fresh colouration (*fide* Weber and de Beaufort, 1913): Dark bluish, underside of head and belly whitish with silvery hue, increasing on sides and tail. Fins dark brown.

Colour in preservative: Brown above, darker at nape; fawn below. Dorsal, upper aspect of pectoral and ventral fins brown, remaining fins dusky yellow. Barbels and peritoneum pale.

DISTRIBUTION

NEW GUINEA: South-draining rivers. Middle Lorentz River.

BIOLOGY

Habitat: Freshwater.

Maximum size: 200 mm SL (?).

Diet: Unknown.

Breeding: Unknown. Sex of the type specimen is indeterminate (possibly a juvenile).

DISCUSSION

The species appears to have a limited distribution as it was not collected during extensive surveys of more easterly river systems (e.g. by Roberts, Maunsell and partners, D. Gwyther, Haines).

The major differences between C. conorhynchus and C. crassilabris are stated under crassilabris. C. conorhynchus superficially resembles N. dayi but is easily distinguished by characters such as gill raker count and jaw dentition.

TYPES

This species is based on one specimen, ZMA 111.084, 170 mm SL, 210 mm TL.

Condition of type: good. Body rigid; tail bent to the RHS. Longitudinal slits on LHS of body below dorsal fin and above anal; belly slit from breast to ventral bases. Head cut through on RHS from mouth corner to opercular margin and also gill cover partly torn forward below. Fins intact, although some with split membranes; almost all tips of anal and caudal rays lost.

ETYMOLOGY

Greek, konos = cone; konikos = cone-like; Greek, rhynchos = nose, snout. Thus, in reference to the cone-like snout.

MATERIAL EXAMINED

SOUTHERN IRIAN JAYA - 1*, ZMA 111.084, Lorentz River near Van Weelskamp, 29 May, 1907, coll. H.A. Lorentz, 170 mm SL, 204 mm TL (tail tips lost) (= HOLOTYPE).

6.5 GENUS 1

6.5.1 Definition and content

Genus 1

Arius non Valenciennes (in Cuvier & Valenciennes), 1840a

Ariodes non Müller & Troschel, 1849

Type: No type species has been nominated

Genus 1 is distinguished by possession of four autogenous tooth plates (2 pairs) longitudinally arranged on the palate (Character 51B), the "head" of the vomer enlarged or conical and the vomerine arms short (Character 21B) (shared with *truncatus* only), and the distal caudal vertebral centra shortened and extended vertically (Character 41A); in combination with several homoplastic characters: long palatine-lateral ethmoid facet; enlarged metapterygoid extending well beyond hind quadrate margin; barbels moderately thick and fleshy, those on mandible with bases close together and almost aligned; lateral line at tail base bifurcate; swimbladder margin creased in some way; laminar bone on anterior vertebrae moderately extensive, with only a shallow, median excavation; 10-13 rays in pectoral fin; first (outer) branchiostegal very wide; gill opening moderately reduced; vomerine teeth absent; slightly reduced number (41-43) of free vertebral centra. Gonads bilobate.

Known content of the genus:

argyropleuron Valenciennes (marine, east coast of India, Indonesia, to south coast of New Guinea and northern Australia)

polystaphylodon Bleeker (marine, Singapore, Indonesia to north coast of New Guinea)

nella Valenciennes (marine, east coast of India to Philippines and Indonesia, south coast of New Guinea, northern Australia)

[The taxon *dussumieri* Valenciennes (marine, NW Indian Ocean) almost certainly belongs in this genus.]

6.5.2 Key to the Australo-Papuan species of Genus 1

A. Epioccipital anteriorly invading skull roof; sides of swimbladder creased internally; posterior palatal epithelial ridges clearly oblique; some teeth always present on anterior palatal tooth patches .... B

AA. Epioccipital hidden anteriorly, overlain by extrascapular and supracleithrum; swimbladder sides scalloped and creased both internally and externally; posterior palatal epithelial ridges clearly transverse; teeth often missing from anterior palatal tooth patches .... *argyropleuron* (p. 235)

B. Dorsal fin spines without internal partitions; supraoccipital process always triangular, although margins irregular; long axes of posterior palatal tooth patches parallel or (usually) converging distally .... *polystaphylodon* (p. 245)

BB. Dorsal fin spines with internal transverse partitions; supraoccipital process expanding with age; long axes of posterior palatal tooth patches usually diverging distally .... *nella* (p. 251)

DISCUSSION

Ariodes Müller and Troschel, has been associated with this group of taxa (including *dussumieri* Valenciennes) (e.g. Taylor, 1986). However, the type species, *arenarius* Müller and Troschel, does not have the apomorphic character states which distinguish the genus (rather, it belongs in the genus group "*Arius*"). No other generic names are available (refer Table 1).

ETYMOLOGY

There is no available name for this genus.

6.5.3

Genus 1 *argyropleuron* Valenciennes

(Figures 97, 98, 99, 100, 101; Tables 23, 24)

Arius argyropleuron Valenciennes (in Cuvier & Valenciennes), 1840a: 104 (Java) (MS name of Kuhl & van Hasselt)

Arius macrocephalus Bleeker, 1846: 167 (Batavia)

Arius acutus Bleeker, 1846: 167 (Batavia)

Arius Hamiltonis Bleeker, 1846a: 291 (Batavia)

Ariodes macrocephalus: Bleeker, 1858: 82, 85

Ariodes acutus: Bleeker, 1858: 82, 86

Ariodes argyropleuron: Bleeker, 1862: 40

Arius Schlegeli Bleeker, 1863a: 146 (Amoy, China)

Tachysurus argyropleuron: Fowler, 1905: 462

Tachysurus broadbenti Ogilby, 1908: 8 (Cape York)

Hemipimelodus colcloughi Ogilby, 1910: 7 (Croker Island, northern Australia)

Cochlefelis colcloughi: Whitley, 1943: 172

Hexanematichthys broadbenti: Munro, 1957: 40

Arius colcloughi: Taylor, 1964: 76

Arius species "A", species "B": Kailola & Wilson, 1978: 41

Arius species: Haines, 1979: 54

DEFINITION

Palatal teeth granular, in two patches each side of palate, longitudinally arranged; teeth in anterior patch frequently missing; posterior patches oblong-ovate, parallel or with long axes converging distally. Mouth small (24-40 %HL); lips and palate creased. No rakers posteriorly on first and second gill arches. Head depressed, elongate;

snout long; mouth small, subterminal to inferior; eye low-set. Exposed head shield very striate or sharply granular; dorsomedian head groove lanceolate; supraoccipital process narrow, always keeled. Caudal peduncle deep (1.3-2.1 in its length). A 14-21; total GR (first arch) 10-16; vetebrae 15-18+6-7+26-27. Fresh colouration variously brown; adipose fin dusky (and see key characters).

DESCRIPTION

D I,7. P I,10-12. A 14-21. GR (first arch) 10-16 of which 3-5 on upper limb. GR (last arch) 9-15. Number of vertebrae 48-51 (41-43 free).

Body robust and elongate; head depressed and long. Predorsal profile straight and low, convex at nape. Snout evenly rounded, tip fleshy, turned ventrad; lips fleshy and thick, creased and crenulate along margin. Rarely a short crescentic groove on dorsum of snout between nostrils; fine papilla-like structures scattered over snout in larger individuals. Mouth subterminal or subinferior, shallowly curved or truncate; gape small; no to 1/3 premaxillary tooth band exposed when mouth closed. Nostrils oval, posterior one slightly lateral to anterior nostril. Eye oblong-ovate, mostly free from head skin. Lateral ethmoid slightly prominent. Eye situated laterally, partly visible from above, opposite or just before mid-head length; lower eye margin in line with corner of mouth. Gill opening moderately wide, membranes meeting ventrally at shallow angle leaving free margin.

Teeth in jaws long and slender, sharp-tipped; depressible; embedded in spongy tissue. Bands short; 6-8 irregular series of teeth in premaxillary band, 4-6 in lower jaw band which has edentulous space at symphysis. Teeth on palate moderately large, globular or conical with blunt tips (peg-like); arranged into four groups lengthwise on palate. Anterior tooth patches frequently absent, when present represented by 1-4 teeth. Large posterior patches oblong-ovate, each consisting of 20-80 teeth; their long axes parallel or converging posteriorly. Brooding males apparently shed palate teeth. Palate skin smooth to closely papillose or longitudinally creased, forming two moderately large transverse flaps before branchial chambers.

Head shield smooth anteriorly; striate along border of dorsomedian head groove, and clusters of sharp or dull granules at shield margin and extending over supraoccipital process; distinct longitudinal striae on process. Dorsomedian head groove lanceolate, beginning level with nostrils, ending just before process base. Groove moderately deep for most of its length. Supraoccipital process narrow and triangular or oblong, sides almost straight; sharp median longitudinal keel present. Triangular humeral process smooth to rugose, more ossified anteroventrally; shaft oblique and acute, reaching 1/3 distance along pectoral spine. Axillary pore small.

Barbels moderately rounded and fleshy. Maxillary barbel terminates between mid-postorbital distance (adults) and below dorsal spine (juveniles). Mandibulary barbel reaches about 1/2 eye diameter beyond eye to beyond pectoral base. Mental barbel ends opposite hind eye margin and just before pectoral base (juveniles). Chin barbel bases almost aligned transversely.

Gill rakers 1/4-2/3 length of opposing filaments. Rakers absent from posterior of first and second arches (rarely 1-2 on upper limb of second), which are covered with fine papillae; 9-11 rakers along 3rd arch. No to moderate thickening posterodorsally on anterior arches.

Fin spines moderately long, somewhat flattened. Anterior margin granular or rugose, few low serrae distally. Posterior margin with serrae: 4-6 low ones on dorsal, 12-16 larger ones on pectoral. Longest dorsal ray 2.1-4 times length of last ray. Pectoral reaches to below posterior dorsal fin. Ventral narrow in males, not reaching anal origin; fin broader in females, to 3rd-4th anal ray. Sexually mature females with thick pad of epithelial tissue on inner ventral rays. Adipose fin oblong, short-based, above middle or posterior 2/3 of anal fin. Anal margin slightly concave, longest ray 2.7-3 times length of last ray. Caudal lobes broad and short, tapered distally.

Caudal peduncle very deep. Lateral line straight, oblique anteriorly, bifurcate at tail base. Short lines diverge from all of lateral line, more numerous anteriorly; and distinct vertical series of pores along body.

Fresh colouration: Dark or light brown, tan or grey above with yellowish or reddish wash; yellow-white below; dusky adipose fin.

Colour in preservative: Tan, brown or grey above, silvery white to creamy fawn below; undersides often stippled dark brown. Fins dusky, stippled brown; adipose fin (dark) brown. Barbels brown. Peritoneum pale with few dusky spots.

DISTRIBUTION

NEW GUINEA: south coast. Gulf of Papua, Era river delta, to Yule Island.

AUSTRALIA: north coast. Dampier (WA), Croker Island, Melville Island, Gulf of Carpentaria, Edward River, Cape York, Torres Strait, Townsville to Moreton Bay.

SOUTHEAST ASIA: Java, Sumatra, Borneo, Malaya, Thailand, Gulf of Siam to India (Bombay).

BIOLOGY

Habitat: sea and lower estuaries; coastal waters.

Maximum size: 570 mm FL (Haines, 1979; identification uncertain); 373 mm SL (my material); 460 mm TL (Bleeker specimen).

Diet: Stomachs of my material contained mud, parts of soft-bodied organisms (?mollusc; ?annelid) and grit. Stomachs of Haines' (1979) material contained mostly mud and detritus and some prawns.

Breeding: Spawning occurs at the beginning of the wet season. Haines recorded 340 mm FL as size at first maturity.

DISCUSSION

I have no hesitancy in linking *broadbenti* Ogilby with *macrocephalus* Bleeker, and *colcloughi* Whitley with *argyropleuron* Valenciennes. Furthermore, statistical analyses failed to reveal any significant differences between taxa sorted *a priori* into "*macrocephalus*", "*argyropleuron*" and other relevant nominal taxa (refer synonym) (figs 102, 103). These analyses showed that stated and perceived differences between these nominal taxa, such as head length relative to body length, were functions of size.

Genus 1 *argyropleuron* is very variable in form however, which makes it difficult to draw meaningful conclusions. For example, its relationship with *crossocheilus* Bleeker (and *tonggol* Bleeker). Although no subgroup was differentiated within the general group by the analyses, a much wider study of this taxon should be undertaken. My material was limited in the number of collection points throughout its geographic range, the number of size classes represented, and the less-than-perfect condition of some specimens.

Bagrus (Ariodes) arenarius Müller & Troschel is not conspecific with Genus 1 argyropleuron as Bleeker (1858) suggested.

Genus 1 argyropleuron can chiefly be distinguished from congeners nella and polystaphylodon by the much reduced anterior palatal tooth patch, direction of the posterior palatal ridges, slightly more numerous anal rays (fig. 104) and less numerous gill rakers (fig. 105); head shield often having clusters of sharp granules, swimbladder wall not being externally scalloped, more caudal vertebrae, and the autapomorphy of narrow posterior vertebral centra. From crossocheilus it can be distinguished (as adults) by its narrow, straight-sided supraoccipital process (process broader, with convex sides in crossocheilus), and usual absence of anterior palatal teeth (always present and many in crossocheilus). From goniaspis Bleeker, argyropleuron differs in form of the jaw teeth (large and molariform) and size of the posterior palatal tooth patches.

Whitley (1943) compared this species (as colcloughi) with spatula Ramsay and Ogilby and papillifer Herre.

TYPES

Arius argyropleuron: The holotype and only nominated type is at the RMNH, number 3041. It measures 148 mm SL (178 mm TL) (M. Boeseman, pers. comm.) so agreeing with Valenciennes' stated length of "six pouces". Unfortunately, the status of the "types" in RMNH 6895 and BMNH 1863.12.4: 67 is not so clear: these lots must contain the type(s) of Bleeker's taxa acutus and Hamiltonis but, as both species are badly defined and no number of original specimens or their sizes were recorded, they cannot be sorted. Furthermore, Bleeker later collected specimens which he included with his types in the one lot upon recognising that all referred to the taxon argyropleuron Valenciennes. The NMV specimen (number 46581, 368 mm SL), purchased from Bleeker's Collection A (see Hubrecht, 1879) is another possibility for type of one of these nominal taxa.

Bleeker had 12 specimens (1858, 1862) of A. argyropleuron from Java and Moarakompeh in Sumatra, with TL of 180-460 mm. The size range of the 12 (possibly type) specimens in RMNH 6895 is 118-320 mm TL (98-270 mm SL; M. Boeseman, pers. comm.), which suggests there has been some switching of specimens in this lot. Indeed, the 460 mm "type of Ariodes macrocephalus Bleeker" which Ogilby (1908) said is in the BMNH, may be one of these specimens. The TL of the 5 specimens I examined from the RMNH lot ranged from 190-300 mm.

Arius macrocephalus: Bleeker described this species in 1846 and repeated the description in 1847 (p. 33). He (1858; 1862) noted two specimens, 370 and 410 mm TL, which are the presumed types of the species. The smaller specimen is at the BMNH, no. 1863.12.4: 78 (308 mm SL); the other is RMNH 6896, 324 mm SL (385 mm TL) (M. Boeseman, pers. comm.).

Tachysurus broadbenti: Originally there were 3 syntypes in the QM collection, but one has been lost for "over 20 years" (J. Johnson, pers. comm.). The others are I.9745 (290 mm SL) and I.9746 (about 303 mm SL). I have examined the 290 mm specimen.

Hemipimelodus colcloughi: This species is based on one specimen, 158 mm SL (202 mm TL, Ogilby), QM I.1538.

Arius schlegeli: Bleeker nominated two types, 206 and 266 mm TL. AMS B.8123, 178 mm SL is the smaller of these; and I do not know where the other specimen is. Bleeker also (1863a) referred to additional specimens "de cette espece" sent to the Leiden Museum by Schlegel, which are probably the "types" mentioned by M. Boeseman (pers. comm.). I borrowed three of this lot of six specimens (RMNH 3032: 142, 164, 237 mm SL) which are specimens of *Arius arius* Valenciennes.

Condition of types: *argyropleuron*: Five specimens in RMNH 6895, which "includes types", according to Boeseman: Fair to poor. Bodies soft, often bent; belly slit in one specimen; head cut through on RHS in three specimens, LHS of head damaged in another; gill arches cut through in some. Fins tattered, especially anal; some spines broken, fin tips lost. The BMNH specimen (1863.12.4: 67) is in poor shape: belly split, RHS of head cut through, branchiostegals on LHS torn; LHS humeral process split; all fins tattered.

Arius macrocephalus: BMNH 1863.12.4: 78. Poor. Body soft; belly slit, part of gut removed. RHS of head cut through (including hanging branchiostegal) to above pectoral base; RHS gill arches partly missing. Fins tattered; part of dorsal rays lost, anal torn, 1/2 of caudal broken off, pectoral bases damaged.

Arius schlegeli: AMS B.8123. Fair, though body soft. Mouth cut on RHS; caudal, ventral and anal rays tattered.

Hemipimelodus colcloughi: QM I.1538. Fair condition.

Tachysurus broadbenti: QM I.9745. Poor condition, though body firm. Backbone removed (hence fish curled up), body gutted. Head cut through ventrally.

ETYMOLOGY

Greek, *argyros* = silver; *pleura* = side. Refers to the fish's silvery sides ("aux flancs argentes" - Valenciennes, 1840a: 104).

MATERIAL EXAMINED

SOUTHERN P.N.G. - 2, AMS I.29290-001, Gulf of Papua, 1975, coll. A.K. Haines, 145 & 162 mm SL; 1*, NTM S.12596-001, same data, 190 mm SL; 1*+3, unreg., same data, 71 mm, other SL's not noted; 1*, KFRS F02079, NW of Yule Island, 5 May 1970, coll. P. Kailola & J. Koaia, 147 mm SL; 1*, KFRS F01580, same data, 133 mm SL; 2*, unreg., Gulf of Papua, 17 July 1981, coll. S. Frusher, 125 & 156 mm SL; 1*, unreg., Kerema Bay, no date, 225 mm SL; 1*, QM I.26083, Arehava, 8-9 Sept. 1974, coll. A.K. Haines, 215 mm SL; 1*, KFRS F.4279-03, Karama River mouth, no date, 154 mm SL; 1*, KFRS F04096, off Oreke River, May 1973, 168 mm SL; 1*, KFRS F01028, Yule Island, June 1966, 148 mm SL; 1*, AMS I.29286-001, Morowan, Ini Island, 15 March 1975, coll. A.K. Haines, 338 mm SL.

QUEENSLAND - 1*, QM I.9745, Cape York, "before 1908", 290 mm SL (= SYNTYPE of _Tachysurus_ _broadbenti_ Ogilby); 1*, JCU TP 163, Cleveland Bay, Townsville, 26 Nov. 1980, coll. W.R. Dowd, 71 mm SL; 1*, JCU 4189, Bohle River estuary, Cleveland Bay, no date, coll. M. Leet, 330 mm SL; 1*, QM I.7141, Cape Cleveland, 4 April 1941, 191 mm SL; 1*, QM I.6116, Cape Cleveland, 25 Feb. 1938, 318 mm SL; 2*, QM I.11502, Moreton Bay, 1950, coll. T.C. Marshall, 281 & 373 mm SL; 1*, unreg., beach at Edward River township, 4 Jan. 1981, coll. D.B. Carter, 172 mm SL; 1*, AMS I.26859-014, Karumba, no date, 234 mm SL; 1*, CSIRO C.3603, 16°49'S, 140°38'E, 25 May 1965, coll. "Rama", 109 mm SL; 1*, AMS I.15557-040, Gulf of Carpentaria at 16°19'S, 141°08'E, 19 April 1964, coll. I.S.R. Munro, 118 mm SL; 1, CSIRO C.4367, Norman River, 1971, coll. I. Munro, 305 mm SL; 1, CSIRO C.3795, Norman River, 1969, coll. D.J. Turner, 320 mm SL; 1, AMS I.15552-005, Norman River at 17°30'S, 140°45'E, 1963, head only, SL not stated: 115 mm HL.

NORTHERN TERRITORY - 1*, QM I.1538, Croker Island, no date, 158 mm SL (= HOLOTYPE of Hemipimelodus colcloughi Ogilby); 1*, NTM S.11567-001, Woods' Inlet, Darwin Harbour, 13 Jan. 1985, coll. R. Williams & P.A. Alderslade, 310 mm SL; 1*, NTM S.11850-002, Leaders' Creek mouth, Gunn Point, Darwin, 5 May 1976, coll. G.Webb & M. King, 248 mm SL; 1*, MNHN 1989-1084, Shoal Bay, Melville Island, 28 March 1973, coll. D.L. Grey, 49 mm SL.

WESTERN AUSTRALIA - 1*, unreg., Dampier, 12 July 1983, coll. M. Dunning, 355 mm SL.

INDONESIA - 5*, RMNH 6895 (in part), East Indies Archipelago - incl. Batavia, coll. P. Bleeker, 150-260 mm SL (possibly incl. type(s) of A. acutus Bleeker and A. hamiltonis Bleeker); 1*, NMV 46581, East Indies Archipelago, coll. P. Bleeker, 368 mm SL; 1*, BMNH 1863.12.4: 67, no locality, coll. P. Bleeker, 141 mm SL (stated by BMNH as presumed type of A. acutus Bleeker); 1*, BMNH 1863.12.4: 78, Batavia, coll. P. Bleeker, 308 mm SL (= COTYPE of Arius macrocephalus Bleeker); 1*, unreg., Teluk Penyu, Cilacap, Java, 18 Dec. 1980, coll. P. Kailola, 119 mm SL; 5*, unreg., same locality, 20 Dec. 1980, coll. P. Kailola, 142-320 mm SL; 1*, unreg., Muarakarang, Jakarta, 4 Dec. 1980, coll. P. Kailola, 178 mm SL; 2*, unreg., same locality, 24 Dec. 1980, coll. P. Kailola, 200 & 297 mm SL; 4, MCZ 30885, Pelabuhan Ratu, 1909, 91-? mm SL; 4, USNM 72539, same data, 70-140 mm SL.

CHINA - 1*, AMS B.8123, Amoy, purch. by AMS in 1885, 178 mm SL (= COTYPE of Arius schlegeli Bleeker).

MALAYSIA - 1, MCZ 23706, Penang, no date, 178 mm SL.

INDIA - 1, AMS B.7954, Bombay, purch. by AMS in 1885, 350 mm TL.

6.5.4

Genus 1 polystaphylodon Bleeker

(Figures 106, 107, 108, 109; Tables 23, 24)

Arius polystaphylodon Bleeker, 1846a: 172 (Batavia-Java; Priaman-Sumatra)
Ariodes polystaphylodon: Bleeker, 1858: 90

DEFINITION

Granular teeth arranged into 2 patches each side of palate, one behind the other: teeth always present in anterior patches, posterior patches elongate, parallel or slightly converging posteriorly. Dorsomedian head groove deep and straight, from just behind nostrils to supraoccipital process base; process triangular, sides irregular proximally. Mouth terminal. No rakers on posterior of first two arches, gill rakers (first arch) 12-17. A 15-20; total vertebrae 21+7+22. Longest barbel 17-38 (mean 31) %SL. Fresh colouration dark blue-charcoal, white below. (And see key characters).

DESCRIPTION

D I,7. P I,10-12. A 15-20. GR (first arch) 12-17, of which 4-6 on upper limb. GR (last arch) 11-14. Number of vertebrae 50 (43 free).

Moderately slender fish, anterior 2/3 of body cylindrical in cross section. Predorsal profile straight, thence slightly convex at nape. Head tapered before eyes; snout slightly rounded; lips moderately thick and "rubbery", inner margins very creased and crenulate. Mouth subterminal; gape moderately broad, usually no premaxillary teeth exposed when mouth closed. Nostrils moderately large, rounded; anterior one slightly median to posterior nostril. Short, shallow crescent on dorsum of snout between nostrils. Eye ovate, moderately large, dorsolateral, its border free of head skin; eye situated just before or at mid-head length. Lateral ethmoid somewhat prominent, forming a "shelf" between eye and nostril. Gill opening wide, membranes meeting ventrally at obtuse angle, margin broadly free from isthmus.

Teeth in jaws conical, fine or slender, tips blunt or sharp; depressible, often embedded in thick, spongy tissue. Between 8 and 10 irregular series of teeth in premaxillary band; 4-5 series in mandibulary band which is divided at symphysis by edentulous space. Palate teeth in four groups. Anterior patches complete at all stadia: rounded, at about level of posterior nostrils; each with 8-18 conical, stout teeth. Posterior tooth patches elongate, broadest anteriorly, long axes parallel or slightly converging distally, posterior tip not, or only slightly turned outward; patches situated at about eye level. Posterior patches with 40-80 peg-like or conical, blunt or sharp-tipped teeth. Palate epithelium thick and convoluted anteriorly, thin and rather smooth posteriorly; broad fold of epithelial tissue extends from each side of palate before branchial chamber.

Anterior of head smooth. Head shield behind eye apparent: rugose, with many fine granules; rough striae form edge of shield laterally and bound posterior dorsomedian head groove. Groove narrow and long, extending from level of posterior nostrils almost to supraoccipital process base; moderately deep and slightly lanceolate medially. Supraoccipital process with low rugae and median keel; process roughly triangular posteriorly and irregularly convex anteriorly. Humeral process triangular; rugose, moderately ossified anteroventrally; its shaft oblique, sharp-tipped; extends 1/3 along pectoral spine. Axillary pore small.

Barbels moderately compressed. Maxillary barbel extends to or almost to head margin, or below dorsal spine in juveniles. Mandibulary barbel terminates just before head margin in adults, beyond pectoral base in juveniles. Mental barbel extends to just past eye, or to short distance beyond ventral head margin in juveniles. Chin barbel bases close together, slightly staggered.

Gill rakers short and conical, half as long as opposing filaments. Rakers absent from posterior aspect of first arch; none (sometimes 1 or 2) on back of second arch; 11-14 rakers (mean 12.7) along posterior of third arch. Gill arches dimpled and fleshy; long, medially-escavated fleshy pad of tissue posterodorsally on second gill arch.

Fin spines acute; compressed, laterally smooth but roughened with fine oblique striae near margin. Anterior (leading) margin of spines conspicuously granular, serrated near tip; posterior (trailing) margin with fine, low striae: 5-12 along dorsal, 15-22 along pectoral. Pectoral spine subequal to or slightly shorter than dorsal spine. Longest dorsal ray 2-4.2 times longer than last ray. Pectoral fin extends to or beyond base of last dorsal ray. Ventral thin-based in males and not reaching as far as anal origin; broad-based in females and reaching opposite 1st to 5th anal ray. Fifth and 6th ventral rays somewhat thickened in maturing females (there were no ripe females in my samples). Adipose fin moderately high, rounded, above middle of anal. Anal margin truncate or slightly concave, longest ray 2.1-2.6 times longer than ray. Caudal lobes broad and pointed.

Caudal peduncle stout. Lateral line oblique anteriorly, thence straight to tail base. At tail base, line curved slightly dorsad (rarely) or bifurcate. Short oblique or vertical lines of pores diverge from lateral line along its length.

Fresh colouration: Bluish charcoal, sides silvery, white below, sometimes stippled dusky. Back and upper sides with metallic sheen. Barbels cream, sometimes dusky. All fins fawn, edged brown.

Colour in preservative: Brown to dark brown above, creamy below. Fins dusky. Peritoneum pale or fawn.

DISTRIBUTION

NEW GUINEA: north coast - Humboldt Bay to the Ramu River mouth.

ASIA: Java, Sumatra, Singapore, Celebes (Weber and de Beaufort, 1913).

BIOLOGY

Habitat: Appears to favour shallow, turbid coastal waters and river mouths (in rivers? - ref. Weber and de Beaufort, 1913).

Maximum size: 340 mm SL (Weber, 1913a).

Diet: No information.

Breeding: Probably spawns in the early - mid wet season. A series of male specimens caught in May have undeveloped gonads; and a female specimen caught in January appears to be spent (small ova remain in anterior part of each gonad). The female specimen from Bali is in an early maturation stage (collected in June).

DISCUSSION

Bleeker only had two juvenile specimens on which to base his description, 150 and 160 mm TL.

Genus 1 *polystaphylodon* is most similar to genus 1 *nella*. However, that species has chambered fin spines (not chambered in *polystaphylodon*), a supraoccipital process expanding with age, a more granular head, and diverging posterior palatal tooth patches. Compared to nella, the barbels of polystaphylodon, fin spines and adipose fin base are slightly longer (figs 110, 111, 112, 113), (and compare other meristics and morphometrics in figs 104, 105, tables 4, 23, 24). Genus 1 polystaphylodon is not synonymous with crossocheilus and appears to be distinct from goniaspis. Characters ontogenetically labile in nella and argyropleuron (e.g. head shield pattern, tooth patches) appear to be quite stable in this taxon. "A". dussumieri Valenciennes mainly differs from polystaphylodon in having expanded lateral ethmoid processes.

This species exhibits little change with growth: i.e. the four palate tooth patches remain well developed at all stadia. It probably attains a small maximum size. Very little is known of its habits and biology, suggesting that it has been confused with other ariid taxa throughout its range.

Jayaram (1984) recorded Genus 1 polystaphylodon from the east coast of Africa. However, that record was based on a skull, probably misidentified (M.M. Smith, pers. comm.). The species is not recorded from other areas of the western Indian Ocean, and indeed, of all the Indo-Australian estuarine ariids, it has a poorly-documented distribution. It does not occur on the south coast of New Guinea, where it is apparently replaced by Genus 1 nella.

TYPES

Syntype: BMNH 1863.12.4: 98, 123 mm SL. The second syntype could not be located. It is not at the RMNH, Leiden; and it was not listed for sale in Bleeker's collection (Hubrecht, 1879).

Condition of type: poor. Body soft and shrunken; head cut through along RHS, lower jaw damaged and sagging. Branchiostegals and gill membranes torn; first gill arch on RHS lost, 2nd and 3rd cut through medially. Fins broken; dorsal spine lost.

ETYMOLOGY

Greek, poly = many; staphyle = bunch or cluster of grapes. Refers to the clusters of granular tubercles on the head shield or, to the palatal teeth.

MATERIAL EXAMINED

NORTHERN IRIAN JAYA - 1*, RMNH unreg., Holtekang, Humboldt Bay, 24 May 1955, coll. L.D. Brongersma, 152 mm SL.

NORTHERN P.N.G. - 1*, KFRS F.4176-10, Broken Water Bay, 30 May 1974, coll. D. Whitcombe, 186 mm SL; 1* ANSP 164916, Murik Lakes, Jan. 1980, coll. J. Campbell, 228 mm SL; 1*, unreg., same data, 294 mm SL; 1*, RMNH 30316, same data, 229 mm SL; 1*, CSIRO H1680-01, same data, 253 mm SL; 1*, QM I.26085, Vanimo, May 1980, coll. A. Richards, 160 mm SL; 1*, unreg., same data, 175 mm SL; 2*, NTM S.11903-001, same data, 179 & 223 mm SL; 1*, USNM 288557, same data, 226 mm SL; 4*, AMS I.16753-021, off Ramu River mouth, 19-20 Oct., coll. J. Paxton, 103-145 m SL.

INDONESIA - 1*, BMNH 1863.12.4: 98, Batavia or Priaman, no date, coll. P. Bleeker, 123 mm SL (= SYNTYPE); 1*, AMS I.27412-001, Muarakarang, Jakarta, 24 Dec. 1980, coll. P. Kailola, 165 mm SL; 1*, AMS I.27412-002, same data, 278 mm SL; 2*, unreg., Teluk Penyu, Cilacap, Java, 19 Dec. 1980, coll. P. Kailola, 122 & 129 mm SL; 3*, ZMB 31874, Teluk Penyu, Cilacap, 20 Dec., 1980, coll. P. Kailola, 105, 113 & 149 mm SL; 2*, unreg., same data, 151 & 173.5 mm SL; 1, NTM S.10733-030, Jimbarang, Bali, 21 June 1983, coll. P. Kailola & T. Gloerfelt-Tarp, 275 mm SL.

MALAYSIA - 2, CAS SU27670, Sabah, Borneo, June 1929, coll. A.W. Herre, 136 & 156 mm SL.

6.5.5

Genus 1 nella Valenciennes

(Figures 60A, 114, 115, 116, 117; Tables 23, 24)

Silurus Russell, 1803: 55

Nalla jellah Russell, 1803: 55, pl. 170 (type loc. implied: Vizagapatam, Coromandel coast, India)

Pimelodus? nella Valenciennes (in Cuvier & Valenciennes), 1840a: 162

Arius leiotetocephalus Bleeker, 1846a: 292 (Batavia, Java)

Bagrus (Ariodes) Meyenii Müller and Troschel, 1849: 9 (unknown; "Java, Celebes, Singapore", acc. to Ogilby, 1908)

Ariodes meyenii: Bleeker, 1858: 79, 82?

Hemipimelodus nella: Bleeker, 1858: 207

Ariodes leiocephalus: Bleeker, 1858: 80, 81, 83, 88

Arius liocephalus: Günther, 1864: 165

Arius nella: Day, 1877: 465

Tachysurus meyenii: Ogilby, 1908: 10

Tachysurus leiotetocephalus: Smith, 1934: 299

Tachysurus nella: Chandy, 1953: 8, pl. 1 fig. 6, pl. 3 fig. 2

Arius sp. (in part): Kailola, 1975: 39

Arius sp. "G": Kailola and Wilson, 1978: 39, 41

DEFINITION

Granular teeth arranged into two patches each side of palate, one behind the other: teeth always present in anterior patch; posterior patch elongate, long axes diverging distally. Mouth terminal. Dorsomedian head groove lanceolate; head shield rugose; supraoccipital process triangular in young, becoming ovate with convex sides with age. No gill rakers posteriorly on first two arches; first arch gill rakers total 13-16. A 14-17; total vertebrae 20-22+4-6+22-24. Caudal fin sublunate. Fresh colouration reddish brown to charcoal blue above, sides often scattered with small violet/olive-brown dots. (And see key characters.)

DESCRIPTION

D I,7. P I,11-13. A 14-17. GR (first arch) 13-15, of which 4-6 on upper limb. GR (last arch) 11-14. Number of vertebrae 47-50 (41-43).

Body fusiform, anteriorly somewhat rounded, posteriorly compressed. Predorsal profile straight to slightly convex, slightly elevated at nape; interorbital concave. Snout blunt (acute in juveniles), projecting beyond slightly curved lower jaw; lips only moderately thick, deeply crenulate along inner margin. Short crescentic groove may be present on dorsum of snout between nostrils. Mouth slightly curved, subterminal; 1/4-3/4 premaxillary tooth band exposed when mouth closed. Nostrils ovate, anterior slightly median to posterior one. Eye ovate, free of head skin; situated dorsolaterally and at mid-head length. Lateral ethmoid rugose and prominent, especially in larger fish. Gill opening moderately wide, membrane margin concave at isthmus and free.

Jaw teeth conical and slender, slightly curved; depressible. Premaxillary teeth in 6-8 irregular series, forming short, broad band, wider than long. Lower jaw teeth in 3-4 irregular series, the narrow band interrupted at symphysis by moderately broad naked space. Teeth on palate peg-like or globular, posterior ones somewhat longer; embedded in spongy tissue (thicker in larger fish) and in four autogenous groups: rounded anterior patch on each side of palate, containing 3-12 teeth; posterior patches elongate, with about 40 to more than 80 (large fish) teeth. Palatine patches parallel for most of their length; anterior part rounded, distal portion narrower and turned slightly outwards. Palate skin thick and papillose; short, oblique ridge of epithelial tissue on each side posteriorly, before branchial chambers.

Exposed head shield smooth anteriorly. Rugae or granules form patches along lateral border of shield, more extensive posteriorly; supraoccipital process varies from very granular or almost smooth. Dorsomedian head groove lanceolate, flat or shallow, almost reaching base of supraoccipital process and flanked posteriorly by prominent striate ridges. Supraoccipital process keeled, straight-sided and triangular in younger fish; keel reduced, process much expanded and laterally rounded (almost shield-like) with age. Triangular humeral process broadbased; almost smooth and moderately ossified anteroventrally. Broad shaft of process horizontal, acute, extending 1/3 distance along pectoral spine. Axillary pore a very small slit.

Barbels thick and flat. Maxillary barbel more or less reaches head margin and pectoral base. Mandibulary barbel reaches or falls well short of ventral head margin. Mental barbel reaches hind eye margin or preopercular ridge. Chin barbel bases almost transversely aligned.

Gill rakers short, half length of opposing filaments. Rakers absent from posterior aspect of first arch, 0-2 posterodorsally on second arch, 10-14 (mean 11.9) posteriorly on third arch. Low, muscular or fleshy epithelial pad with crenulate margin posterodorsally on second gill arch.

Fin spines thick, compressed, outer 1/3 of lateral aspect patterned with fine ridges and rugae. Anterior spine margin with low, sharp granules and 2-5 serrae distally. Six-10 low serrae along posterior (trailing) margin of dorsal spine, 15 to more than 20 along posterior of pectoral spine. Last dorsal ray 2.5–3.5 shorter than longest ray. Pectoral extends to or beyond last dorsal ray, its hind margin noticeably concave. Ventral narrow, ending well short of anal origin [no mature females available for comparison]. Adipose fin short-based, beginning behind anal origin. Anal margin concave, last ray 2–2.7 shorter than longest ray. Caudal fin crescentic or sublunate, its lobes broad and moderately short.

Caudal peduncle moderately thick and deep. Lateral line elevated anteriorly, almost straight, bifurcate at tail base. Vertical lines of fine pores branch off along length of lateral line.

Fresh colouration: Charcoal, reddish brown, leaden blue or olive above; body and tail pearly or bluish white below, covered with small violet or olive-brown dots. A metallic, silvery lustre or sheen over body. Caudal fin dull yellow; adipose, dorsal, ventral and anal fins with dark brown margin; pectoral fin dark bluish brown above. Barbels brown or dusky.

Colour in preservative: Dark brown, reddish brown or charcoal above, breaking into fine dark brown or fawn dots or specks over all of cream or fawn lower sides, underhead and belly; more dense under head. Maxillary barbels dark brown, other barbels fawn. Fins fawn or tan, caudal yellowish, all stippled dusky: upper aspect of pectoral fin and outer half or third of dorsal and adipose fins dark brown or charcoal; margin of anal and ventral fins brown. Peritoneum grey; gill rakers sometimes dark-tipped.

DISTRIBUTION

NEW GUINEA: Gulf of Papua.

AUSTRALIA: Northwest coast, Melville Island, Gulf of Carpentaria, east Queensland coast.

INDIA - SOUTHEAST ASIA: East coast of India (Coromandel, Vishakhapatnam [= Vizagapatnam], Puri-Orissa coast, Andhra), Bay of Bengal, Gulf of Siam, Thailand (including Bangplasor, Sriracha), Penang, Malaya (Kuala Pahang, Muar River, Malacca), Singapore, Riau (= Rhio) Strait, Java (Jakarta, Surabaya), the Philippines (Luzon Island, Leyte Island), North Borneo (specimen in CAS, collected by Herre, 1929) and Celebes (Makassar).

BIOLOGY

Habitat: sea and estuaries.

Maximum size: 871 mm TL, 745 mm SL (holotype of *Ariodes meyenii*); 810 mm FL and 710 mm FL (C. Jones, unpubl., Cairns, Sept. 1985).

Diet: Gut contents of specimens 78-149 mm SL included grit, sea urchin spines and plant material. No other dietary information is available.

Breeding: Sightings of these fish spawning in huge aggregations in shallow water, have been made in eastern Queensland over consecutive years in September and October (local fishermen; identification confirmed). One authenticated report by Queensland fishermen of spawning, covers 2-3,000 fish of 5-10 kg aggregating in an area of approximately 50 m^2. The spawning covered several hours, females releasing the large (15.5-19.2 mm diam.) ova which were fertilised and scooped up by the males in their mouths.

This species appears to migrate. Smith (1934; 1945: 412) observed that Genus 1 nella is the most abundant of Thailand's sea catfishes and that the "appearance of the fish in a given section is irregular and the abundance varies greatly from month to month and year to year." It occurs in huge schools and is caught in immense numbers in traps (e.g. 5,000 fish in one day in one trap!) and in "large quantities" in fish traps in Luzon (Herre, 1926). This phenomenon is also witnessed in Queensland.

DISCUSSION

Genus 1 nella is based on Russell's (1803) drawing and brief description of "Nalla jellah". Valenciennes (1840a) provisionally placed the fish in Pimelodus Lacepede; followed by Bleeker (1858) who included it in his genus Hemipimelodus. Day (1877), having deduced from Russell's text that the dentition was "sub-granulous" on the palate, placed "Nalla jellah" in the genus Arius Valenciennes.

The fresh colouration in Russell's painting and the tail shape, agree with that of my recently-caught material. Furthermore, I find very close agreement between Chandy's (1953) description, figures and measurements of three specimens she determined as A. nella (Valenciennes) with similar-sized Australo-Papuan material; and they also match well with Bleeker's types of leiotetocephalus. Misra (1976) also recognised A. nella, largely repeating Chandy's description. Tachysurus nella was one of several species poorly known from Indian waters (Jayaram and Dhanze, 1978), and in later publications on Indian ariids, Jayaram (1982, 1984) omitted mention of the species completely.

Reasons for poor recognition of Genus 1 nella in Indian waters would included: 1) ignorance of the growth changes in the form and texture of the supraoccipital process; 2) scientific surveys being conducted in water not frequented by the species, and its irregular appearance at local fishing grounds (e.g. statements in Smith, 1934; 1945); and 3) its similarity with *A. dussumieri* Valenciennes (both share similar dentition, head shape and lateral ethmoid prominence). (I have examined correctly identified material of *A. dussumieri* [refer Appendix A]).

Information supplied on the type of *Bagrus* (*Ariodes*) *meyenii* Müller and Troschel clearly places the taxon in the synonymy of Genus 1 *nella*. Weber and de Beaufort (1913), Herre (1953) and Whitley (1964) for example, had earlier recognised its affinity with *A. leiotetocephalus*.

Bleeker (1862) and Smith (1945) noted that the very distinct shape of the supraoccipital process sets Genus 1 *nella* apart from other species with a similar dentition. The process is easily detached from the dried skull, and Smith recorded that it may often be seen in numbers on beaches where carcasses have disintegrated. *Arius grandicassis* Valenciennes exhibits similar variation in the shape of this process. Bleeker's figure (pl. 60), his specimen in the NMV, and the *Bagrus* (*Ariodes*) *meyenii* type all have the ovate or expanded, wedge-shaped process developed from the moderately slender process of smaller fish.

Genus 1 *nella* was recorded from Australia for the first time by Ogilby (1908 - as *A. meyenii*), his record followed by McCulloch (1929). Whitley (1964) recorded it as the synonym *leiotetocephalus* Bleeker. Munro (1957) made no mention of either species. Kailola and Wilson (1978) compared their small specimens with *A. goniaspis* Bleeker. Specimens called *A. dussumieri* collected on the *Oshoro Maru* cruise to northwestern Australia (Anon., 1964) must be referable to Genus 1 nella. (A. dussumieri is restricted to the NW Indian Ocean - at least Arabian Gulf to Burma; possibly east Africa.)

The distinguishing characters of Genus 1 nella have already been discussed (refer key; figs 104, 105, 110 to 113; tables 4, 23, 24; polystaphylodon and argyropleuron discussions). This species is recognised from other taxa with four palatal tooth patches by their size and shape, the supraoccipital process shape, caudal shape, less number of haemal vertebrae and slightly longer snout (mean 43 %HL). Young fish in which the supraoccipital process has not expanded are similar to dussumieri, but they lack the prominent lateral ethmoid processes.

Arius magatensis Herre, 1926 from higher altitude, freshwater rivers of northern Luzon (Philippines) is morphologically very similar to Genus 1 nella; and the two almost certainly form a species pair. However, magatensis has 19-21 anal rays (cf. 14-17 in nella) and 18 gill rakers on the first arch (cf. 13-16 in nella). The shape of the posterior tooth patches (if that can be relied upon) are more ovate and the supraoccipital process is triangular with straight sides. I have examined a 129 mm SL specimen (CAS (SU) 29983) which is very comparable to similar-sized nella. Although this species attains a maximum SL of "half a meter or more in length" (Herre, 1926: 398), I have no information whether the supraoccipital process expands with age. The type series of magatensis is probably lost (D. Catania, pers. comm., 1989).

Genus 1 nella has not been recorded from the north coast of PNG where it apparently is replaced by Genus 1 polystaphylodon (and compare the reverse distribution of polystaphylodon).

TYPES

Arius leiotetocephalus: Bleeker (1862) stated that he had 12 specimens. At the sale of his collection they were split into 5 lots: 8 to Series A, one each to series B-E (Hubrecht, 1879). The A Series, bought by the RMNH, is catalogued as RMNH 5276. The Victorian Museum houses one of Bleeker's specimens (NMV 45964, 255 mm SL) - believed to have been the specimen allocated to the C Series (Dixon and Huxley, 1982). The whereabouts of the remaining 3 specimens is unknown.

Ariodes meyenii: The stuffed and mounted type is in the ZMB, registered as ZMB 3002. Relevant measurements (taken by H.J. Paepke) are: TL 871 mm; SL 745 mm; head length 203 mm; eye diameter (approx.) 18 mm; maxillary barbel length 100 mm; adipose fin base 26 mm; anal base 86 mm; dorsal base 55 mm; interdorsal space 256 mm; predorsal length 312 mm; snout length 80 mm; occipital process length 87 mm; process width 60 mm; mouth width 70 mm. Paepke also enclosed sketches of the occipital process and the mouth and a photograph of the whole fish. The anteriorly rounded body, small adipose fin, projecting snout and colouration clearly place Müller and Troschel's species in the synonymy of *A. nella*.

Nalla jellah Russell: The nine-inch type no longer exists.

Condition of types: *Ariodes leiotetocephalus* (on NMV 45964): fair. Body firm; RHS head cut through and first two gill arches severed; branchiostegals damaged; anal fin and tips of pectoral and ventral fins tattered; caudal lobes broken.

Ariodes meyenii: stuffed and mounted, fair. Some damage to skin and most fin tips torn. Pectoral spines damaged or absent.

ETYMOLOGY

nella (from *nalla*) is an indigenous name.

MATERIAL EXAMINED

SOUTHERN P.N.G. - 1*, AMS I.26977-001, Gulf of Papua, 13 July 1981, coll. S. Frusher, 125 mm SL; 1*, KFRS F0064, NW of Yule Island, 5 May 1970, coll. P. Kailola & J. Koaia, 115.5 mm SL; 1*, CAS 60486, Kerema Bay, 1975, coll. A.K. Haines, 122 mm SL; 2*, KFRS F02985, off Oreke River mouth, May 1973, coll. J. Koaia, 108 & 4 mm SL; 1*, ANSP 164919, Gulf of Papua, 1978, coll. S. Frusher, 135 mm SL; 1*, CSIRO A.3044, Kerema Bay, 4 April 1955, coll. A.M. Rapson, 82 mm SL;

1, KFRS F.5623-02, Morowan, Ini Island, Jan. 1976, SL not noted.

QUEENSLAND - 1*, QM I.1471, Townsville, 19 Sept. 1913, 291 mm SL;

1*, JCU 4182, Cleveland Bay, 10 Nov. 1981, coll. N. Milward, 232 mm SL; 1*, JCU 4185, same locality, 28 July 1981, coll. N. Milward, 190 mm SL; 1*, JCU 4186, same data, 240 mm SL; 1*, JCU TP163, Townsville?, 116 mm SL; 2*, unreg., heads of large specimens from Cairns, Sept. 1985.

NORTHERN TERRITORY - 4*, NTM S.11908-001, Melville Island, 12-13 Nov. 1979, coll. A. Baker, 143-149.5 mm SL; 1, NTM S.10319-002, Shoal Bay, Melville Island, Oct. 1972, 56 mm SL; 1*, CSIRO H.1913-01, 16°48'S., 139°28'30"E., 15 Dec. 1963, coll. I.S.R. Munro, 142 mm SL;

1, NTM S.12066-001, Arafura Sea, N of Cape Wessel, Nov. 1986, 245 mm SL; 1*, CSIRO C.3302, 17°25'S., 140°42'E., 29 July 1963, 118 mm SL; 1*, CSIRO C.3303, same data, 121 mm SL.

INDONESIA - 1*, NMV 45964, East Indies Archipelago, no date, coll. P. Bleeker, 255 mm SL (= SYNTYPE); 1*, MZB 139, "Golf v. Boni" (= ?Bone, Celebes), 18 Oct. 1910, 123.5 mm SL; 1, USNM 160556, Macassar, Celebes, Dec. 1909, 303 mm SL; 1, USNM 160559, same data, 350 mm SL; 1, USNM 160564, same data, 306 mm SL; 1, USNM 160565, same data, 306 mm SL; 2, USNM 138377, Celebes, no date, SL not noted.

PHILIPPINES - 1, CAS 63620, "Philippines", no date, 203 mm SL; 2*, unreg., Navotas market, Manila, 28 May 1986, coll. P. Kailola, 207 & 216 mm SL; 2, USNM 138376, Samar, no date, 108 & 183 mm SL; 1, USNM 126216, San Fabian, no date, 161 mm SL; 1, USNM 160560, Malampaya River mouth, Dec. 1908, 282 mm SL; 1, USNM 160562, same data, 275 mm SL; 1, USNM 160567, same data, 248 mm SL; 1, USNM 160568, same data, 262 mm SL; 1, USNM 160569, same data, 268 mm SL; 1, USNM 160563, Tacloban market, Leyte Island, April 1908, 246 mm SL.

SOUTH CHINA SEA - 1, CAS 63621, no date, 96 mm SL.

VIETNAM - 5, UMMZ unreg., 09°05'S, 106°22'E, Sept. 1974, 117-138 mm SL; 1, UMMZ unreg., same data, 158 mm SL.

6.6 "ARIUS"

6.6.1 Synonymy, definition and content

Genus group "Arius" Valenciennes, 1840a

A full synonymy of "Arius" Valenciennes as presently understood is presented here. It is by circumstance incomplete, as I did not fully investigate the character states of several Western Hemisphere nominal genera (Aspistor Jordan & Evermann, Leptarius Gill, Notarius Gill, Sciadeichthys Bleeker and Selenaspis Bleeker). This synonymy should be compared with that presented by earlier authors (e.g. Fowler, 1941; Herre, 1953; Misra, 1976).

Arius Valenciennes, 1840a:53 (type species, Pimelodus arius Hamilton-Buchanan, 1822, by absolute tautonomy)

Ariodes Müller & Troschel, 1849:6 (type species, Bagrus (Ariodes) arenarius Müller & Troschel, 1849, by subsequent designation)

Genidens Castelnau, 1855:33 (type species, *Bagrus genidens* Valenciennes, 1840, by absolute tautonomy)

Netuma Bleeker, 1858:23, 61, 62, 67, 93 (type species, *Bagrus netuma* Valenciennes, 1840, by absolute tautonomy)

?*Guiritinga* Bleeker, 1858:62, 67 (type species, *Pimelodus commersonii* Lacepède, 1803, by monotypy)

Hexanematichthys Bleeker, 1858a:2 (type species, *Bagrus sundaicus* Valenciennes, 1840, by monotypy)

Ariopsis Gill, 1862:56 (type species, *Arius milberti* Valenciennes, 1840a, by monotypy)

Hemiarius Bleeker, 1862:7, 29 (type species, *Cephalocassis stormii* Bleeker, 1858, by original designation)

Pseudarius Bleeker, 1862:8, 35 (type species, *Pimelodus arius* Hamilton-Buchanan, 1822, by original designation)

Neoarius Castelnau, 1878:237 (type species, *Arius curtisii* Castelnau, 1878, by monotypy)

Nemapteryx Ogilby, 1908:3, 10 (type species, *Arius stirlingi* Ogilby, 1898, by original designation)

Brustiarius Herre, 1935:388 (type species, *Arius* (*Brustiarius*) *nox* Herre, 1935, by original designation)

Pararius Whitley, 1940:409 (type species, *Arius proximus* Ogilby, 1898, by original designation)

Cochlefelis Whitley, 1941:8 (type species, *Arius spatula* Ramsay & Ogilby, 1886, by original designation)

The genus group "*Arius*" is an unnatural group of species and hence, cannot be characterised. For the purpose of *formal classification* (6.1.1) however, the group needs to be defined. This definition cannot be other than "generalised", as it relies on a mixture of synapomorphies and symplesiomorphies.

Mouth curved or transverse, inferior to terminal; lips fleshy to tightly applied. Jaw teeth very small to moderate, slender or conical, sharp and depressible or fixed; forming 4-25 irregular series in band along each jaw. Mandibulary pores small to large. Chin barbel bases close together or well-separated. Palatal dentition present or absent: when present, teeth conical and sharp, or peg-like or molariform, and grouped into two, four or six patches. Vomerine tooth plates when present, firmly fixed to vomer; other tooth plates autogenous, with or without teeth. Vomer T-shaped. Head shield and posterior cleithral process granular, rugose or almost smooth. Mesethmoid front margin deeply excavated to prominently apexed, cornua reduced or divergent; lateral ethmoid often distinct; posterior dorsomedian cranial fontanelle absent, small or long. Frontals narrow or broad posteriorly, anterior arms slender or broad. Temporal fossa open or reduced; extrascapular distinct. Subvertebral cone low to well-developed. Eye lateral or dorsolateral, orbit more or less free from head skin. Infraorbital series of four bones. Metapterygoid moderate to extensive; suture between it and hyomandibular short or long. Gill openings wide or less wide; branchiostegals 5-7. Rakers along anterior and posterior face of gill arches, not infrequently absent from posterior face of first two arches. First pharyngobranchial situated along shaft of first epibranchial or near its angle. Posterior cleithral process short to moderately long. Fin spines thick or thin, smooth to rugose. Pectoral with 8-12 branched rays; anal with 8-30 rays. Adipose fin base short or moderately long, situated above or extending beyond anal. Lateral line turned dorsad or bifurcate at caudal base. Swimbladder shape variable, from flat and oblong to ovate. Gonads bilobate.

Within Australo-Papuan members of "Arius", synapomorphies and sets of homoplasies define four subgenera and three species groups:

- subgenus Brustiarius (freshwater, northern New Guinea)
- subgenus Cochlefelis (fresh and brackish water, southern New Guinea)
- subgenus Hemiarius (freshwater to marine, [Sumatra, Borneo], southern New Guinea and northern Australia)
- subgenus Hexanematichthys (marine and estuarine, [SE Asia], southern New Guinea and northern Australia)
- species group Netuma (marine and estuarine, [East Africa] to New Guinea and northern Australia)
- species group A (freshwater, southern and northern New Guinea)
- species group B (marine to freshwater, southern New Guinea to northern Australia)

Seven individual species (marine to freshwater, New Guinea and northern Australia) do not belong in these categories, nor form groups.

Finally, two taxa are incertae sedis. Although their definition and position within the Ariidae is unstable, I suggest they remain temporarily in "Arius".

6.6.2 Key to SUBGENERA, species groups and species of "Arius" (including distribution, where NNG = northern New Guinea, SNG = southern New Guinea, NA = northern Australia)

A. Buccopharyngeal cavity either: dusky or charcoal, sometimes also gill arches; or series of longitudinal furrows in skin on upper sides, behind head; 8-10 pectoral rays; usually more than 20 gill rakers on first arch . ... B

AA. Buccopharyngeal cavity and gill arches not dark ....D

B. No teeth on palate ... [Incertae sedis] ... species 4 (SNG, NA; p. 459)

BB. Four patches of palatal teeth forming 3 or one patch .... [BRUSTIARIUS] C

C. Total GR on first arch more than 50 (mean 60.6); pads of epithelial tissue on palate and gill arches enlarged .... nox (NNG; p.269)

CC. Total GR on first arch 19-30 (mean 23.1); epithelial tissue pads not as large as in nox and irregular in shape . solidus (NNG; p.277)

D. Snout spatulate; jaw teeth in broad bands, premaxillary band largely exposed; barbels long; mandibulary pores very small
.... [COCHLEFELIS] .... E

DD. Snout not spatulate; jaw teeth not in broad bands .... F

E. Total of 15-17 GR on first arch; 20-23 anal rays; maxillary barbel reaches pectoral base at most, 17-28 (mean 20) %SL; membranous inner margin of barbels; lip broad .... spatula (SNG; p.285)

EE. Total of 18-24 GR on first arch; 21-27 anal rays; maxillary barbel to below dorsal fin, 23-38 (mean 32) %SL; no membrane on barbel inner margin; lip narrow .... danielsi (SNG; p.292)

F. Snout "shark"-like; jaw teeth strong, caniniform, fixed; head shield often smooth; mandibulary pores large
.... [HEMIARIUS] .... G

FF. Snout not "shark"-like; teeth more or less depressible .... H

G. Swimbladder cardiform, moderate, sides scalloped; eye free from head skin; lachrimal and nasal bones not irregular in shape; fin spines half-chambered; caudal vertebrae 28-29; snout length 32-41 %HL; maxillary barbel 15-25 %SL; laminar bone of anterior vertebrae reduced; Müllerian Ramus curved .... species 1 (SNG; NA; p.299)

GG. Swimbladder very large, flat, ovate; eye covered by head skin; lachrimal and nasal irregularly shaped; fin spines thin; high number of caudal vertebrae (36); snout length 28-32 %HL; maxillary barbel 11-16 %SL; laminar bone irregular and discontinuous; Müllerian Ramus angular .... species 5 (SNG; NA; p.306)

H. Nuchal ("predorsal") plate expanded with age; peritoneum dark; head depressed, granular
.... [HEXANEMATICHTHYS] .... mastersi (SNG; NA; p.310)

HH. Nuchal plate always narrow; peritoneum pale I

I. Snout prominent, slightly notched at level of nostrils; lips absent except at mouth corners; barbels long, 33-44 %SL; GR total (first arch) 12-16 .. [Incertae sedis] .... macrorhynchus (SNG; p.465)

II. Snout not notched; lips always present .... J

J. Small-based adipose fin over posterior 2/3 of anal; heart-shaped swimbladder with scalloped sides; lateral line often bifurcate at tail base .... (Netuma) .... K

JJ. Swimbladder with smooth, unnotched sides; lateral line never bifurcate at tail base .... M

K. Six patches of teeth on palate (3 on each side) L

KK. Four patches of teeth on palate (2 on each side); GR (first arch) 10-13 .... proximus (SNG; NA; p.345)

L. Snout prominent and somewhat pointed, mouth inferior; A 14-17; paired vomerine tooth patches always separate at midline; body iridescence coppery or golden ..... thalassinus (NNG; SNG; NA; p.319)

LL. Snout rounded, not prominent, mouth subterminal; A 17-21; paired vomerine tooth patches unite across palate midline with age; body iridescence bronze .... bilineatus (NNG; SNG; NA; p.332)

M. No or two (one each side) patches of teeth on palate; posterior rakers absent from full length of first two gill arches .... (species group A) .... N

MM. Four or two (one each side) patches of teeth on palate (if two, posterior rakers present) .... P

N. One oval patch of teeth each side of palate; barbels short, maxillary barbel 9-10 %SL .... species 7 (NNG; p.369)

NN. No teeth on palate (*very rarely* one patch); maxillary barbel 16-32 %SL .... O

O. Posterior aspect of first two gill arches without rakers and papillae; body dark green to olive above, sides iridescent gold; vertical series of small, golden spots along body; 5 haemal vertebrae .... *taylori* (SNG; p.364)

OO. Some rakers may be present on upper posterior limb of first two gill arches; papillae present on all or lower part of posterior aspect of gill arches; body bluish grey; 6-7 haemal vertebrae .... *velutinus* (NNG; p.353)

P. Posterior rakers present along length of all gill arches .... (species group B) .... Q

PP. Posterior rakers largely absent from first two gill arches .... S

Q. One oblique, oval patch of low, conical teeth on each side of palate; strong serrae along inner margin of pectoral spine .... species 3 (SNG; NA; p.397)

QQ. Two oval patches of villiform teeth on each side of palate (rarely one), or vomerine patches united to form one large patch medially; serrae on pectoral spine moderate .... R

R. Crescentic groove always present between nostrils; maxillary barbel reaches dorsal spine base, further in juveniles; eye large, 16-32 %HL; gill arch epithelial pads large with crenulate margins; long axis of vomerine tooth patches oblique; body bluish black to violet brown .... *berneyi* (SNG; NA; p.388)

RR. Crescentic snout groove sometimes present in juveniles; maxillary barbel reaches pectoral base, to dorsal spine base in juveniles; eye moderate, 10-28 %HL; gill arch epithelial pads moderate to small with smooth margins; long axis of vomerine tooth patches horizontal; body colour variable, usually dark brown, blue or fawn .... *graeffei* (SNG; NA; p.374)

S. Jaw teeth barely depressible; chin barbel bases well-separated, staggered; large mandibulary pores .... T

SS. Jaw teeth clearly depressible; chin barbel bases not well-separated, slightly staggered; mandibulary pores moderate or small .... U

T. Barbels short, maxillary barbel 10-12 %SL; dorsomedian head groove tapered posteriorly; body olive to vivid blue, white below .... *augustus* (SNG; p.410)

TT. Barbels long, maxillary barbel 30-56 %SL; dorsomedian head groove deep and elliptical posteriorly; body golden brown to greyish pink, fin margins blackish .... *armiger* (SNG; NA; p.401)

U. Adipose fin base 12-19 %SL, longer than anal base length; outer patches of palatal teeth much (2-3 times) larger than vomerine patches; low papillae on palate and back of gill arches; snout fleshy, mouth subinferior .... species 6 (SNG; p.455)

UU. Adipose fin base 6-14 %SL, shorter than anal base length; outer patches of palatal teeth equal to or slightly larger than vomerine patches; palate and gill arches usually smooth; snout not fleshy V

V. Snout truncate; head oblong, its width 56-75 (mean 66) %HL; first arch GR 10-17 (mean 13); A 16-19 (mean 18); maxillary barbel usually reaches head margin .... *midgleyi* (NA; p.437)

VV. Snout rounded to acute; head not oblong, its width 64-83 (mean 74) %HL; first arch GR 13-22 (mean 17); A 16-24 (mean 20); maxillary barbel usually extends beyond head margin (as far as last dorsal ray in juveniles) .... W

W. Interorbital flat or concave, nape slightly elevated; snout rounded (acute in juveniles); half premaxillary tooth band exposed when mouth closed; maxillary barbel 17-39 (mean 21) %SL; eye diameter 13-27 (mean 20) %HL; large, thick and fleshy epithelial pad posterodorsally on second gill arch; body dark green to yellowish, sides iridescent bronze .... *latirostris* (SNG; p.416)

WW. Interorbital flat or slightly convex; snout rounded; usually no teeth visible when mouth closed; maxillary barbel 23-51 (mean 35) %SL; eye diameter 10-23 (mean 14.5) %HL; low to moderate epithelial pad posterodorsally on second gill arch; body sides with vertical series of golden spots X

X. Body noticeably tapered distally; caudal peduncle depth 6-8 %SL; head low, its height 1-1.5 (mean 1.2) in its width; head skin thin; eye situated slightly before mid-head length and visible from above; 7 haemal vertebrae .... species 2 (NNG; p.447)

XX. Body moderately tapered; caudal peduncle depth 7-10 %SL; head height 1.2-2.4 (mean 1.5) in its width; head skin thick; eye situated well before mid-head length and just visible from above; 4-6 haemal vertebrae .... *leptaspis* (SNG; NA; p.426)

DISCUSSION

Pimelodus arius Hamilton-Buchanan, 1822 is the type of *Arius* Valenciennes, by absolute tautonomy (Wheeler and Baddokwaya, 1981; refer also Chapter 1.5). Bleeker however (1863b) nominated *grandicassis* Valenciennes as the type of *Arius* (and *arius* as the type of *Pseudarius* Bleeker). Day (1877) and Ogilby (1898) supported Bleeker's position. Issues raised by these and later authors were: *grandicassis* was first-named in Valenciennes' listing; whether the Hamilton-Buchanan's lost *arius* type is conspecific with Valenciennes' *Arius arius*; and whether members of *Arius* have granular palatal teeth (e.g. *arius*) or villiform (e.g. *grandicassis*).

Day (1877) placed *arius* Hamilton-Buchanan in the synonymy of his species *Buchanani*. W.R. Taylor (pers. comm., 1988) questioned the identity of *arius*: is it conspecific with *maculatus* Thunberg, 1792, or *gagora* Hamilton-Buchanan - which has page priority?

With such nomenclatural uncertainty, coupled with the broad geographical distribution, variety of phenotypes and habitats displayed by this family, it is perhaps not surprising that many nominal genera are, realistically, synonyms of "*Arius*". That the genus is paraphyletic (refer 6.1.1; 6.6.1) is symptomatic of this confusion.

I have shown that five nominal Australo-Papuan genera are synonyms of "*Arius*". Whereas three (*Nemapteryx* Ogilby, *Brustiarius* Herre and *Cochlefelis* Whitley) are based on sound character states, *Neoarius* Castelnau and *Pararius* Whitley are not. Indeed, Whitley himself (1940; 1941) and Munro (1957) appeared to experience difficulty identifying these genera whilst allocating to them a number of "*Arius*" species.

Study of additional, extralimital ariid taxa should enable recognition of the nature of "*Arius*" and its phylogenetic relationships.

ETYMOLOGY

Greek, *Ares*, *Areos* = god of war.

6.6.3 Subgenus Brustiarius definition and content

Brustiarius Herre, 1935: 388

Type: Arius (Brustiarius) nox Herre, 1935

The apomorphic dark buccopharyngeal cavity (Character 39A) defines this group, in conjunction with several homoplastic character states: in adults, temporal fossa much reduced or absent; metapterygoid enlarged, its hind border opposite hind margin of quadrate; short suture uniting metapterygoid and hyomandibular; small-based adipose fin over posterior 2/3 of anal; tendency for vomerine tooth patches to expand and/or alter shape; trend for reduced cranial ossification, plus thin premaxillary and thinning and shelving of pectoral girdle; slender epibranchials and urohyal; long palatine-lateral ethmoid facet; extreme meristics in pectoral fin (8-10 rays) and gill rakers on first arch (19-67 total). Jaw tooth series reduced; teeth small and curved or conical; lips thin; body darkly pigmented.

Known content of the subgenus:

nox Herre (freshwater, Sepik and Ramu River systems, northern New Guinea)

solidus Herre (freshwater, Mamberamo to Ramu River systems, northern New Guinea)

6.6.3.1

"Arius" (Brustiarius) nox Herre

(Figures 118, 119, 120; Tables 25, 26)

Arius (Brustiarius) nox Herre, 1935: 388 (in part) (Nyourangi, Sepik River)

Tachsysurus nox: Fowler, 1949: 52 (in part)

Brustiarius nox: Munro, 1958: 123 (in part)

DEFINITION

Front of palate with four patches of small, curved teeth arranged transversely: inner patches square, confluent with age; outer patches ovate, larger. Head slightly attenuated; lips and jaws thin, upturned at symphysis; mouth terminal. Posterior aspect of first gill arches with none to 12 rakers, and double epithelial pad dorsoposteriorly; total first arch gill rakers 56-67. Eye large, 4-6 %SL, not visible from above; barbels thin and rounded in cross-section, maxillary barbel 22-30 %SL. Fin spines thin; pectoral rays 8-9; adipose fin short-based, 4-7 %SL. Free vertebrae 44-46, including 9-10 trunk vertebrae. Fresh colouration very dark above, clearly demarcated from yellowish undersides.

DESCRIPTION

D I,7. P I,8-9. A 18-21. GR (first arch) 56-67 of which 16-20 on upper limb. GR (last arch) 48-57. Number of vertebrae 51-53 (44-46 free).

Slender catfish, body cylindrical, anteriorly depressed and posteriorly compressed. Predorsal profile flat and slightly concave to above operculum, rising more steeply at nape. Snout rounded; lips thin and tightly applied (more so on upper jaw), present as fleshy lobes at mouth corners. Jaws thin, noticeably upturned at symphysis; mouth terminal or lower jaw included; lateral part of premaxillary tooth band sometimes exposed when mouth closed. Nostrils almost rounded, well separated; anterior nostril directly in front of posterior one. Eye large and rounded, its border free from head skin. Eye situated laterally, almost in line with corner of mouth, orbit barely, or not, visible from above. Mid-head length noticeably behind eye. Gill opening wide and extending well forward, membranes meeting ventrally at an acute angle; broad, free membrane margin.

All teeth embedded in tissue. Teeth on jaws fine, conical and sharp-tipped; only slightly depressible: on upper jaw forming emarginate band of 4-8 irregular series; on lower jaw in 2-5 similar series, each side separated by moderate edentulous space. Teeth on palate small, conical, sharp or blunt-tipped; clustered into four groups arranged across front of palate. Outer palatal tooth patches ovate, inner patches square or laterally emarginate. Number of teeth increase with age, gaps between them diminish, and inner groups become confluent. Palate smooth with two low, fleshy oblique ridges of epithelial tissue posteriorly.

Bony head shield partly obscured by thick skin. Many fine granules extend over most of shield and supraoccipital process; and thin granular striae parallel dorsomedian head groove and extend towards orbit. Groove flat and lanceolate, deeper and narrow posteriorly, originating at nostrils and reaching almost to supraoccipital process base. Process almost triangular, with low median keel. Triangular humeral process smooth or rugose, thickened anteroventrally and forming flange over pectoral spine base. Process moderately acute, with upturned apex; extends 1/4-1/3 along pectoral spine. Axillary pore tiny.

Barbels rounded ("tubular") in cross section, thinner at extremities. Maxillary barbel usually reaches head margin, often to tip of humeral process. Mandibulary barbel reaches pectoral base. Mental barbel extends to head margin or pectoral spine base. Chin barbel bases moderately staggered.

Gill rakers long, equal to length of opposing gill filaments. Posterior face of gill arches smooth; upper limb of first arch with 0-7 (mean 1.3) low rakers, upper limb of second arch with 0-12 (mean 5.3) low rakers; posterior face of third arch with 39-57 (mean 45.6) rakers. Thick double pad of epithelial tissue surrounds upper insertion of first two arches.

Fin spines thin, moderately compressed, smooth laterally; sometimes short filament at tip. Anterior spine margin with sharp rugae and 3-4 low serrae distally; posterior (trailing) margin with sharp, low serrae: 10-14 on dorsal, 12-18 on pectoral. Pectoral spine subequal to dorsal spine. Last dorsal ray 2.5-3.3 in longest ray. Pectoral base situated low on sides; fin extends to below posterior dorsal rays. Ventral oblong, terminating 1/2-one eye diameter before anal origin in males and extending up to 4th anal ray in females. Sexually mature females possess moderately thick cushion of epithelial tissue along upper proximal part of 6th ventral ray, featuring an obtuse lateral flap. Adipose fin short-based, rounded in outline, situated above posterior 1/3 of anal fin. Anal margin slightly concave, last fin ray 2.4-3 shorter than longest ray. Caudal lobes narrow and tapered, upper lobe slightly the longer.

Caudal peduncle compressed and slender. Lateral line straight, elevated anteriorly and directed obliquely dorsad at tail base. Numerous oblique venules diverge from line along its length.

Fresh colouration: Back and sides blackish brown or charcoal, clearly separated from dusky white or yellowish underside of head and lower sides. Iridescent blue or violet sheen over head and body. Fins brown to dark brown, dusky yellow on outer 1/3 of anal, adipose and caudal fins, and on ventral aspect of paired fins. Barbels black.

Colour in preservative: Charcoal to blackish brown above, counter-shaded fawn or yellow below. Fins blackish brown, ventral aspect of pectoral and ventral fins dusky yellow. Barbels black. Gill filaments grey or brownish; peritoneum pale fawn or grey, sparsely speckled brown.

DISTRIBUTION

NEW GUINEA: north-draining rivers. Sepik and Ramu River systems.

BIOLOGY

Habitat: Freshwater. This species prefers the quieter waters of the floodplain and permanent billabongs and backwaters off the main river where the pH ranges from 6.2-7, water temperature from 28-34°C at the surface and 26-30°C at 10m depth. Water clarity varies from turbid to very clear (to 1.8 m visibility) (Coates, Osborne and Redding-Coates, 1983). The depth of water on the floodplain rarely exceeds 2 m; and the floodplain is dry during most of June through to November (Coates, 1983).

Maximum size: 285 mm SL (D. Coates, pers. comm.).

Diet: "*Arius*" *nox* exhibits increased feeding activity on the floodplain where the main dietary components are probably abundant during the wet season. These are small insect larvae and crustaceans, some plant material as well as fine and coarse detritus. Coates (1983) found evidence of selectivity for food items, many individuals having fed exclusively on one type in preference to other available food of a similar nature. The intake of smaller insect larvae and nymphs remains high throughout the year with reduced feeding on small crustaceans and detritus during the dry season (May to October). Conversely, an increase in the consumption of plant material (e.g. *Salvinia* root hairs) during the dry season, reflects the movement of fish off the dried floodplains to the river backwaters. According to Coates, "*A*". *nox* exhibits an annual feeding pattern in opposition to all other Sepik ariids, in that feeding activity (based on mean stomach fullness) decreases during the dry season. Fat storage also increases during the wet season (in most other ariid species, fat deposition is higher during the late dry season).

Breeding: Most spawning takes place between late January and March-April, although D. Coates (pers. comm.) collected material in breeding condition throughout the year. He recorded a maximum number of 30 ova.

DISCUSSION

Two of Herre's paratypes belong to "*A*". *solidus* Herre as they have total GR count (first arch) of 28 (CAS SU 24451) and 26 (FMNH 17200). The total GR count of the remaining paratype series ranges from 51-60. Although Herre's gill raker count for this species is therefore erroneous, any other discrepancies (e.g. colouration, general morphology) produced by inclusion of these two *solidus* specimens in the type series have been masked by the close morphological similarity of both taxa.

Roberts (1978) also noted that Herre had included *A. solidus* (as *A. kanganamanensis*) in the *nox* type series. He further surmised that the two species (and *Hemipimelodus bernhardi* Nichols) were closely related, sharing such features as an increase in gill raker number, thinning of the upper jaw and anterior portion of the cranium.

Ready parallels were drawn by Roberts (1978) and D. Coates (pers. comm.) between "*A*". *nox* and *Nedystoma dayi* (Ramsay & Ogilby) of southern New Guinea. I have earlier addressed the similarities between these taxa (Chapters 3, 5).

Coates (1983) observed that nox directs the barbels from the mandible forward, possibly using them to seek out small invertebrates from the sediment, plant material and surrounding water.

"A". nox can be distinguished from other Australo-Papuan ariids chiefly by its high gill raker count, low pectoral count, dark colouration, barbel form, large eye, flat snout and terminal mouth, and long, slender caudal lobes.

TYPES

Herre described A. nox on 12 specimens, collected from Nyourangi and Kanganaman on the Sepik River. The holotype and five paratypes are at FMNH, the remainder at CAS. Register numbers and data are: FMNH 17195, Nyourangi, 22 May 1929, 192 mm SL (= HOLOTYPE); 17196-17200 (3 from Nyourangi, 2 from Kanganaman) (= PARATYPES); CAS(SU) 24451 from Kanganaman (3 specimens), CAS(SU) 24452 from Nyourangi (3 specimens). One paratype from CAS(SU) 24451 and paratype FMNH 17200 are specimens of "A". solidus.

I have seen all paratypes. FMNH 17196, 176 mm SL; FMNH 17197, 174 mm SL; FMNH 17198, 208 mm SL; FMNH 17199, 163 mm SL; CAS(SU) 24451, 208 mm SL + 162 mm SL; CAS(SU) 24452, 168 mm SL + 163 mm SL + 171 mm SL. [See "A". solidus for other types.]

Condition of types: The four FMNH paratypes are in reasonably good condition. The gill rakers and top edge of operculum are severed in FMNH 17196; most fins and barbels are intact although all caudal fin tips are damaged; belly is slit and the body bent posteriorly in all. The CAS paratypes are in good condition. All have short slits (and holes) in the back and along the belly; the otolith is removed from the 168 mm specimen; the RHS operculum cut in the 168 and 171 mm specimens.

ETYMOLOGY

Latin, noctis = night. In reference to the very dark body colouring of this species.

MATERIAL EXAMINED

NORTHERN P.N.G. - 1*, FMNH 17196, Nyourangi, Sepik River, 22 May 1929, coll. A.W. Herre, 176 mm SL (= PARATYPE); 1*, FMNH 17197, same data, 174 mm SL (= PARATYPE); 3, CAS(SU) 24452, Nyourangi, Sepik River, 1929, 163-171 mm SL (= PARATYPES); 1*, FMNH 17198, Kanganaman, Sepik River, 15 May 1929, 208 mm SL (= PARATYPE); 1*, FMNH 17199, same data, 163 mm SL (= PARATYPE); 2, CAS(SU) 24451, Kanganaman, Sepik River, 1929, 162 & 208 mm SL (= PARATYPES); 2*, KFRS F.5518-03, Angoram, Sepik River, Jan. 1982, coll. D. Coates, 102 & 264 mm SL; 2*, WAM P.28225-001 (in part), Sepik River, no date, coll. D. Coates, 101 & 214 mm SL; 2*, WAM P.27837-003, Chambri Lakes, 21 Oct. 1982, coll. D. Coates & G.R. Allen, 215 & 222 mm SL; 6, KFRS F.4356-01, Chambri Lakes, Oct. 1972, SL's not noted; 2*, AMS I.27407-001, Angoram, Sepik River, Jan. 1982, coll. D. Coates, 180 & 282 mm SL; 5, WAM P.28223-001, Sepik River, 1982, 97-200 mm SL; 13, WAM P.28225-001 (in part), Sepik River, no date, 87-238 mm SL; 1*, WAM P.27846-004, 8km downstream from Pagwi, 27 Oct. 1982, coll. D. Coates & G.R. Allen, 131 mm SL; 2*, QM I.25056, Angoram, Oct. 1981, coll. D. Coates, 206 & 274 mm SL;
1*, NHRM A88/1981428.4230, same data, 169 mm SL; 2*, UMMZ 214018, same data, 183.5 & 192 mm SL; 1, AMS I.27407-002, Angoram, Jan. 1982, 192 mm SL; 5, KFRS F.5467-02, Bunapas Mission, Ramu River, April 1987, SL's not noted.

6.6.3.2

"Arius" (Brustiarius) solidus Herre

(Figures 57, 121, 122, 123, 124; Tables 25, 26)

Arius solidus Herre, 1935: 385 (Timbunke, Sepik River)

Arius kanganamanensis Herre, 1935: 387 (Kanganaman, Sepik River)

Arius microstomus Nichols, 1940: 2 (Bernhard Camp, Idenburg River)

Hemipimelodus bernhardi Nichols, 1940: 3 (Bernhard Camp, Idenburg River)

Tachysurus kanganamensis: Fowler, 1949: 52

Tachysurus solidus: Fowler, 1949: 52

Netuma microstomus: Munro, 1958: 122

Netuma microstoma: Munro, 1967: 82 (emend.)

DEFINITION

Palate either with small, curved teeth in four distinct patches, or in a "butterfly"-shape, or in a very large, single patch; or palate naked. Posterior aspect of first two gill arches with none to 8 low rakers; 17-23 anal rays; 8-10 pectoral rays; 19-30 rakers on first gill arch; 44-48 free vertebral centra of which 10-12 are trunk centra. Adipose fin base 4-9 %SL, above posterior 2/3 of anal; eye moderately large, visible from above, 4-7 %SL; maxillary barbels thin and rounded in cross-section, 23-26 %SL; lips moderately thin. Fresh colouration dark bluish brown; fins dark.

DESCRIPTION

D I,7. P I,8-10. A 17-23. GR (first arch) 19-30 of which 7-12 on upper limb. GR (last arch) 19-30. Number of vertebrae 52-56 (44-48 free).

Body moderately slender, depressed anteriorly. Predorsal profile straight, slightly concave at level of interorbital. Snout slightly rounded; lips moderately thin and tightly applied, thicker and fleshy at mouth corners. Jaws upturned at symphyses; mouth curved, almost terminal; teeth not visible when mouth closed. Nostrils well-separated; anterior nostril rounded, directly before ovate posterior nostril. Eye large, rounded, free from head skin. Eye situated dorsolaterally and almost entirely visible from above, well before mid-head length; horizontal line from jaw symphysis passes through pupil. Gill opening wide, membranes uniting at slightly acute angle, leaving broad, free margin.

Teeth small, fine and curved, slightly depressible, arranged in 5-8 irregular series in upper jaw, 3-6 series in lower; edentulous space in mandibulary tooth band at symphysis. Teeth on front of palate fine and conical or curved, tips sharp or blunt; clustered into 4 transversely placed patches. Outer patches ovate; vomerine patches squareish in juveniles, lengthened and laterally emarginate in larger fish. Palate dentition variable, irrespective of age (fig. 57): patches remain distinct; or vomerine patches assume an "hourglass" shape; or all unite to form a "butterfly"-shape; or a large unbroken patch; or teeth shed, only partly covering tooth plates. Palate either smooth or with fine papillae; with two low, oblique ridges of epithelial tissue posterodorsally.

Bony head shield barely concealed by thin skin, rugose to closely packed fine granules extending forward to above eye and posteriorly over supraoccipital process; granular striae border dorsomedian head groove posteriorly. Head groove lanceolate, extending from nostrils to slightly before supraoccipital process base; flat, deeper posteriorly.

Process triangular or oblong, sides slightly convex, median longitudinal keel reduced. Triangular humeral process smooth or slightly rugose, more heavily ossified anteroventrally. Process oblique, acute, extending 1/4-1/3 distance along pectoral spine. Axillary pore tiny.

Barbels very thin, flattened. Maxillary barbel reaches to or just beyond head. Mandibulary barbel extends to pectoral base. Mental barbel reaches ventral head margin or beyond. Chin barbel bases staggered.

Gill rakers half length of opposing filaments. Posterior face of arches smooth, rakers absent (rarely 1-8 rakers on upper limb) on first and second arches; 18-28 along posterior of third arch. Posterodorsal epithelial pad development on first two arches varies from absent to moderately thick and crenulate, and fleshy, better developed on second.

Fin spines moderately thick or thin, compressed, sides finely striate; anterior (leading) spine margins sharply rugose, few low spines distally; posterior margin with 5-10 low, sharp serrae (dorsal spine) or 8-12 larger serrae (pectoral). Spines sometimes tipped with short filament. Last dorsal ray 2-3.6 shorter than longest ray. Pectoral reaches to or beyond posterior dorsal rays. Ventral oblong, falling short of anal origin in males, to opposite origin and as far as 3rd-5th anal rays in females. Sexually mature females with convex pad of epithelial tissue along dorsal aspect of 6th ray. Adipose fin oblong, short-based, above posterior of anal fin. Anal margin slightly concave, last ray 2.1-3.5 shorter than longest anal ray. Caudal lobes narrow and tapered, upper lobe slightly the longer.

Caudal peduncle compressed. Lateral line straight, elevated anteriorly, obliquely dorsad at tail base. Numerous short lines diverge above and below full length of lateral line.

Fresh colouration: Dark bluish brown above, undersides cream, freckled dark brown; back and upper sides with bluish sheen. All fins dark brown.

Colour in preservative: Dark brown to brown above, fawn to creamy below. Fins dark brown, underside of pectoral and ventral paler. Barbels dark. Peritoneum dusky, pinkish cream or stippled dark grey.

DISTRIBUTION

NEW GUINEA: north-draining rivers. Mamberamo, Idenberg, Sepik and Ramu River systems.

BIOLOGY

Habitat: Freshwater. River channels and oxbow lakes, more commonly in the lakes. Occasionally over the floodplain in the wet season. [Water quality information the same as that for "*A*". *nox*.]

Maximum size: 490 mm SL (Coates, 1983).

Diet: Omnivorous. Stomach contents include larger and smaller insect larvae, *Caridina* spp., *Macrobrachium* spp., plant material (including root hairs and decaying wood), green filamentous algae, fine and coarse detritus, whole small fish (small *Tilapia*, *Ophieleotris* spp.) and loose fish scales, some earthworms (Coates, 1983). Similar items had been ingested by my specimens.

Breeding: Spawning takes place almost all year round, with a peak in the months of the early wet season. Coates (pers. comm.) recorded fecundity between 8-90 ova, with first maturity at about 200 mm SL.

DISCUSSION

The highly labile nature of the palatal dentition in this species has engendered considerable confusion for both systematists and fisheries workers conducting ecological studies. Not only is the degree of dental development independent of size (fig. 57), but the teeth are differently shaped.

The species has peaks in abundance in March-April and December. During his surveys of the Sepik River, Coates (1983) observed that "*A*". *solidus* made up 67% by weight of gill net catches and 21% of market landings. Hence, the species is very important in the local fishery. This species displays the habit of lepidophagy (Sazima, 1983) along with several other Australo-Papuan ariids.

"*Arius*" *solidus* is most similar to "*A*". *nox*, from which it can easily be distinguished by the number of gill rakers (more than 50 on first arch of "*A*." *nox*). Cluster analysis and scattergrams (using the bivariate scatter plots subprogramme) did not reveal any real morphological differences between 48 individuals determined *a priori* as *kanganamanensis* Herre, *microstomus* Nichols, *Hemipimelodus bernhardi* Nichols and *solidus*. This series included types of all nominal species.

TYPES

Arius solidus: This species is based on a holotype and 22 paratypes, all collected from the Sepik River. They are distributed as follows: FMNH 17201 (holotype); paratypes FMNH 17202-17210 (one from Timbunke, 4 from Kanganaman, 4 from Nyourangi); CAS (SU) 24445 (4 from Nyourangi); CAS (SU) 24444 (5 from Kanganaman); CAS (SU) 24447 (1 from Timbunke); CAS (SU) 24448 (1 from Koragu); CAS (SU) 24449 (1 from Kabarao). One paratype from Timbunke is missing. I have examined 18 paratypes, SL range 135-287 mm.

Arius kanganamanensis: Described on two specimens in poor condition; one locality. Holotype is FMNH 17194 (178 mm SL), paratype is CAS (SU) 24450 (176 mm SL). I have seen the paratype.

Arius microstomus: Based on two specimens, one locality. Holotype AMNH 15041 (137 mm SL), paratype AMNH 20929 (74 mm SL). I have seen the paratype.

Hemipimelodus bernhardi: This species is based on four specimens, one locality. Holotype AMNH 15039 (157 mm SL), paratypes AMNH 15040 (108.5, 138 & 173 mm SL). I have seen all paratypes.

Condition of types: *A. solidus*: sound. All have a slit along RHS of belly, often short cuts on back. Body of some twisted; or mouth cut at corner; fin rays torn; often parts of fins (e.g. caudal) lost or tattered.

A. kanganamanensis: poor. Head intact. Belly skin removed between girdles exposing viscera. Slits in body above anal and ventral, also below dorsal fin. Anal fin cut off; all of caudal missing; pectoral on LHS missing; RHS pectoral rays dislocated.

A. microstomus: Sound condition.

H. bernhardi: Sound condition; most fins intact.

ETYMOLOGY

Latin, *solidus* = dense, hard, thick, firm. In reference to the palatal dentition: "... the palate largely covered by a homogeneous plate, which merely becomes broader and longer in the adult" (Herre, 1935: 386).

MATERIAL EXAMINED

NORTHERN IRIAN JAYA - 1*, ZMA 116.458, Pioniersbivak, Mamberamo River, 19 Dec. 1920, coll. W.C. van Heurn, 270 mm SL; 1*, AMNH 20929, Bernhard Camp, Idenberg River, May 1939, coll. R. Archbold & J. Richardson, 74 mm SL (= PARATYPE of *Arius microstomus* Nichols); 2*+1, AMNH 15040, same data, 108. -173 mm SL (= PARATYPES of *Hemipimelodus bernhardi* Nichols).

NORTHERN P.N.G. - 1*, FMNH 17204, Kanganaman, Sepik River, 15 May 1929, coll. A.W. Herre, 154 mm SL (= PARATYPE); 1*, FMNH 17203, same data, 175 mm SL (= PARATYPE); 1*, FMNH 17206, same data, 185 mm SL (= PARATYPE); 1*, FMNH 17205, same data, 150 mm SL (= PARATYPE); 1*, FMNH 17202, Timbunke, Sepik River, 17 May 1929, coll. A.W. Herre, 189 mm SL (= PARATYPE); 1*, FMNH 17207, Nyourangi, Sepik River, 22 May 1929, coll. A.W. Herre, 197 mm SL (= PARATYPE); 1*, FMNH 17208, same data, 185 mm SL (= PARATYPE); 2*, WAM P.27837-002, Chambri Lakes, 21 Oct. 1982, coll. G.R. Allen & D. Coates, 101 & 222 mm SL; 1*, KFRS F.5517-03, Keram, 17 April 1980, coll. C. Brooks, 242 mm SL; 3*, WAM P.27846-003, 8 km downstream from Pagwi, 27 Oct. 1982, coll. G.R. Allen & D. Coates, 140-147 mm SL; 1*+1, WAM P.27846-002, same data, 99 & 127 mm SL; 1*, KFRS F.5518-02, Angoram, Jan. 1982, coll. D. Coates, 171.5 mm SL; 2*, QM I.25057, Angoram, 1981, coll. D. Coates, 230 & 247 mm SL; 3*, unreg. same data, 165.5 mm SL (other SL's not available); 2*, NHRM A88/1982405.4228, Magendo 2, Sepik River floodplain, 8 Oct. 1982, coll. D. Coates, 112 & 127 mm SL; 3*, KFRS F.5519-01, same data, 89-114 mm SL; 2*, MNHN 1988-804, same data, 80 & 108 mm SL; 7*, unreg., same data, 85-130.5 mm SL; 6, AMNH 58711, same data, SL not noted; 5, RMNH 30324, same data, SL not noted; 15, CSIRO H 1686-01, same data, SL not noted;

59, USNM 288560, same data, 52-82 mm SL; 3, MZUSP unreg., same data, 94-97 mm SL; 4, AMS I.27409-001, Magendo 2, Dec. 1976 & Aug. 1981, 81-176 mm SL; 1*, FMNH 17200, Kanganaman, Sepik River, 15 May 1929, coll. A.W. Herre, 149 mm SL (= PARATYPE of *A.* (*B.*) *nox* Herre); 4*, KFRS F02815, Annanberg, Ramu River, 17 Dec. 1970, coll. L. Vargu, 138-195 mm SL (138 mm SL specimen also as: AMS I.30116-001); 1*, KFRS F.5518-01, Angoram, Jan. 1982, coll. D. Coates, 143 mm SL; 1*, AMS I.27408-002, Angoram, 1982, coll. D. Coates, 206 mm SL; 1*, CAS 60487, same data, 145 mm SL; 2*, AMS I.27408-001, same data, 155 & 260 mm SL; 1, CAS (SU)69115 (ex CAS (SU)24451), Kanganaman, May 1929, 153 mm SL (= PARATYPE of *A.* (*B.*) *nox* Herre); 1, CAS (SU)24450, Kanganaman, May 1929, 176 mm SL (= PARATYPE of *A.* *kanganamanensis* Herre); 4, CAS SU24445, Nyourangi, Sepik River, May 1929, 135-191 mm SL (= PARATYPES); 5, CAS (SU)24444, Kanganaman, May 1929, 140-234 mm SL (= PARATYPES); 1, CAS (SU)24447, Timbunke, May 1929, 224 mm SL (= PARATYPE).

6.6.4 Subgenus *Cochlefelis* definition and content

Cochlefelis Whitley, 1941: 8

Type: *Arius spatula* Ramsay & Ogilby, 1886

This group is characterised by a depressed head, broad, curved mouth and wide bands of jaw teeth in which the number of often spatulate teeth increases with age and long, flattened barbels; in combination with a number of homoplasies: chin barbel bases very widely separated; lateral ethmoid very extensive ventrally, obscuring space between frontal arms; posterior dorsomedian fontanelle open at all stadia; mesethmoid with very broad cornua, anterior margin only slightly excavated; mandibulary pores very small; a higher total number of vertebrae (56-59), including more numerous caudal vertebrae; and 20-28 anal rays.

Known content of the subgenus:

spatula Ramsay & Ogilby (freshwater, southern New Guinea)

danielsi Regan (estuarine to freshwater, southern New Guinea)

6.6.4.1

"*Arius*" (*Cochlefelis*) *spatula* (Ramsay & Ogilby)

(Figures 125, 126, 127, 128; Tables 27, 28)

Arius spatula Ramsay & Ogilby, 1886: 15 (Strickland River)

Arius nudidens Weber, 1913: 538, fig. 15 (Lorentz River)

Tachysurus spatula: Fowler, 1928: 62

Tachysurus nudidens: Fowler, 1928: 62

Cochlefelis spatula: Whitley, 1941: 9

DEFINITION

Tooth tips flattened or spatulate. Four patches of teeth in line across front of palate: vomerine pair rounded, well separated; outer pair elongate. Mouth wide; nearly all of broad premaxillary tooth band exposed when mouth closed; upper lip 2/3 width of eye diameter. Eye dorsolateral; snout depressed; barbels with a shallow, membranous inner margin. A 20-23; total gill rakers on first arch 15-17; no posterior rakers on first two arches. Adipose fin base larger than or equal to dorsal base length. Fresh colouration blue or lilac above, white below.

DESCRIPTION

D I,7. P I,11-12. A 20-23. GR (first arch) 15-17, of which 4-6 on upper limb. GR (last arch) 14-16. Number of vertebrae 56-59 (50-52 free).

Body elongate, elevated before dorsal fin; anterior part of head depressed. Predorsal profile moderately steep and straight, slightly concave at interorbital. Snout well-rounded and fleshy, spatulate to slightly tapered when viewed from above; width of lip between tooth band and snout rim 2/3 eye diameter; lips moderately thick at mouth corners. Jaws strong; mouth distinctly inferior, gape broad and curved; almost all premaxillary tooth band exposed when mouth closed. Nostrils rounded, anterior nostril placed slightly lateral to posterior one. Eye ovate, its margin almost completely free from head skin; situated dorsolaterally, at or well before mid-head length. Gill opening wide, membranes meeting ventrally at a moderately acute angle, leaving broad, free margin.

Teeth conical, some acute, most with slightly spatulate or flattened tip; depressible in jaws; embedded in fleshy tissue. Curved premaxillary band with 10-25 irregular series of teeth, the number increasing with age. Lower jaw curved band with 7-17 series of teeth, band divided at symphysis by edentulous space. Palate teeth smaller than jaw teeth and arranged into four groups forming a band across front of palate: vomerine group ovate and widely separated at midline, contiguous with elongate and twice wider outer groups. Palate smooth with two very low, oblique ridges of skin before branchial chambers.

Head shield moderately smooth anteriorly. Broad band of striae flanking dorsomedian head groove posteriorly, striae radiating onto margins and over supraoccipital process, becoming rugose and granular with increasing age. Dorsomedian head groove lanceolate, very shallow anteriorly, ending well before supraoccipital process base. Process oblong, slender, with almost parallel sides. Sides of head with moderately conspicuous venules in larger fish. Humeral process smooth with few striae, broadly triangular; moderately ossified anteroventrally. Shaft oblique, acute. Axillary pore slit-like and small.

Barbels ribbon-like, compressed, with a membranous inner margin in larger fish. Maxillary barbel inserted nearly opposite posterior nostril, reaching to well short of head margin or to distal pectoral base. Mandibulary barbel begins opposite eye pupil, reaching pectoral base or as far as dorsal origin. Mental barbel inserted in line with posterior nostril, reaching as far as preopercular or opercular margin. Bases of chin barbels strongly staggered.

Gill rakers as long as opposing gill filaments. Arches smooth, posterior face of first and second arches lacking rakers; 12-15 rakers along posterior aspect of third arch. Low, muscular swelling posterodorsally on second arch.

Fin spines rounded and moderately thick, with fine longitudinal striae on sides. Outer (anterior) margin roughened and granular, few antrorse serrae near tip; posterior (trailing) margin of dorsal with 8-12 small serrae; posterior margin of pectoral with 12-16 slightly larger serrae. Spines tipped with short filament, and dorsal spine longer than pectoral. Longest dorsal ray 2.7-3 times last ray. Pectoral extends to below posterior dorsal rays. Ventral broad-based in females and reaching as far as 6th anal ray; narrow-based in males, reaching to, or short of, anal origin. In sexually mature females, 6th (inner) ray of ventral has thickened pad of epithelial tissue bearing a small "hook" on its inner margin. Adipose fin large, long-based, somewhat rectangular in shape, originating just before anal origin and terminating opposite 14-16th anal ray. Anal moderately high, margin truncate, longest ray 2.8-3.3 times last ray. Caudal fin almost lunate when extended, its lobes moderately long and tapered.

Caudal peduncle moderately slender. Lateral line oblique anteriorly, thence straight and turned dorsad at tail base. Vertical series of pores intersect with line above and below, and shorter oblique lines diverge along its length.

Fresh colouration: Vivid blue, mauve or dusky mauve above, silvery on lower sides, white below. Chin barbels white. Fins brown or bluish brown, anal and ventral fins reddish in sexually mature individuals.

Colour in preservative: Dark grey, brown or tan above, grey to cream below; snout freckled dark in small specimens. Dorsal, adipose and caudal fins brown, as well as upper aspect of pectoral, ventral and basal half of anal fins. Fin margins sometimes pale. Barbels brown, those on chin cream. Peritoneum pale, sometimes with scattered dark spots.

DISTRIBUTION

NEW GUINEA: South-draining rivers. Middle Lorentz River, middle (Hardenberg, 1936) and upper Digoel River, upper, middle (Roberts, 1978) and lower Fly River, upper and middle Strickland River, tributary of Pie River, middle Purari River to middle Lakekamu River.

BIOLOGY

Habitat: Almost exclusively freshwater. It is rare in the upper delta slightly saline areas (Haines, 1979). Haines and Maunsell and partners (1982) caught few specimens, although Roberts (1978) stated that it is fairly common in large tributaries of the upper and middle Fly. Haines found "A". spatula in a variety of habitats, from very saline water to still and flowing, turbid freshwater billabongs and main rivers. Roberts' specimens (all large individuals) came from turbid, flowing water and swampy lagoons, pH 6.7, temperature 25.5°C (one station).

Maximum size: 546 mm SL (Roberts, 1978); 570 mm FL (Haines, 1979); 640 mm TL (Maunsell and partners, 1982).

Diet: Carnivorous, almost exclusively on prawns and yabbies. Roberts (1978) found that Macrobachium and Caridina spp. were dominant, but always smaller than 40 mm carapace length [cf. "A". danielsi]. A few terrestrial insects and small fish had also been consumed. Maunsell and partners (1982) found mostly yabbies and prawns, a few fish and aquatic insects. Haines (1979) examined 13 stomachs and of the 11 containing food items, 8 held prawns, 3 had some fish. The stomachs of my material were empty.

Breeding: Females in full spawning condition have not been collected, although some of Roberts' (1978) specimens (collected end of the dry season/beginning of the wet season) were mature, the females with pads on the inner ventral rays. The assumption that "A". spatula spawns in the early wet season is further supported by the absence of mature individuals in Maunsell and partners (1982) survey, which was conducted mid-year; and my smallest specimen (0+ year-class) was caught in March. However, the 500 mm SL RMNH specimen, caught in March, is a female at gonad maturity stage IV-V, which suggests that spawning continues through to the early dry season. Haines' (1979) smallest size at maturity was 470 mm FL.

DISCUSSION

I concur with Munro (1958) and other recent authors who followed Whitley's (1941) decision to synonymise the nominal Arius nudidens Weber with "A". spatula.

Although Ramsay and Ogilby's description is based on the AMS type specimen, M. Gomon (NMV) informed me (1986) that the NMV fish register lists a "co-type" of "Arius" spatula. We have so far been unable to locate this specimen in the collection.

Tortonese (1964) tentatively recorded the synonym nudidens from Katau, based on a badly-preserved specimen of 115 mm. Although his material is not available for study I consider it unlikely that he had a specimen of "A". spatula, because of its seaside capture locality.

"A". spatula is most similar to "A". danielsi. The key characters best distinguish these taxa; and in addition: spatula has a smaller mouth gape (42-45 %HL cf. 44-59 %HL in danielsi), a shorter interdorsal (22-25 %SL cf. 26-34 %SL in danielsi) and all of the eye is visible from above (eye lateral, only partly visible from above in danielsi). No other Australo-Papuan ariids can be mistaken for these taxa.

TYPES

Arius spatula: One stated type, AMS B.9937 ("12 3/4 inches"), 254.5 mm SL (and see Discussion).

Arius nudidens: Weber listed four syntypes, of which three are at the Zoological Museum, Amsterdam: ZMA 111.508 (487 mm TL, figured specimen), ZMA 111.507 (183 mm SL, 232 mm TL) and ZMA 111.509, 105 mm TL. The remaining syntype, from 17th May 1907 collection, is in the MZB, number 129 (66.5 mm SL, 85 mm TL).

Condition of types: A. spatula: sound. Body somewhat rigid and dessicated, strongly bent at level of the adipose fin. Snout wrinkled; belly slit and some gut everted. Fins intact although slightly dislodged and dorsal membrane split behind the spine.
A. nudidens, syntype ZMA 111.507: sound. Body rigid, tail bent to RHS; head cut through on LHS, and one maxillary barbel damaged. Belly slit between pectoral girdle and ventral fins. All fins intact. I examined syntype MZB 129 in 1980 but did not note its condition.

ETYMOLOGY

Latin, spatula = spoon, shovel; broad, flat. Refers to the snout shape.

MATERIAL EXAMINED

SOUTHERN IRIAN JAYA - 1*, ZMA 111.507, Lorentz River near Van Weelskamp, 29 May 1907, coll. H.A. Lorentz, 183 mm SL, (= SYNTYPE of Arius nudidens Weber); 1*, RMNH 28817, Digoel River at Tanah Tinggi, 10-11 March 1956, coll. Lt. Romer, Roy. Netherl. Navy, 500 mm SL; 1, MZB 129, Lorentz River, 17 May 1907, 66.5 mm SL, (= SYNTYPE of A. nudidens).
SOUTHERN P.N.G. - 1*, AMS B.9937, Strickland River, Papua, registered Jan. 1886; coll. Roy. Geogr. Soc. Exped., 254.5 mm SL (= HOLOTYPE); 1*, AMS I.22461-001 (ex USNM 217083), Wai Ketu, NE of Kiunga, 21-24 Oct.

1975, coll. T.R. Roberts, 485 mm SL (not 508 mm); 1*, unreg., Kuku Creek near Bevan Rapids, Purari River, 12 May 1975, coll. A.K. Haines, 380 mm SL; 1*, unreg., billabong, mid Purari River, 5 May 1975, coll. A.K. Haines, 166 mm SL; 1*, AMS I.25997-002, same data, 143 mm SL;
2, KFRS F.4538-01, Kubiri Creek, Dec. 1974, 178 & 230 mm SL;
2, KFRS F03997, Lakekamu River, Oct. 1971, 259 & 260 mm SL;
1, KFRS F03775, Fly River at Kiunga, Oct. 1973, 200 mm SL;
2, KFRS F03998, Pie River at Baimuru, Sept. 1971, 260 & 273 mm SL;
1, KFRS F.4683-01 (ex USNM 217085) mouth of Binge River, Nov. 1975, 546 mm SL; 1, AMS I.22461-001 (ex USNM 217083), Wai Ketu, trib. of Elevala River, Oct. 1975, 508 mm SL; 3, unreg., Gwaimasi village, upper Strickland River, Aug.1986 - Nov.1987 (dried skulls only), 112-203 mm length (no SL's stated).

6.6.4.2

"*Arius*" (*Cochlefelis*) *danielsi* Regan

(Figures 129, 130, 131, 132; Tables 27, 28)

Arius (*Hemiarius*) *Danielsi* Regan, 1908a: 154 (Fly River)
Arius *Danielsi*: Weber, 1913: 542
Hexanematichthys *danielsi*: Munro, 1958: 123
Cochlefelis *danielsi*: Roberts, 1978: 45

DEFINITION

Jaw teeth numerous, tips flattened or spatulate; in broad bands. Four patches of teeth aligned across front of palate. Premaxillary tooth band exposed when mouth closed, upper lip 1/4-1/3 width of eye diameter. Eye lateral; head depressed; mouth very wide, 44-59 %HL. A 24-27; total gill rakers (first arch) 18-24; no rakers on posterior of first two gill arches. Barbels long. Adipose fin base equal to or 2/3 of dorsal base length. Fresh colouration bronze or brown above, white below.

DESCRIPTION

D I,7. P I,10-11. A 24-27. GR (first arch) 18-24 of which 6-9 on upper limb. GR (last arch) 20-24. Number of vertebrae 56-58 (49-51 free).

Body elongate and compressed; head depressed, more so in larger fish. Predorsal profile straight; interorbital flat. Snout broad and well-rounded; lips thin and firm, thicker at mouth corners; width of lip between tooth band and snout rim 1/4-1/3 eye diameter. Jaws strong; mouth gape very broad and curved; lower jaw elevated at symphysis. Snout projects beyond inferior mouth such that all or most of premaxillary tooth band exposed when mouth closed; very fine papilla-like structures developed on snout area in large fish. Nostrils lateral; anterior nostril directly anterior to posterior one. Eye moderately large, rounded or slightly ovate, its margin free from head skin. Eye lateral, situated slightly before mid-head length. Gill opening wide, membranes joining at an acute angle, leaving broad, free margin.

Teeth in jaws and on palate embedded in fleshy tissue. Teeth slightly depressible, conical, with flattened, spatulate tip; palatal teeth a little stouter. Both jaws with irregular series of 10-20 teeth, the number increasing with age; lower jaw band interrupted at symphysis by narrow edentulous space. Four ovate patches of teeth transversely arranged at front of palate: smaller, vomerine pair separated at midline by short space and contiguous with twice-broader outer patches.

Palate smooth with barely developed oblique ridges of epithelial tissue before branchial chamber.

Head shield finely granular or rugose, especially posteriorly, and mostly concealed by thin skin. Dorsomedian head groove lanceolate, shallow, originating between nostrils and terminating 1-2 eye diameters before supraoccipital process base; groove bordered posteriorly by band of fine serrae. Lateral ethmoid slightly prominent. Supraoccipital process elongate, with straight sides and low keel. Venules over sides of head moderately well developed. Triangular humeral process smooth or slightly rugose, heavily ossified anteroventrally, its shaft oblique, acute, extending 1/3 along pectoral spine. Axillary pore small and slit-like.

Barbels strap-like. Maxillary barbel extends from head margin to below dorsal fin. Mandibulary barbel usually reaches dorsal origin. Mental barbel reaches ventral head margin or as far as pectoral base. Chin barbel bases strongly staggered.

Gill rakers slender, as long as opposing filaments. Arches smooth, first two arches lacking posterior rakers, and 19-24 rakers along posterior aspect of third arch. Arches not thickened posterodorsally.

Fin spines moderately slender, slightly rounded; with fine, longitudinal striae laterally. Anterior spine margin with low granules and few antrorse serrae towards tip. Posterior margin serrate: dorsal with 11-18 low serrae; pectoral with 18-22 stronger, rather prominent serrae. Spines subequal in length and tips with short filament. Longest dorsal spine 2.4-3.8 longer than last ray. Pectoral extends to below or beyond dorsal fin. Ventral reaches anal origin, fin slender in males and broader in females. (I have no mature female specimens to examine for pad development). Adipose fin margin convex, short-based; situated above posterior half of anal fin. Anal anteriorly elevated, longest ray 2.5-3.5 longer than last ray. Caudal lobes slender and well-tapered.

Caudal peduncle compressed and moderately deep. Lateral line straight, curved dorsad at tail base and slightly elevated below dorsal. Many oblique, short lines arise from whole length of main line, and vertical series of pores extend across back and onto lower sides.

Fresh colouration: Grey, bronze or dark brown above, lilac on midsides, silvery white below. Maxillary barbel brown, other barbels white. Dorsal, caudal and adipose fins dark grey, their outer half dark brown or blackish. Other fins dusky yellow, dark brown basally on dorsal aspect of pectoral and ventral fins and anterior of anal.

Colour in preservative: Dark brown to charcoal above, dusky yellow or fawn on sides. Barbels brown. Dorsal, adipose and caudal fins brown, margins of other fins dark brown or blackish. Peritoneum fawn.

DISTRIBUTION

NEW GUINEA: south-draining rivers. Varen River, Lorentz River system, middle and lower Fly River, Strickland River (Roberts, 1978), Kikori River and delta (Anu and Kasila Creeks, Aird Hills, Aird and Newbury Rivers), Era River and delta (Morowan, Kaivu), Purari River and delta (Bevan Rapids, Kuku Creek, mid Purari River, Wame River, Arehava, Amipoke Island, Alele Passage). [Not to the Vailala River.]

BIOLOGY

Habitat: Common to abundant in the lower mangrove, *Pandanus*-*Nypa*-*Sonneratia* saline water zones of the Gulf of Papua rivers, very occasionally present upstream in the freshwater delta and main river with its sides branches (Haines, 1979). Roberts (1978) collected "*A*". *danielsi* from large, strongly-flowing rivers to swampy lagoon habitats, water quality ranging from grey and turbid, to clear, reddish brown and alkaline (pH 7.5). Maunsell and partners (1982) found "*A*". *danielsi* common in the lower Fly River and delta regions, and only recorded one large adult (520 mm TL) as far upstream as 750km from Toro Pass.

Maximum size: 550 mm FL (Haines, 1979); 450 mm SL (Roberts, 1978).

Diet: "*A*". *danielsi* is carnivorous, feeding mostly on prawns and other crustacea. Roberts (1978) found that, as with "*A*". *spatula*, "*A*". *danielsi* ingested whole specimens of *Macrobrachium* and *Caridina* spp. He also recorded some terrestrial insects and one lizard from *danielsi* stomachs. ["*A*". *danielsi* can ingest larger *Macrobrachium* (more than 70 mm carapace length) than can "*A*". *spatula* (Roberts, 1978).] Maunsell and partners (1982) found that crabs and prawns are the most abundant food items, although they also identified beetles, grasshoppers, mantis, termites, some aquatic insects, plant material and vertebrate remains in "*A*". *danielsi* stomachs. Of 107 food-containing stomachs checked by Haines (1979) there were prawns in 65, crabs in 49, fish in 4, insects in 8, detritus and algae in 2, and a coelenterate in one. "*A*". *danielsi* is the dominant ariid prawn-eater in the lower river and estuaries of the Purari system (Haines, 1979). Stomachs of material I examined contained crabs, whole prawns and fragments, crustacean fragments, bristles, insects, insect pupae, plant detritus, sticks and pulpy (fruit?) material.

Breeding: Spawning usually occurs between October and February in the estuaries and lower reaches of Gulf rivers (Haines, 1979). Maunsell and partners (1982), who sampled mid-year, found that gonads in large fish were immature or developing. Haines recorded a significantly different sex ratio in 113 specimens of 3 males, 71 females and 39 immature; and the smallest size at sexual maturity of 260 mm SL.

There is evidence of a downstream breeding migration in "A". danielsi. Only large fish with immature or developing gonads have been caught in freshwater sections, whilst mature fish and juveniles have only been caught in brackish water (Roberts', Haines' and Maunsell and partners' studies).

DISCUSSION

Although Roberts (1978) partly characterised Cochlefelis by its possession of a membranous lower margin to the barbels, this feature is not or scarcely developed in "A". danielsi.

Haines (1979) found evidence of an "ecological replacement" within this species pair, i.e. "A". spatula occurs only upstream in freshwater whilst danielsi occurs downstream in the deltas and estuaries, infrequently entering freshwater.

Differences between this species and "A". spatula are stated under spatula.

Regan (1908a) compared this species with Arius stormii Bleeker.

TYPE

Arius danielsi: Based on a single specimen, BMNH 1905.8.15: 21, 148 mm SL.

Condition of type: fair. Specimen rigid, gill membranes expanded. Belly cut from pectoral girdle to vent; large hole in upper side on RHS, mid-length of body. Most of caudal fin missing; dorsal membrane connecting rays and spine split, otherwise fins intact.

ETYMOLOGY

Named for W. Cooke Daniels who collected the type specimen.

MATERIAL EXAMINED

SOUTHERN P.N.G. - 1*, BMNH 1905.8.15: 21, Fly River, no date, coll. W. Cooke Daniels, 148 mm SL, (= HOLOTYPE); 1*, AMNH 13989, Sturt Island, Fly River, Oct. 1936, coll. R. Archbold, A. Rand & G. Tate, 201 mm SL; 1*, AMS I.22457-001 (in part), (ex USNM 217087), area of Lake Bosset & Wam River, middle Fly River, 27 Nov. 1975, coll. T.R. Roberts, 425 mm SL; 2*, KFRS F0077, Kikori River, Dec. 1956, 120 & 163 mm SL; 1*, KFRS F.4537-001, no data, 160 mm SL; 1*, NTM S.11910-001, Kubiri Creek, 3 Dec. 1974, coll. A.K. Haines, 178 mm SL; 2*, AMS I.26972-002, same data, 139 & 154 mm SL; 1*, AMS I.26972-003, same data, 210 mm SL; 1*, unreg., same data, 303 mm SL; 1*, QM I.26080, billabong, mid Purari River, 5 May 1975, coll. A.K. Haines, 355 mm SL; 1*, USNM 288551, Arehava, 19 Jan. 1975, coll. A.K. Haines, 209.5 mm SL; 1*, UMMZ 214019, Wame River, 1975, coll. A.K. Haines, 206 mm SL; 1*, RMNH 30317, Moinamu, 11 Aug. 1976, coll. A.K. Haines, 161 mm SL; 1, KFRS F.4680-01 (ex USNM 217087), area of Lake Bosset and Wam River, middle Fly River, Nov. 1975, SL not noted; 2, AMS I.22457-001, (ex USNM 217087) area of Lake Bosset and Wam River, middle Fly River, Nov. 1975, 431 & 450 mm SL; 1, NTM S.11909-001, Moinamu, Aug. 1976, 138 mm SL; 1, unreg., Moinamu, Aug. 1976, 68 mm SL; 1, NTM S.12599-001, Aird Hills, Dec. 1974, 220 mm SL.

6.6.5 Subgenus *Hemiarius* definition and content

Hemiarius Bleeker, 1862: 7, 29

Type: *Cephalocassis stormii* Bleeker, 1858

This subgenus is defined by combination of homoplasies: a convex, broad mesthmoid; metapterygoid enlarged and extending beyond the hind margin of the quadrate (not in *stormii*); large mandibulary pores; laminar bone not extensive and deeply excavated medially, well-staggered chin barbel bases (not in *stormii*); barbels strap-like; moderately smooth to striate neurocranium; strong, caniniform teeth in very few series, and teeth fixed (not depressible); seven branchiostegals (not in *stormii*) and fin spines chambered (possibly not in species 5).

Known content of the subgenus:

stormii Bleeker (brackish water to marine, Sumatra, Thailand, Borneo, possibly remainder of Indonesia and Malaya)

species 1 (freshwater to estuaries, central southern New Guinea and northern Australia)

species 5 (estuaries, central southern New Guinea and northern Australia)

6.6.5.1

"*Arius*" (*Hemiarius*) species 1

(Figures 133, 134, 135; Tables 29, 30)

Hexanematichthys sp. Kailola, 1975: 41 (in part)

Hexanematichthys sp. "Y" Kailola and Wilson, 1978: 42

Arius cf. stirlingi: Roberts, 1978: 37, fig. 16a

Arius sp. Maunsell and partners, 1982: 181

DEFINITION

Teeth very strong, non-depressible; in narrow bands in jaws and in four patches arranged across front of palate. Snout prominent, jaw teeth exposed; mouth wide. Head venulose, head shield almost smooth. Eye small, free, 7-14 %HL; few (10-11) first arch gill rakers; no rakers on posterior of first two arches; gill opening (very) wide. Body, lips and inside mouth covered with orange or yellow mucus; teeth frequently reddish.

DESCRIPTION

D I,7. P I,11-12. A 17-20. GR (first arch) 10-11 of which 3-4 on upper limb. GR (last arch) 9-11. Number of vertebrae 49-50 (42-43 free).

Body robust anteriorly, tapered and well-compressed posteriorly. Predorsal profile straight anteriorly, convex at nape. Snout prominent, well-rounded, lips thin to moderately thick, their inner margin scalloped. Jaws very strong; mouth very wide and curved, subterminal or inferior. Tooth band in upper jaw almost completely exposed when mouth shut, outer rows of teeth on lower jaw also visible in closed mouth. Nostrils large, ovate, anterior one directly before posterior one. Eye ovate, moderately small, its margin completely free from head skin; eye situated dorsolaterally, well before mid-head length. Gill opening wide, membranes broadly scalloped and meeting at an acute angle, leaving broad, free margin.

All teeth very sharp and strong, conical, not depressible. Premaxillary tooth band of 4-6 irregular series of teeth; mandibulary tooth band with 4-5 series of teeth, almost continuous across symphysis. Four patches of teeth in row across anterior of palate; two inner (vomerine) patches separated by narrow gap at midline and half as wide as outer, curved patches; 3-4 rows of teeth in each group. Palate smooth anteriorly, longitudinally creased posteriorly and with two long, low ridges of epithelial tissue before branchial chambers.

Head smooth anteriorly, few groups of sharp granules in head shield laterally; distinct parallel striae adjacent to distal third of dorsomedian head groove and extending over supraoccipital process. Dorsomedian groove narrow, lanceolate and flat, extending from between nostrils to process base. Supraoccipital process with sharp, distinct keel and straight to slightly convex sides. Predorsal plate angular and striate. Numerous, anastomising venules over anterior 2/3 and sides of head, continuing onto shoulder. Humeral process rugose, anteroventrally well-ossified and forming narrow flange; acute, triangular shaft of process reaching 1/4-1/3 along pectoral spine. Axillary pore very small and slit-like.

Barbels very thin distally. Maxillary barbel attains end of humeral process in juveniles, to well before head margin in adults. Mandibulary barbel reaches head margin in young, preopercular margin in adults. Mental barbel extends short distance behind eye. Chin barbel bases well staggered.

Gill rakers rigid, pungent, 1/2-2/3 length of opposing filaments. No rakers along posterior face of first two gill arches, 9-11 along third arch. Low, muscular thickening posterodorsally on arches.

Fin spines thick, slightly curved and rounded, patterned with fine rugae and granules. Anterior margin of spines with distinct granules proximally and 6-10 antrorse, low serrae distally; posteror margin with 8-30 serrae or dentae. Short filament on spine tips.

Longest dorsal ray 1.9-3.2 longer than last ray. Pectoral fin low, extends to below dorsal fin. Ventral fin narrow in males, ends well before anal fin origin. Fin in females broad, attains anal origin or beyond; inner rays thicken and form pad of tissue in sexually mature individuals. Adipose fin moderately high, oblong, originating approximately opposite anal origin. Anal margin almost truncate, longest ray 2.1-3.6 times last ray. Caudal lobes broad-based and strongly tapered, upper lobe slightly longer than lower.

Caudal peduncle shallow and extended. Lateral line straight, oblique below dorsal fin and strongly upturned at tail base. Short lines and ascending rows of pores branch off from lateral line, dense and extensive anteriorly.

Fresh colouration: Greenish or pale bluish grey above; white or cream below. Bright yellowish orange mucus over all of body; lips and inside of mouth also yellow. Teeth reddish. Fins bluish grey or yellowish, dusky towards margins. Snout and head of some individuals blotched black. The yellow mouth and flanks and reddish teeth distinguish this species.

Colour in preservative: Pinkish brown or tan above, cream or pale fawn below, top of head darker brown. Fins brown or light tan, margin of dorsal and caudal dark brown; upper aspect of pectoral, ventral and mid-anal rays darker brown. Maxillary barbel dark brown, others pale. Peritoneum grey.

DISTRIBUTION

NEW GUINEA: Southern coast and rivers. The middle and lower Fly River and Fly River delta throughout the Gulf of Papua, including the Kikori, Era, Pie and Purari River systems and deltas, Vailala River mouth, Murua River, Lakekamu and Oreke Rivers.

AUSTRALIA: northern coast and rivers from the Adelaide and Alligator Rivers to the Gulf of Carpentaria and the Norman River.

BIOLOGY

Habitat: Coastal and lower mangrove areas, estuaries into main rivers and lagoons; into freshwater. Although found throughout the Gulf Rivers (Papua) it is nowhere common.

Maximum size: 1.2 m FL (Haines, 1979); 1.2 m SL (Roberts, 1978); 19 kg whole weight (T. Coleman, pers. comm.). Local (Papuan) villagers have reported that this species can attain 2 m length and I have measured a 950 mm SL (1030 mm TL) specimen from the Adelaide River. N. Haysom and T. Davis have collected 1-2 m, "40 kg" (!) fish from the Alligator and Norman Rivers (pers. comm., July 1987).

Diet: Carnivorous. Food items in 18 stomachs (Haines, 1979) were: fish in 16, prawns in 3, crabs in one. In Gulf rivers, "*Arius*" species 1 is a major piscivore in the coastal through to the freshwater zones above the delta. Stomachs of Adelaide River specimens (530-570 mm SL) contained fish bones, crustacean fragments and plant material.

Breeding: In Papuan rivers, breeding occurs in the estuarine delta and *Nypa* areas (where juveniles also predominate) between July and September-October. Haines caught ripe fish and incubating males in July and August; T. Coleman (pers. comm.) caught sexually mature females (gonad stages III-VI) between January and August in northern Australian rivers. Three ripe females 720, 750 and 760 mm SL, 7-11kg whole weight from the Adelaide River in July 1989, had fecundity of 71, 47 and 85 respectively, ova diameter 16-22 mm. Haines (1979) found significantly more females than males in his material, and recorded the smallest size at first maturity as 30 cm FL.

"Arius" species 1 may migrate. Support for this comes from several observations: (1) it is not always in evidence. K. Makeu and other coastal Papuans have informed me that many large fish suddenly appear only at a certain time of the year; and individuals disappear completely from fishing grounds in northern Australia in the wet season (T. Coleman, pers. comm.); (2) it is seasonally common in estuaries (Haines, 1979); (3) whereas breeding appears to occur in the coastal zones and lower river in mid-year, large fish are caught further upriver later in the year (Haines, 1979; Roberts, 1978).

DISCUSSION

"Arius" species 1 is comparable to "A". stormii (Bleeker, 1858), a SE Asian species growing to over 500 mm (according to Weber and de Beaufort, 1913). However, "A". stormii possesses the following unique features: dorsal spine subequal to head length (equal to head length without snout in "Arius" species 1); caudal peduncle depth 2.6-2.8 in its length (1.9-2.3 in "Arius" species 1); anterior nostrils lateral to posterior ones (anterior); total gill rakers on the first arch 17-18 (10-11); serrae on front margin of dorsal spine directed upwards (directed downwards); fin spines very broad (moderately broad); adipose fin begins before anal origin (opposite or behind in "Arius" species 1).

"Arius" species 1 is also similar to "A". armiger (venulose head; small eye; strong teeth). The taxa can easily be distinguished however, on gill raker and anal fin meristics, maxillary barbel length and colouration.

Smith (1945) recorded a single "ovigerous" female of "A". stormii 400 mm long, from the river above Bangkok, 30 April 1928; and I suggest that stormii's biology is similar to that of "Arius" species 1.

In late 1976, this species was the second most important commercial species at Kikori after barramundi (*Lates calcarifer* (Bloch)) (Haines, 1979).

TYPES

No types have been nominated.

ETYMOLOGY

This species has not been named.

MATERIAL EXAMINED

SOUTHERN P.N.G. - 1, KFRS F.5627-01, Tirere village, N bank of Daru Island, April 1988, 350 mm SL; 1, KFRS F.5626-03, Sagero, N bank of Daru Island, Sept., 1988, 330 mm SL; 1, KFRS F.5729-03, Daru Island, 30 Sept. 1983, 166 mm SL; 1*, KFRS F04094, off Oreke River mouth, May 1973, coll. J. Koaia, 200 mm SL; 1*, AMS I.29292-001, Gulf of Papua, 11 July 1981, coll. S. Frusher, 159 mm SL; 4* + 6, KFRS F03992, Pie River at Baimuru, 28 Sept. 1971 (juveniles from mouth of an adult male, 104 cm SL), 84-89 mm SL (89 mm specimen also as: AMS I.30115-001); 1, KFRS F04099, old Kukipi village, Lakekamu River mouth, 18 Oct. 1971, 328 mm SL.

QUEENSLAND - 1*, CSIRO C.3798, Norman River at Karumba, 1969, coll. D.J. Turner, 430 mm SL; 2*, AMS I.15557-041, Gulf of Carpentaria at 17°26'S., 140°40'E., 23 Dec. 1963, coll. I.S.R. Munro, 103 & 172 mm SL.

NORTHERN TERRITORY - 2*, NTM S.11190-001, Northern Territory coast (exact locality unknown), June 1983, coll. P. Mundy, 450 & 460 mm SL; 9, unreg., Adelaide River, coll. T. Coleman, May-June 1989, 360-950 mm SL.

6.6.5.2

"Arius" (Hemiarius) species 5

(Figures 136, 137, 138; Tables 29, 30)

Hexanematichthys sp. (in part): Kailola, 1975: 41

Hexanematichthys sp. "D": Kailola & Wilson, 1978: 40,42

DEFINITION

Head and anterior body depressed; ribs long and angular, impressed in abdominal body wall. Eye covered with head skin; head smooth. Mouth wide, terminal, jaws upturned at symphysis; teeth fixed, cardiform; in 1-2 series on jaws and palate; four elongate patches of palatal teeth. No rakers on posterior of first two arches; mandibulary barbel longest, reaching dorsal fin. A 20-21; total gill rakers (first arch) 11-12; total vertebrae 24+3+33. Fin spines slender, weak. Fresh colouration grey or yellowish, fins and mouth (bright) yellow or orange.

DESCRIPTION

D I,7. P I,10. A 20-21. GR (first arch) 11-12, of which 5 on upper limb. GR (last arch) 10-13. Number of vertebrae 58-60 (51-54 free).

Body moderately stout, anterior two-thirds very depressed; angular pleural ribs of trunk and anterior caudal vertebrae apparent through body wall, forming a "shelf" along lower sides. Predorsal profile straight, elevated slightly at occipital process. Snout evenly rounded; lips narrow, much thickened at corners, scalloped along inner margin. Jaws very strong, lower elevated at symphysis and slightly longer than upper. Mouth terminal or superior, broad and curved; teeth not visible when mouth closed. Nostrils small and rounded, placed well forward on snout; anterior one directly in front of posterior one. Eye ovate, very small, covered with head skin; almost dorsally situated and about 4 eye diameters before mid-head length. Gill opening wide, membranes meeting well forward; distal margin broad.

Teeth fixed, strong and slightly curved, cardiform. Teeth on both palate and upper jaw arranged in two (rarely one) row(s) with distinct naked space between rows, teeth in inner row longer. One row of teeth on lower jaw and naked space at symphysis. Four elongate patches of teeth across palate: inner pair adjoining and half as wide as curved outer patches. Palate smooth; two long, low ridges of epithelial tissue before branchial chamber.

Head shield striate and rough, covered by thick skin. Dorsomedian head groove lanceolate, flat, beginning well forward on snout and almost reaching base of supraoccipital process. Process narrow, with straight sides and rounded from side to side. Sides of head smooth. Broad-based, triangular humeral process smooth, weakly ossified anteroventrally; its shaft short and oblique, extending 1/4 distance along pectoral spine. Small axillary spine present.

Barbels thin and flattened. Maxillary barbel short, reaching only to preopercular margin. Mandibulary barbel long, extending past head or as far as anterior dorsal rays. Mental barbel reaches ventral head margin or beyond pectoral base. Chin barbels strongly staggered.

Gill rakers stiff and moderately pungent, 1/2 as long as opposing gill filaments. Gill arches smooth; no rakers on posterior face of first two; 10-12 along back of third arch. No thickened tissue posterodorsally on arches.

Fin spines feeble, rounded, pungent in smallest specimen; smooth or roughened along anterior margin, and weakly serrated or roughened along posterior margin (smallest specimen with 8-9 serrae along posterior margin of pectoral spine). Dorsal fin truncate in outline, longest ray 2.3-2.8 longer than last ray. Pectoral fin very low on sides, its base in a horizontal plane. Fin hind margin truncate above, concave below; fin reaching to below dorsal. Ventral of both sexes broad, terminating well short of anal origin. Adipose fin above anterior 2/3 of anal. Anal margin almost straight, longest ray 2.6-3.1 times last ray in length. Caudal lobes broad and short.

Caudal peduncle stout. Lateral line straight, curved dorsad at tail base. Numerous very fine short lines emanate from lateral line, forming dense, branching network anteriorly; and indistinct vertical series of pores ascend from line over upper sides.

Fresh colouration: Very pale grey to yellowish above, white below; colours well-separated. Barbels grey or cream; mouth "honey"-coloured. Dorsal, ventral, anal and pectoral fins bright yellow-orange; caudal fin dull yellow-orange.

Colour in preservative: Charcoal or dark lilac-brown above, upper jaw and undersides pale. Lower sides and under head cream or pinkish, colour extending dorsally along gill membranes; nostrils and eyes also in pale streaks. Dorsal, pectoral and ventral fins dusky yellow basally, charcoal distally or over dorsal aspect; anal and caudal fins dull yellow or orangey. Peritoneum pale.

DISTRIBUTION

NEW GUINEA: Southern coast along the Gulf of Papua.

AUSTRALIA: Northern coast east of Darwin. Probably more widespread.

BIOLOGY

Habitat: Shallow mudflats and river mouths; muddy coastal waters.

Maximum size: 350 mm SL.

Diet: Stomachs empty; large, loose fish scales and detritus adhering to gills of largest specimen. Probably a piscivore.

Breeding: The largest specimen (caught late February) is a mature male, and the 282 mm specimen is female, probably at an early stage of maturity. The RHS ovary has about 20 ova, 2.5-4 mm diameter (probably two size classes). Nothing else known.

DISCUSSION

This species is very distinct (in dentition, body form, colouration) and exhibits several autapomorphies, such as form of the swimbladder, anterior vertebrae laminar bone, lachrimal and nasal.

TYPES

Types have not been nominated.

ETYMOLOGY

This species has not been named.

MATERIAL EXAMINED

SOUTHERN P.N.G. - 1*, AMS I.28960-001, Gulf of Papua, 1978, coll. S. Frusher, 282 mm SL; 1*, KFRS F03302, 1/2 mile inside Pai'a Inlet, 6 May 1967, F.R.V. Tagula, 188 mm SL (also as: AMS I.30111-001); 1*, KFRS F.5526-01, off Kerema, 11 Oct. 1983, coll. D. Witton, D. Coates & R. Watson, 270 mm SL.

NORTHERN TERRITORY - 1*, NTM S.11189-001, mouth of Wildman River, 28 February 1984, coll. P. Mundy, 350 mm SL.

6.6.6 Subgenus *Hexanematichthys* definition and content

Hexanematichthys Bleeker, 1858a: 2

Type: *Bagrus sundaicus* Bleeker, 1858 (= junior synonym of *Arius sagor* Hamilton-Buchanan)

This subgenus is defined by possession of a dark peritoneum (Character 38A) and the size of the nuchal plate ("predorsal plate") which increases and becomes square or "butterfly"-shaped with age (Character 42A); in combination with the homoplasies of temporal fossa reduced with age and head low; and neurocranium very granular.

Known content of the subgenus:

sagor Hamilton-Buchanan (marine and estuarine, east coast of India, SE Asia to Borneo and Indonesia)

masteri Ogilby (marine and estuarine, southern New Guinea and northern Australia)

6.6.6.1

"*Arius*" (*Hexanematichthys*) *mastersi* Ogilby

(Figures 139, 140, 141; Tables 39, 40)

Arius gagorides: Macleay, 1881: 213 (Port Darwin)

Arius mastersi Ogilby, 1898: 34 (northern Australia - Darwin)

Tachysurus mastersi: McCulloch, 1929: 59

Arius sagoroides Hardenberg, 1941: 221, fig. 2 (Merauke)

Tachysurus (*Pararius*) *godfreyi* Whitley, 1941: 11, fig. 8, nos. 3,4 (Port Darwin)

Netuma sagoroides: Munro, 1958: 122

Netuma mastersi: Munro, 1957: 39, fig. 278

Netuma godfreyi: Munro, 1957: 39

Pararius godfreyi: Whitley, 1964: 36

DEFINITION

Three patches of teeth each side of palate: two aligned transversely at front, a third posteriorly and at right angles. Head depressed, broad; head shield granular and extensive; supraoccipital process broad and short; predorsal (nuchal) bone expands with age, becoming broad, oblong and "butterfly"-shaped. Barbels strap-like; no rakers on posterior aspect of first two gill arches. A 16-20; total gill rakers (first arch) 12-18; total vertebrae 23-24+5+32. Caudal peduncle noticeably compressed. Fresh colouration grey to olive above with cream spots over back; white below; peritoneum dark grey or brown.

DESCRIPTION

D I,7. P I,9-11. A 16-20. GR (first arch) 12-18, of which 4-6 on upper limb. GR (last arch) 12-18. Number of vertebrae 60-61 (52-54 free).

Body depressed and broad anteriorly, well-compressed to cylindrical posteriorly. Predorsal profile straight or slightly convex, more oblique at nape. Snout evenly curved, lips moderately thick and firm, creased along inner margins. Jaws very strong; mouth subterminal, gape very broad; none or anterior 1/3 of premaxillary tooth band visible when mouth closed. Nostrils rounded or ovate, anterior one directly before posterior opening. Distinct crescent-shaped groove on dorsum of snout between nostrils; and very fine papilla-like structures scattered over snout in many different-sized individuals. Eye almost rounded, dorsolateral, its border free of head skin; eye situated just to well before mid head length. Deep pouch below suborbital extending from maxillary barbel base to beyond pupil. Gill opening wide, membranes united ventrally in obtuse angle leaving broad, free margin.

Teeth on jaws very small: slender, sharp and depressible; embedded in spongy tissue. About 12-16 irregular series of teeth in premaxillary band; 8-12 in mandibulary band which is divided at symphysis by edentulous space. Teeth on palate stout and conical, in six groups, three each side of midline: four rectangular patches across anterior of palate, two ovate patches posterior and at right angle to anterior band. All groups distinctly separated in juveniles; the four anterior patches coalescing laterally and joining the expanding posterior groups in larger fish, so forming a single patch. Vomerine tooth patches smaller than outer patches, and posterior patches becoming crescentic or concave with age. Two low, diagonal epithelial ridges occasionally present posteriorly on palate.

Head shield extensive, broad and very granular, concealed by thin skin. Granules extend forward to level of nostrils in large fish, at least to eye in juveniles. Dorsomedian head groove shallow anteriorly, deep and narrow posteriorly, sometimes partly concealed by bone overgrowth. Groove usually reaches supraoccipital process base. Process triangular in young, becoming broad and almost semicircular in large fish - as broad as long; bears sharp, low median keel. Adjacent predorsal bone narrow and crescentic in juveniles, expanding and lengthening with increasing fish size to assume a wide "butterfly" shape. Sides of head smooth, often venulose. Triangular humeral process sharply granular, striate, heavily ossified anteroventrally. Process shaft oblique and acute, extending 1/3-1/4 along pectoral spine. Axillary pore small.

Barbels robust, strap-like and compressed. Maxillary barbel reaches below last dorsal rays in juveniles, to beyond humeral process in large fish. Mandibulary barbel reaches from ventral head margin to beyond pectoral base; mental barbel reaches to or just beyond hind eye margin. Chin barbel bases moderately staggered.

Gill rakers strong and rigid, moderately long, half length of opposing filaments. Gill arches smooth; no rakers on posterior face of first arch, none (rarely 1-3) on posterior face of second; 11-17 on third. Thick pad of tissue posterodorsally on second gill arch.

Fin spines strong, compressed; with coarse or granular longitudinal striae on sides. Anterior (leading) spine margin dentate or granular, few low serrae near tip; posterior (trailing) margin with 3-9 low serrae (dorsal spine) and 16-22 stout serrae (pectoral spine). Spines tipped with filament at all sizes. Longest dorsal ray 2.3-3 longer than last ray. Pectoral fin reaches to or beyond dorsal fin. Ventral moderately slender in males, reaching just to anal origin; moderately broad to very broad in females, reaching from anal origin to 3rd ray. Large, flat pad of tissue on dorsal aspect of 5th and 6th ventral rays in sexually mature females. Adipose fin long-based, convex in outline, originating opposite or just behind anal origin and terminating before 4th last anal ray. Anal moderately elevated, anteriorly rounded, longest ray 2.3-3.4 times last ray. Caudal lobes broad and pointed; upper lobe noticeably longer than lower.

Caudal peduncle well compressed. Lateral line straight for most of its length, turned dorsad below dorsal and at tail base. Numerous short, diagonal lines and few vertical series of pores diverge from line along its length - often difficult to discern in thick body skin.

Fresh colouration: Pale silvery grey to dark olive grey above, silvery on sides, creamy white below; many pale (cream) spots scattered over back. Colour separation between dorsum and ventrum clearly defined. Fins pinkish-grey, dorsal and adipose dusky or grey, especially near margins; dorsal aspect of ventral and pectoral fins often dusky. Barbels dark or light brown.

Colour in preservative: Dark brown to grey above with faint paler spots on head and back; lower body dusky or creamy orange. Dorsal, adipose and upper lobe of caudal fin grey or dusky, basal anterior part of anal, upper aspect of pectoral and ventral fins dusky. Barbels brown or grey. Peritoneum dark grey or dark brown, often scattered with black dots.

DISTRIBUTION

NEW GUINEA: southern coast from Oetakwa River mouth to Merauke, Kerema, Purari River delta area and Galley Reach.

AUSTRALIA: northern coast. Derby to Melville Island and Darwin, Gulf of Carpentaria to Cape York (western drainage).

BIOLOGY

Habitat: Turbid, shallow coastal waters, tidal mudflats, estuaries and beaches adjacent to river mouths. Taylor's (1964) specimen was from a rocky cove over sandy bottom.

Maximum size: 510 mm SL (pers. comm., D. Carter; identification confirmed).

Diet: "A". mastersi is mostly predaceous. Twelve of the 14 stomachs examined by Haines (1979) contained food items: prawns in

5, crabs in 5, fish in 2, mud, algae and detritus in 4 (all FL's more than 320 mm). The gut contents of fish I have examined were: a small fish, fish remains, loose scales, parts of crustacea, algae, gravel and detritus.

Breeding: "*A*". *mastersi* spawns at the beginning of the wet monsoon. I have examined females with gonad stages III to VI caught October to November; and one male caught in December had mature gonads. Haines (1979) noted 34cm FL as the size at first maturity for this species. Fecundity is low, one ovary of a mature (stage VI) female I examined contained 14 large, yolked ova of 10.5-11.9 mm diameter.

DISCUSSION

The holotype of "*A*". *mastersi* bears a label reading "*A. gagorides* Cuv. & Val., Port Darwin" and is 243 mm SL. It appears to be Macleay's specimen (no length stated). By overlooking its posterior palatal tooth patches, Macleay erred in determining his specimen (now the type) as the Indo-Malay species *Arius gagorides* Valenciennes. Day (1877), Chandy (1953), Misra (1976) and others consider *A. gagoroides* as a synonym of *A. sona* (Hamilton-Buchanan, 1822). In recognising Macleay's specimen as new, Ogilby (1898) correctly remarked that it bears only a superficial resemblance to *A. sona*.

"*Arius*" *mastersi* is very similar to "*A*". *sagor* (Hamilton-Buchanan, 1822), from SE Asia, the type of the (sub)genus. I have examined 31 specimens of "*A*". *sagor* (Appendix A), a species which can be distinguished from "*A*". *mastersi* largely on possession of four instead of 6 patches of teeth on the palate and 53-55 vertebrae (total) *cf.* 60-61 in *mastersi*. Ogilby (1898) and Hardenberg (1941) (who named *mastersi* as *sagoroides*) also observed that it resembles "*A*". *sagor* in habitat and appearance.

Hardenberg's paratypes from Japero were 24 and 30 cm (?SL), and it is likely that the specimen I examined in the Jakarta collection from Japero (NCIP 516) is one of them. It was collected in 1937 and is 242 mm SL.

Whitley (1941) misidentified 12 small specimens from Mapoon (Cape York) and nominated them as paratypes of "*A*". *berneyi*.

Ogilby (1898) briefly contrasted *mastersi* with "*A*". *thalassinus* (Rüppell), which also possesses 6 autogenous tooth plates on the palate. Munro (1958) must have followed this comparison when he included *mastersi* in *Netuma* Bleeker.

In comparison with Australo-Papuan species, "*A*". *mastersi* is most similar to *leptaspis* Bleeker, in having an extensive, granular head shield and short dorsomedian head groove. However, the characters of dentition, peritoneal colour, supraoccipital and predorsal plate size easily distinguish *leptaspis* (and all other Australo-Papuan ariids) from *mastersi*.

TYPES

A. *mastersi* is based on a single specimen, AMS I.25690-001 (ex MAMU F.153); 243 mm SL.

Tachysurus (*Pararius*) *godfreyi* is based on one specimen, AMS I.5270; 305 mm SL.

The type specimens of *Arius sagoroides* Hardenberg have not definitely been identified in collections (but see Discussion).

Condition of types: *Arius mastersi*: sound. Body bent posterior to adipose fin; belly slit. Oblique tear on LHS of head through mouth and eye; first gill arch severed. Most fins intact though edges frayed;

ventral fin tattered. All colour lost: specimen silvery grey, pale fawn above.

Tachysurus (*Pararius*) *godfreyi*: fair. Body slightly soft, belly sunken, skin rubbed on LHS; a slit and few tears on belly; edges of gill membranes frayed. Fins intact but edges slightly tattered. LHS maxillary barbel frayed and damaged. Specimen silvery-brown above, white below.

ETYMOLOGY

Named for Mr George Masters, curator, the Macleay Museum, Sydney University.

MATERIAL EXAMINED

SOUTHERN IRIAN JAYA - 1*, NCIP 516, Japero, Oetakwa River mouth (NCIP stn 1), Oct. 1937, 242 mm SL (?= TYPE of *A. sagoroides*). SOUTHERN P.N.G. - 1*, AMS I.26973-001, Avioua, 28 July 1976, coll. A.K. Haines, 197 mm SL; 1*, USNM 288559, Arehava, 19 Nov. 1974, coll. A.K. Haines, 194 mm SL; 1, ZMA 119.484, Barea, Feb. 1976, 287 mm SL; 1, NTM S.11913-001, Akoma, Nov. 1976, 325 mm SL; 1*, AMNH 58709, off Kerema, June 1978, coll. S. Frusher, 224 mm SL; 1*, KFRS F.4303-44 (in part), Galley Reach, 27 July 1972, coll. L.F. Reynolds, 181 mm SL. QUEENSLAND - 12*, AMS I.8077 - 8088, Mapoon, no date, coll. W.S. Park, 79-116 mm SL (= PARATYPES of *A. berneyi* [Whitley]); 1*, QM I.22649, Chapman River mouth, 21 Dec. 1980, coll. D.B. Carter, 243 mm SL; 1*, QM I.22650, same data, 340 mm SL; 2*, unreg., Chapman River mouth, 16 Nov. 1980, coll. D.B. Carter, 290 & 395 mm SL; 1*, MZUSP unreg., same data, 248 mm SL; 1*, CSIRO C.3325, 17°36'S., 140°16'E., 31 July 1963, coll. CSIRO, 231.5 mm SL; 1, CSIRO C.4001, Gulf of Carpentaria, 10 Aug. 1963, coll "Rama", 350 mm SL; 1, CSIRO 3796, Norman River at Karumba, 1969, 350 mm SL.

NORTHERN TERRITORY - 1*, AMS I.25690-001 (ex MAMU F.153), Port Darwin, coll. W. Macleay, 243 mm SL, (= HOLOTYPE); 1*, AMS I.5270, Port Darwin, April 1902, coll. H.W. Christie & C.F. Godfrey, 305 mm SL (= HOLOTYPE of _T. godfreyi_); 2, NTM S.11537-001, Vesty's Beach, Darwin, 22 Nov. 1984, coll. G. Cole & C. Errity, 290 & 355 mm SL; 1, NTM S.11507-003, Ludmilla Creek, Darwin, 19 Dec. 1984, coll. G. Cole & A. Howard, 424 mm SL; 1, USNM 173566, Nightcliff, Darwin, March 1948, coll. R. Miller, 315 mm SL; 1*, (not kept), off Melville Island, mid 1982, coll. A. Baker, 360 mm SL; 1*+1, NTM S.10101-002, Shoal Bay, Melville Island, 17 Sept. 1973, coll. D. Grey, 79 & 161.5 mm SL; 2*+1, NTM S.10319-001, Shoal Bay, Melville Island, 19 Oct. 1972, coll. D. Grey, 89, 103 & 130 mm SL.

WESTERN AUSTRALIA - 1*, AMNH 51647, mudflats around Derby jetty, 20-21 April 1969, coll. J. Nelson, H. Butler & D. Rosen, 90 mm SL.

6.6.7 _Netuma_ Species Group

The species group _Netuma_ Bleeker in New Guinea and Australia contains three taxa: _thalassinus_ Rüppell, _bilineatus_ Valenciennes and _proximus_ Ogilby. They have in common several homoplasies: a small-based adipose fin over the posterior 2/3 of the anal; heart-shaped swimbladder with scalloped sides; 5 branchiostegals (6 in _proximus_); lateral line bifurcate at tail base (infrequently in _proximus_); and a higher average number of haemal vertebrae (6-9).

6.6.7.1

"*Arius*" (*Netuma*) *thalassinus* Rüppell, 1837

(Figures 142, 143, 144, 145; Tables 31, 32)

Bagrus thalassinus Rüppell, 1837: 75, pl. 20, fig. 2 (Massaua, Red Sea)

Bagrus netuma Valenciennes (in Cuvier & Valenciennes), 1840: 438, pl. 417 (Pondicherry, India)

Bagrus laevigatus Valenciennes (in Cuvier & Valenciennes), 1840: 439 (Red Sea)

Arius nasutus Valenciennes (in Cuvier & Valenciennes), 1840a: 45 (Malabar, India: Red Sea)

Catastoma nasutum (Kuhl & van Hasselt) Valenciennes, 1840a: 60 (Java) (manuscript)

Bagrus carchariorhijnchos Bleeker, 1846a: 291 (Batavia)

Bagrus carchariorhynchos Bleeker, 1847: 7, 9 (emend.)

Sarcogenys rostratus (Kuhl & van Hasselt) Bleeker, 1862: 28 (manuscript name in synonymy)

Arius andamanensis Day, 1870: 699 (in part) (Andaman Islands)

?*Arius serratus* Day, 1877: 462, pl. 95, fig. 3 (Sind, Pakistan)

Ariodes aeneus Sauvage, 1883: 160 ("Iles Raffles" = Singapore)

Netuma thalassina jacksonensis Whitley, 1941: 12, fig. 8, nos 1, 2 (Port Jackson, NSW)

Only primary synonymy is given for this species (refer Discussion). The generic names employed in literature has ranged from *Bagrus* through *Arius*, *Tachysurus*, *Netuma* and *Galeichthys*.

DEFINITION

Fine teeth arranged into 3 patches on each side of palate, generally forming a large triangle: one vomerine and two autogenous patches; vomerine tooth patches of each side always separated at midline. Snout angular in young, prominent and acute with age; mouth inferior. Head shield finely granular; termination of dorsomedian head groove margined by a "V" formed by the frontals; supraoccipital process a broad-based triangle with straight or convex sides. Caudal fin lobes slender and tapered; adipose fin short-based and situated posteriorly. Usually no posterior rakers on first two gill arches. A 14-17; first arch gill rakers 11-14; total vertebrae 19-20+6+19-22. Body colouration greyish blue to fawn, back and sides iridescent coppery or golden; outer half of adipose fin blackish.

DESCRIPTION

D I,7. P I,10-12. A 14-17. GR (first arch) 12-15, of which 4-6 on upper limb. GR (last arch) 11-14. Number of vertebrae 46-48 (38-44 or 45 free).

Body robust, elongate. Predorsal profile straight. Snout angular to rounded in smaller fish, generally broadly pointed or elliptical, to prominent in large individuals. Lips moderately thick, crenulate along inner margin; mouth moderately to strongly curved; subterminal in smaller fish, inferior in larger fish; 1/4 to all of premaxillary tooth band exposed when mouth closed. Nostrils ovate. Eye ovate to rounded, free from head skin; situated dorsolaterally, and at or slightly before mid-head length. Lateral ethmoid usually prominent before eye. Gill opening moderately wide; gill membranes broad and free, meeting in a right angle over isthmus.

Jaw teeth slender, sharp and depressible, their bases surrounded by fleshy tissue; arranged in 5-9 series on premaxillary and 4-7 series on mandible. Lower jaw band divided at symphysis by edentulous space.

Palate smooth to slightly villose; anteriorly with 6 patches of sharp teeth (finer and shorter than jaw teeth): a vomerine and two autogenous patches on each side, together forming a triangle. Vomerine patch rounded; anterolateral patch transversely ovate; posterior patch elongate, ovate-triangular, becoming contiguous with both anterior tooth patches with age. Narrow, medial gap separates vomerine tooth patches at all stadia. Two low to moderate, oblique, epithelial ridges posteriorly on palate.

Head shield (when apparent) smooth to moderately granular, rugae or fine granules radiating in oblique series over supraoccipital process and laterally on shield, extending to above and before eye. Dorsomedian head groove flat to shallow, broadly lanceolate and tapered posteriorly; beginning at level of nostrils and almost reaching supraoccipital process base; frontal margins bordering groove posteriorly slightly elevated, so forming a "V" junction. Supraoccipital process moderately broad, triangular, sides straight to convex, with median keel. Humeral process smooth to rugose, slightly oblique or horizontal; broadly triangular and heavily ossified anteroventrally; apex blunt or acute; process extending 1/2 distance along pectoral spine. Axillary pore small, rounded.

Barbels moderately thick. Maxillary barbel fails to reach head margin by distance of about 1/2 an eye diameter, or to slightly beyond humeral process. Mandibulary barbel slightly exceeds or falls short of ventral head margin. Mental barbel ends opposite or slightly beyond posterior eye margin. Chin barbel bases moderately staggered.

Gill rakers 1/2-2/3 length of opposing filaments. Gill arches smooth, no rakers on posterior aspect of first and second arches (rarely 1-5 on upper limb of second arch), posterior of third arch with 9-12 short rakers. Low to moderate epithelial pad development on upper limb of second gill arch.

Fin spines moderately thick. Anterior spine margin with moderate to low rugae, and serrae near tip; posterior margin of dorsal with 5-11 low serrae and posterior margin of pectoral with 11-26 stronger serrae. Last dorsal ray 2.2-3.6 shorter than longest ray. Pectoral fin reaches to below mid-dorsal fin. Ventral narrow in males, ending 1/2-1 eye diameter's distance before anal origin; fin broader in females, reaching past anal origin up to 4th ray. Inner rays thickened in sexually mature females and forming a thick pad. Anal margin concave, longest ray 2-2.8 times length of last ray. Oblong adipose fin short-based, situated above posterior 1/3 of anal. Caudal lobes narrow and tapered, upper lobe slightly longer than lower lobe; fin deeply forked.

Caudal peduncle moderately compressed and slender. Lateral line oblique anteriorly, thence straight, bifurcating over both caudal lobes (rarely, turns dorsad only). Short, oblique lines diverge from lateral line for most of its length.

Fresh colouration: Upper body grey, bluish or olive fawn, coppery on head; iridescent gold, green or silvery over sides of head, back and caudal peduncle (sometimes as narrow crossbands); sides fawn, golden or silvery; belly white to dusky cream, occasionally stippled brown. Fins tan or fawn, outer 1/2-2/3 of adipose fin blackish. Barbels fawn to cream.

Colour in preservative: Tan or fawn above, sides greyish silver or coppery; white below, often dark-stippled. Fins fawn to dark brown, outer 1/2 of adipose fin dark brown or black. Barbels fawn or brown. Peritoneum pale grey or cream.

DISTRIBUTION

NEW GUINEA: northern and southern coasts.

AUSTRALIA: Sydney (Port Jackson), north to Queensland, Northern Territory as far as Exmouth Gulf, W.A.

INDO-PACIFIC: central to northern East Africa, Red Sea to Persian Gulf, India and neighbouring coastal states, Thailand, Vietnam, Burma, Malaysia, Philippines, South China Sea and Indonesia; southern Japan?.

BIOLOGY

Habitat: Coastal waters onto the continental shelf. Juveniles are found in estuaries and near-shore areas. Adults commonly occur in deeper water than do "A". bilineatus adults: recorded at 150 m (FRV Courageous cruises, 1978), and probably inhabit greater depths. "A". thalassinus is not common in trawl catches from shallow to moderate depths. South Javanese fishers handline for large individuals several kilometres offshore (pers. comm.).

Maximum size: 1.05 m SL (Dmitrenko, 1974); to 1.3 m (pers. obs.).

Diet: Apparently opportunistic carnivores. In my material, stomachs of juveniles contained fish bones, sea-urchin fragments, loose fish scales, detritus, annelids and mud; whereas stomachs of larger specimens contained decapods (crabs, prawns, euphasids), loose fish scales and whole teleosts (Clupeidae, Engraulididae, Ophichthidae, Carangidae, Leiognathidae). Mojumder (1972, for combined "A". bilineatus + "A". thalassinus) observed variation in stomach content taxa with peaks of abundance of prey items. The diet consisted of: prawns, crabs, Squilla species and crustacean fragments (together comprising 67% gut contents), a variety of teleosts (22% contents) and mollusc (4% - cephalopod, gastropod, lamellibranch), amphipods, polychaetes, starfish and sea-cucumbers, isopods, sand and mud. Al-Hassan *et al*. (1988) identified fish and crab remains in *thalassinus* stomachs.

Breeding: Spawning takes place from the late dry season, through the wet season, into the early dry. Ripe and recently spent fish (my material) were present in June, September, December, January and March, incubating males in December, February and April. Dmitrenko (1974) found "*A*". *thalassinus* individuals spawning in summer (northern hemisphere; equivalent December-February in Australia), later than "*A*". *bilineatus* spawning. It is possible that cooler temperature at depths inhabited by *thalassinus* delayed spawning. Fecundity (my material - one gonad only examined) ranged from 22-34 mature ova, 19-24 mm diameter. Individual males probably inhabit the less saline coastal waters, where small juveniles are found.

Whereas "*A*". *thalassinus* individuals appear to be solitary at non-spawning periods, they form huge aggregations for spawning. For example, in mid-July 1989, a Taiwanese trawler in Australian waters caught 6.9 tonnes of ripe "*A*". *thalassinus* in *one* shot (between 2.30-8pm, 75m depth, 10°10'S, 134°35'E) (W. Anderson, pers. comm.); and K. Mochizuki (pers. comm., 1986) observed numerous large, sexually mature *thalassinus* at Songhkla market, Thailand (caught by pair trawler) on one day (only) in late November, 1985.

[See also, information under "*A*". *bilineatus*.]

DISCUSSION

"*A*". *thalassinus* and "*A*". *bilineatus* are distinguished from all other Australo-Papuan (and Asian) ariids by their possession of two large, tripartite palatal tooth patches. Other characters which identify them are: a short-based, posteriorly situated adipose fin, fusiform body, strong caudal peduncle and slender-lobed fin, scalloped swimbladder, and bifurcate lateral line posteriorly. The only other ariid in the region with 6 palatal tooth patches is "*A*". *mastersi*, which can be readily distinguished by its depressed, granular head, expanded predorsal plate and dark peritoneum.

These two ariids are usually thought to be one taxon. I have examined the basis for this (Kailola, 1986a) and the confused nomenclatural situation, which culminated in study of types and/or descriptions of 13 available names (see also "*A*". *bilineatus* discussion).

Distinguishing features I recognise are largely supported by Al-Hassan *et al*. (1988), and are (based on *thalassinus*):
(1) The *free vertebral count* ranges from 38-44 (45-52 in *bilineatus*) (figs 76, 146); (2) the anterior or *mid-caudal vertebral centra* (figs 39D and E, 147) are much larger than other vertebral centra (Character 41 - Chapter 3) (all centra of approximately equal size in *bilineatus*); (3) the *snout tip length* is almost always longer than that of *bilineatus* (fig. 151) at all ages and both sexes (Kailola, 1986a; figs 148, 149), reflecting the different form of the mesethmoid (Character 18 - Chapter 3); (4) *anal rays* 14-17 (17-21 in *bilineatus*; fig. 146) (5) there are 13-14 *trunk* and 6 *haemal vertebrae* (11-12 and 7-9 respectively, in *bilineatus*; (6) the *form and arrangement of granules on the head shield* differs between taxa: more extensive in *thalassinus* and coarser in *bilineatus*; (figs 144A, 152A);
(7) *supraoccipital process* usually with convex sides and broad-based (with concave sides and narrower in *bilineatus*); (8) *maximum size* of more than 1 m (little more than 60 cm in *bilineatus*); (9) the triangular, tripartite *tooth patches* on each side of the palate are

longer and always separated at the midline (shorter and uniting with age in *bilineatus*); (10) the *body colour* is usually fawn with coppery lustre (bluish or reddish brown with bronze lustre in *bilineatus*); (11) *some body proportions* (Al-Hassan *et al.*, 1988) distinguish the taxa, notably body weight/length and anal fin basal length/dorsal fin basal length; (12) *fin spines* are more robust and *maxillary barbel* slightly shorter (less robust spines and slightly longer barbel in *bilineatus*).

Masuda *et al.*'s (1984: pl. 60G) illustration of "*A*. *maculatus* (Thunberg)" from southern Japan, is of "*A*". *thalassinus*.

TYPES

Bagrus thalassinus: based on four specimens from Massaua, Red Sea, all at SMF. Holotype is SMF 544, approximately 130 mm SL; paratypes are SMF 5414, approximately 135 mm SL, SMF 5740, skeleton, and SMF 2627, dried.

Bagrus netuma: single type specimen, MNHN 9345; approximately 400 mm SL.

Bagrus laevigatus: type specimen is MNHN B.710, 129 mm SL.

Arius nasutus: three specimens, all at MNHN: MNHN A.9407, approximately 740 mm SL and A.9408, 650 mm SL - both from Malabar in India; MNHN A.9409, approximately 640 mm SL, from the Red Sea.

Bagrus carchariorhynchos: Bleeker apparently nominated one specimen as type, yet had others. He put them in the one jar with his *rhodonotus* types (refer Kailola, 1986a; see "*A*". *bilineatus* discussion). At least two of the 16 remaining at RMNH (number 6885) are referable to *thalassinus* (137, 370 mm SL, both with 41 free vertebrae); as is NMV 46590, a Bleeker specimen from the same lot. The 370 mm SL specimen is probably the type.

Arius andamanensis: the number of types was not stated, and Day's (1870) description spans both *thalassinus* and *bilineatus*. One "type" specimen in the ZSI (number 1307) has 43 free vertebrae, and so belongs with *thalassinus*.

Arius serratus: although Day (1877) nominated only one type, a ZSI and an AMS specimen claim to be that specimen. The AMS specimen is referable to *bilineatus*, but the characteristics of the ZSI specimen (number 467) have not been determined.

Ariodes aeneus: both types are at MNHN, number A.5155, 113 and 117 mm SL.

Netuma thalassina jacksonensis: Whitley nominated two types. The holotype is AMS I.10095, 275 mm SL; but the paratype, said to be 2 foot 3 inches, has not been located.

Condition of types: *thalassinus*. None examined; two are in alcohol, one dried, another skeletonised.

netuma: stuffed and mounted, varnished. Moderate condition for its preserving medium. Barbels curled and dried; eye replaced with glass; fins damaged; stitching and stuffing have obscured some features.

laevigatus: good. Head cut on RHS below; tips of dorsal spine, half of upper caudal lobe missing; lower caudal lobe partly severed.

nasutus: stuffed and mounted. Same comment as for *netuma*.

carcarhiorhynchos: very poor. Body slightly soft; RHS head and snout skinned, eye removed as well as some muscle tissue around orbit, and operculum; head groove excavated and skinned. Tissue and skin missing on RHS as far as dorsal fin; supraoccipital, neural spines and swimbladder exposed. Tissue also removed from LHS under operculum. RHS branchiostegals loose; RHS pectoral spine tip embedded in body wall. Two cuts across back behind dorsal; half of dorsal spine missing; anal and ventral fin tips damaged; lower caudal lobe broken off; upper lobe bent and cracked, but intact.

andamanensis: fair. Specimen moderately dessicated; snout squashed. Belly slit to vent; cavity eviscerated. Dorsal spine tip lost; LHS pectoral spine broken but attached; anal tattered; both caudal lobes broken off.

aeneus: fair. Body soft, but intact (both specimens). Predorsal plate broken in 117 mm specimen. Belly slit, pectoral and anal rays slightly tattered; skin on lower jaw symphysis torn and jaw loose in 113 mm specimen.

thalassina jacksonensis: Moderate. Body curved; anal fin frayed; predorsal plate broken.

ETYMOLOGY

Greek, thalassios = of the sea. Refers to the marine habitat of this species.

MATERIAL EXAMINED

NORTHERN P.N.G. - 2, WAM P.28215-001, Murik Lakes, 1982, 371 & 373 mm SL.

SOUTHERN P.N.G. - 1, CSIRO A.3041, Kerema Bay, 4 April 1955, coll. A.M. Rapson, 64 mm SL; 1, CSIRO A.3042, same data, 75 mm SL; 1*, KFRS F03399, Port Moresby harbour, 8 Sept. 1971, coll. E. Tarr, 739 mm SL.

NEW SOUTH WALES - 1*, AMS I.10095, Port Jackson, Aug. 1909, 293 mm SL (= HOLOTYPE of Netuma thalassina jacksonensis); 1*, MAMU F.152A, Port Jackson, no date, 259 mm SL; 1, AMS IA.6076, off North Head, Port Jackson, May 1934, 594 mm TL, head only kept.

QUEENSLAND - 1*, QM I.14918, 17°00'S, 140°15'25"E, 27 Feb. 1964, 125 mm SL; 1*, QM I.17350, Torres Strait, 25 March 1974, 132 mm SL; 1*, WAM P.26501-001 (in part), Gulf of Carpentaria, Oct. 1964, coll. R.W. George, 132 mm SL; 1*, CSIRO C.4134, NE of Robinson River, Gulf of Carpentaria, 1978, 150 mm SL; 4, AMS I.15557-044, Gulf of Carpentaria at 16°46'S, 139°30'E, Oct. 1963, 108-173 mm SL; 1*, JCU TP162 (in part), Townsville?, no date, 114.5 mm SL; 1, AMS E.2774, 4-20 mi. NE of Gloucester Head, Aug. 1910, 187 mm SL; 3, AMS E.2880-2, 11-14 mi. NW of Pine Peak, Aug. 1910, 168 - 178 mm SL; 1, AMS I.9788, Cape Grenville, pre-1908, 500 mm SL.

NORTHERN TERRITORY - 4*, NTM S.10031-092, N of Smith's Point, Coburg Peninsular, 18 Oct. 1981, coll. H.K. Larson & N.R. Anson, 138-153 mm SL; 4*, NTM S.11611-026, Arafura Sea at 10°26'S, 136°24'E, 8 March 1985, coll. W. Houston, 245-340 mm SL; 1, NTM S.10985-001, Arafura Sea, 1983, 470 mm SL; 1, not kept, Arafura Sea at 10°35'S, 137°03'E, March 1985, 255 mm SL; 6*, unreg., Melville Island, Aug. 1980, coll. A. Baker, 146-570 mm SL (mean SL = 255 mm); 1, NTM S.0442, N of Melville Island, June 1975, 126 mm SL; 1, NTM S.0443, same data, 134 mm SL; 1, NTM S.0613, N of Coburg Peninsular, Sept. 1975, 124 mm SL; 1, NTM S.0615, same data, 132 mm SL; 1, NTM S.0617, same data, 121 mm SL; 1, NTM S.0841, N of Melville Island, Oct. 1975, 121 mm SL; 1, NTM S.0842, same data, 140 mm SL; 1, NTM S.0844, same data, 128 mm SL; 1, NTM S.0851, same data, 143 mm SL; 1, NTM S.0854, same data, 138 mm SL; 1*, CSIRO C.3699, 08°55'S, 138°00'E, 4 Dec. 1968, coll. CSIRO, 213 mm SL; 1*, CSIRO A.2204, 17°21'S, 139°53'E, 1978, coll. CSIRO, 119 mm SL; 1*, CSIRO A.2205, same data, 113 mm SL; 1*, MNHN 1989-1083, N of Darwin, 1980, coll. A. Baker, 142 mm SL; 2*, AMS I.29288-001, same data, 128 & 137 mm SL; 1, not kept, near

Milingimbi, Nov. 1984, 760 mm FL, 860 mm TL; 4, not kept, 11°07'S, 131°30'E, July 1980, 115-123 mm SL.

WESTERN AUSTRALIA - 1*, WAM P.24229, Napier Broome Bay, July 1973, coll. W.A. Fish & Fauna Dept, 98 mm SL; 1*, CSIRO CA284, NNW of Nickol Bay at 19°27'S, 116°33'E, 16 May 1978, coll. CSIRO, 337 mm SL; 1*, WAM P.4532, Exmouth Gulf, 14 Sept. 1958, 173 mm SL; 1*, not kept, 19°44'S, 116°02'E, 2 Dec. 1979, coll. CSIRO, 395 mm SL; 1*, unreg., 19°46'S, 116°00'E, 3 Dec. 1979, coll. CSIRO, 501 mm SL; 1*, unreg., 19°29'S, 115°59'E, 3 Dec 1979, coll. CSIRO, 376.5 mm SL; 2*, not kept, 18°08'S, 119°22'E, 12 June 1980, coll. CSIRO, 380 & 390 mm SL; 1*, unreg., 18°00'S, 119°10'E, 12 June 1980, coll. CSIRO, 388 mm SL; 1*, unreg., 17°49'S, 120°18'E, 15 June 1980, coll. CSIRO, 455 mm SL; 2*, unreg., 18°09'S, 120°02'E, 15 June 1980, coll. CSIRO, 395 & 413 mm SL; 1*, CSIRO C.3898, Exmouth Gulf, no date, 97 mm SL.

INDONESIA - 2*, RMNH 6885 (in part), Batavia, pre-1879, coll. P. Bleeker, 137 & 370 mm SL (larger specimen prob. = TYPE of _Bagrus carchariorhynchos_); 1*, CSIRO H 1683-01, Cirebon, 1986, coll. K. Taylor, 470 mm SL; 1, not kept, South Java, Aug. 1981, 460 mm SL; 1, not kept, Roti Island, Aug. 1981, SL not noted; 1, unreg., Pasar Sanglah, Bali, Aug. 1981, 193 mm SL; 1, S of Lombok Island, Aug. 1981, 169 mm SL; 1, NCIP 201, 06°13'S, 105°44'E, April 1983, 390 mm SL; 1, NMV 46590, East Indies Archipelago, coll. P. Bleeker, pre-1879, SL not noted (= type?).

PHILIPPINES - 4*, unreg., Navotas market, Manila, 28 May 1986, coll. P. Kailola, 151-198 mm SL; 1, USNM 56076, Bulan, pre-1906, 400 mm SL; 1, CAS 27674, Tayabas, Luzon, 1931, 116 mm SL; 1, CAS 6356, Manila Bay, no date, 186 mm SL; 2, CAS(SU) 29565, Manila Bay, no date, 158 & 236 mm SL; 2, CAS 38203, Iloilo, August 1940, 181 & 221 mm SL; 1, ANSP 77351, Philippines, no date, 166 mm SL.

CHINA - 1*, ASIZB 640596, no data supplied, 290 mm SL.

SINGAPORE - 2*, MNHN A.5155, "Iles Raffles" (= Singapore), Expedition de *La Zelee*, 1840, 113 & 117 mm SL (= COTYPES of *Ariodes aeneus*); 1, CAS 39338, Singapore, no date, 140 mm SL.

VIETNAM - 1, UMMZ unreg., Vietnam, no date, 142 mm SL; 11, UMMZ unreg., Vietnam at 09°00'N, 106°20'E, Sept. 1974, 110-142 mm SL.

THAILAND - 1*, ZMB 31873, Songhkla market (from S Gulf of Thailand), 26 Nov. 1985, coll. K. Mochizuki, 119.5 mm SL; 2, CAS 63617, off Phu-Quoc, Gulf of Thailand, no date, 128 & 143 mm SL; 1, CAS 2566, Gulf of Thailand at 11°34'N, 99°52'E, 176 mm SL; 2, CAS 63635, SE of Ko-Prong, Gulf of Thailand, Dec. 1968, 82 & 102 mm SL; 1, CAS 63831, Gulf of Thailand at 11°59'N, 102°44'E, Oct. 1957, 65 mm SL.

INDIA - 1*, MNHN A.9407, Malabar, no date, 740 mm SL (= SYNTYPE of *Arius nasutus*); 1*, MNHN A.9408, same data, 650 mm SL (= same status); 1*, MNHN A.9345, Pondicherry, no date, 400 mm SL (= TYPE of *Bagrus netuma*); 1*, ZSI 1307, Andaman Islands, no date, coll. F. Day, 246 mm SL (= COTYPE of *Arius andamanensis*); 1, CAS 29587, Arabian Sea near Bombay, no date, 135 mm SL; 2, CAS(SU) 41040, Maharanipeta Beach, no date, 130 & 180 mm SL; 12, USNM unreg., Visakhapatnam, April 1963, SL not noted; 2, USNM unreg., Mandapan, Sept., 1966, 223 & 234 mm SL.

PAKISTAN - 1*, LACM 38133-70, 3-4 km W of Turshian Creek mouth, Sind, 26 April 1978, coll. CCS78-21, 173 mm SL; 2, LACM unreg. (ex 38129-94), near Paitani Creek mouth, Sind, April 1978, 126 & 222 mm SL.

PERSIAN GULF - 1, USNM unreg., N of Qatar, Feb. 1977, 370 mm SL.

RED SEA - 1*, MNHN B.710, Mer Rouge, no date, 129 mm SL (= TYPE of *Bagrus laevigatus*); 1*, RMNH 3043, Red Sea, no date, 269 mm SL (= stated specimen of *Netuma nasuta*, topotype of *Bagrus thalassinus*).

ETHIOPIA - 1, USNM 207003, 15°40'N, 040°23'E, no date, 309 mm SL.

6.6.7.2

"Arius" (Netuma) bilineatus Valenciennes,

(Figures 150, 151, 152, 153; Tables 31, 32)

Bagrus bilineatus Valenciennes (in Cuvier & Valenciennes), 1840: 434
(Pondicherry, India; Rangoon, Burma)

Bagrus rhodonotus Bleeker, 1846: 157 (Batavia)

Arius andamanensis Day, 1870: 699 (in part) (Andaman Islands)

Arius serratus Day, 1877: 462, pl.95, fig. 3 (Sind, Pakistan)

Netuma osakae Jordan & Kanazawe (in Jordan & Hubbs), 1925: 157, pl. 9,
fig. 1 (Osaka, Japan)

Arius dayi Dmitrenko, 1974: 39, figs 1A, 2 (Masera, Oman)

Only primary synonymy is given for this species (see Discussion). The generic names employed in literature has ranged from Bagrus through Arius, Tachysurus, Netuma and Galeichthys.

DEFINITION

Fine teeth arranged into 3 patches on each side of palate, generally forming a large triangle: one vomerine and two autogenous patches; vomerine tooth patches of each side fused together in larger fish. Snout rounded or slightly truncate; mouth subterminal. Head shield rugose or granular, coarser over supraoccipital process; dorsomedian head groove bordered posteriorly by slightly raised frontals forming a "V"; supraoccipital process a moderately narrow triangle with straight or concave sides. Caudal fin lobes slender and tapered; adipose fin short-based and situated posteriorly. Usually no posterior rakers on first two gill arches. A 17-21; first arch gill rakers 11-16; total vertebrae 20-21+7-9+27-28. Body colouration reddish or bluish brown, with bronze lustre over back and sides; adipose fin dark brown.

DESCRIPTION

D I,7. P I, 10-12. A 17-19(21). GR (first arch) 11-16 of which 4-6 on upper limb. GR (last arch) 10-15. Total vertebral number 53-58 (46-52 free).

Body robust. Predorsal profile straight, more oblique at nape. Snout rounded to slightly truncate. Lips moderately thick; mouth moderately wide and curved, subterminal; up to 1/4 premaxillary tooth band visible when mouth closed. Nostrils ovate, posterior one slightly lateral. Shallow, crescentic groove often present between posterior nostrils. Eye rounded to ovate, free from head skin; situated dorsolaterally and little before mid-head length. Lateral ethmoid somewhat prominent. Gill opening moderately wide; broad, free gill membranes forming a right angle medially over isthmus.

Teeth slender, sharp and depressible, embedded in soft tissue; arranged in 5-8 series on premaxillary and 4-6 series on lower jaw. Lower jaw band divided at symphysis by edentulous space. Palate smooth to slightly villose, anteriorly with 6 patches of sharp, slightly stronger teeth: a vomerine and two autogenous patches on each side. Vomerine tooth patches and anterolateral patches rounded or ovate, with age often contiguous with each other and across midline. Posterior patch elongate and triangular, usually contiguous with anterolateral tooth patch. Two (very) low, oblique epithelial ridges on palate before branchial chamber.

Head shield smooth, rugose or granular, groups of rugae or granules concentrated at anterior and lateral margins and covering much of supraoccipital process; granules coarser along crenulate to rounded median keel of process. Dorsomedian head groove generally shallow and broadly lanceolate, not or almost reaching supraoccipital process base, slightly raised posterolateral border to fontanelle forming a "V" junction before process base. Supraoccipital process a moderately slender triangle, with straight to concave sides. Humeral process with horizontal, anastomosing rugae; broadly triangular and heavily ossified anteroventrally. Process blunt-tipped and only slightly oblique, extending 1/3-1/2 distance along pectoral spine. Axillary pore small, rounded.

Barbels moderately thick. Maxillary barbel usually reaches head margin or to past tip of humeral process. Mandibulary barbel usually attains ventral head margin. Mental barbel ends opposite eye. Chin barbel bases moderately staggered.

Gill rakers 2/3 length of opposing filaments. Gill arches smooth, posterior aspect of first two arches with no rakers (rarely 1-3 on upper limb); posterior of third arch with 8-14 short rakers. Moderate to feeble epithelial pad development on upper limb of first two arches.

Fin spines slender to moderately thick. Low rugae along leading spine margin and few serrae near tip; posterior margin of dorsal with low serrae and 2/3 length of pectoral posterior margin with 9-15 stronger serrae. Last dorsal ray 2.3-3.5 shorter than longest ray. Pectoral fin reaches to below mid-dorsal fin. Ventral narrow in males, not reaching anal origin by distance 1/4-one eye diameter. Ventral broader in females and reaching anal origin to 3rd anal ray, inner rays thickened to form low pad in sexually mature fish. Anal margin concave, last ray 1.5-3.4 shorter than longest ray. Adipose fin short-based, oblong, situated above posterior 2/3 of anal. Caudal lobes narrow and tapered, upper slightly longer; fin deeply forked.

Caudal peduncle compressed and shallow. Lateral line oblique anteriorly, thence straight to caudal base where it bifurcates over both lobes (rarely, turns dorsad only). Short, oblique lines diverge from lateral line for most of its length as well as vertical series of papillae.

Fresh colouration: Upper body dark grey, reddish or bluish brown, often with a bronze lustre ("each of the granules on the head appear to be tipped with gold": Day, 1877: 463); sides iridescent silver or bronze, sometimes narrow, iridescent crossbands present; belly fawn, cream or white, sometimes brown-stippled; fins tan; adipose fin uniformly brown. Barbels fawn.

Colour in preservative: Reddish brown to tan above, becoming pale below; sides often with grey-blue sheen; creamy undersides often stippled brown. Fins yellowish brown; pectoral, ventral and anal paler proximally, outer half dark; most of adipose fin dark brown to blackish. Barbels brown. Peritoneum pale grey, pinkish or white.

DISTRIBUTION

NEW GUINEA: northern and southern coasts.

AUSTRALIA: southeast Queensland (to northern NSW: Grant, 1987), to off Shark Bay, W.A.

INDO-PACIFIC: NW Indian Ocean to India and neighbouring coastal states, Malaysia, Thailand, Vietnam, all of Indonesia, the Philippines, South China Sea to southern Japan (only record is *Netuma osakae*, which O. Okamura suggested [1985] would have been fished in the [warmer] China Sea).

BIOLOGY

Habitat: Coastal waters onto the continental shelf. Juveniles are present in estuaries. Adults are usually in shallower waters than are "*A*". *thalassinus* adults. Thus, this species is more frequently represented in catches, such waters being accessible to smaller fishing craft. Also recorded to 124 m depth (FRV *Courageous* cruises, 1978).

Maximum size: 620 mm SL (western Torres Strait).

Diet: Apparently opportunistic carnivores. In my material, stomachs of juveniles (130 mm SL) contained loose scales, detritus, mud, sea urchin and crustacean fragments; and stomachs of larger fish (300-350 mm SL) contained prawns, loose scales, teleosts (Leiognathidae; indet.) and crustacean fragments. Mojumder's (1972) analysis of stomach content (refer this heading under "*A*". *thalassinus*) equally applies to *bilineatus*. Al-Hassan *et al*. (1988) recorded a variety of teleosts, prawns and crabs in stomach contents of Arabian Gulf *bilineatus* as well as alpheid shrimps, echinoderms and molluscs.

Breeding: Spawning takes place from the late dry season to mid wet season. Ripe and just spent fish (my material) were caught in June, August, November, December; and brooding males in November and March. Fecundity (my material, one gonad examined) ranged from 18 (380 mm FL) to 54 (620 mm SL; mature ova diameter 15.5-18 mm). Moreover, a 310 mm SL fish had 7 and 9 mature ova (both gonads); and a 216 mm SL male (caught in March) was brooding 5 juveniles, 51-55.3 mm SL. Thus, fecundity appears to increase with fish size; and size at first maturity is less than 30 cm. The total number of large ova in 8 "*thalassinus*" from off Cilacap, Java (Sept. 1979) ranged from 61-103 (Anon., 1980).

As with "*A*". *thalassinus*, large spawning aggregations form, often in estuaries and shallower coastal waters. Smith (1945) reported such schools in SE Thailand estuaries; and Grant (1987) noted "boils" in the Gulf of Carpentaria (both presumably, of "*A*". *bilineatus*).

For both taxa, the following information has been gathered: spawning occurs at 20-75m, over a silty substrate, when surface temperature attains 25-28°C; mature ovum diameter 15-24 mm; fecundity range 23-103; incubation period up to 47 days; juvenile size at release (51?)64 mm (Dmitrenko, 1970, 1974; Al-Nasiri and Hoda, 1977; see also Rimmer and Merrick, 1983; pers. obs.).

Dmitrenko's (1970) reporting of "*thalassinus*" were subsequently (1974) found to be based on *bilineatus* (as *Arius dayi*) + *thalassinus*. My observations do not support his conclusion that these taxa have disjunct spawning periods. It is possible that Arabian Gulf populations undertake different spawning regimes than do Indo-Australian *Netuma*, or that other factors (such as water temperature) influence the periodicity.

Mojumder's (1981) attempted analysis of spawning and maturity in *thalassinus* is again clouded through combining two taxa. Nevertheless, he found mature fish for a relatively short period (April to August) and a low fecundity (max. total 42). I suggest he only sampled young adults.

DISCUSSION

This common species has been confused with "*A*". *thalassinus* (Rüppell) since Bleeker, 1858. Hence, prepared descriptions of "*A. thalassinus*" are based on a mixture of *bilineatus* and *thalassinus*.

Bleeker (1858) surmised that too much significance had been placed on appearance in the *Netuma* group which, he decided, were expressions of growth and life expectancy (e.g. the "shark-like" appearance of the head with growth). He (1858; 1862) therefore placed in synonymy, seven nominal taxa (actually representing two valid species): *thalassinus* Rüppell, *netuma* Valenciennes, *bilineatus* Valenciennes, *laevigatus* Valenciennes, *nasutus* Valenciennes, *rhodonotus* Bleeker and *carchariorhynchos* Bleeker. Bleeker was followed by Günther (1864), Day (1877) and most subsequent authors.

Two persistent, erroneous assumptions have remained with fisheries workers for more than 130 years, *viz*: that the snout becomes longer with increasing size; and that only males develop a produced snout (e.g. Weber & de Beaufort, 1913; Jayaram, 1984). As a result of this long-held belief that only one "sea catfish" (*thalassinus*) existed, many works on the distribution, biology and commercial fishery of "*A. thalassinus*" need to be referred to with caution. Examples are: Al-Nasiri and Shamsul Hoda (1977), Mojumder (1972; 1974; 1977; 1981), Sekharan (1973), Pillai (1978) and Randall *et al.* (1978). However, judging by the stated lengths of their study material, mostly *bilineatus* was caught. Mojumder (1977) recorded a moderately rapid growth rate for "*thalassinus*", yet found more than one modal size group in a length-frequency study; whilst Sekharan (1973a) found that "*thalassinus*" preferred two depth zones in the Bay of Bengal. It is likely the presence of two species were reflected in these results.

Characters which distinguish *bilineatus* from *thalassinus* are discussed under "*A*". *thalassinus*.

"Deddi-jella" of Russell (1803: 54, pl.169) is not a manuscript name of "*A*". *bilineatus*, as I earlier supposed (1986a). It appears instead, to belong with "*Arius*" *jella* Day, as it has granular palatal teeth (Day, 1877: 467).

Taylor's (1964) specimens of "*thalassinus*" (USNM 173567) are referable to *bilineatus*, as is Grant's (1987: 69) figure.

TYPES

Bagrus bilineatus: two specimens named as types. One is MNHN A.9344, from Pondicherry, approx. 240 mm SL. The syntype from Rangoon cannot be located and may be lost.

Bagrus rhodonotus: not certainly located. Bleeker (1846) did not state the number of types, and when he synonymised rhodonotus with B. carchariorhynchos and nasutus Valenciennes, he put all of his specimens in the one jar. None of the 23 specimens he then had bears indication that it is a type of rhodonotus, although 14 of the 16 from his total now as RMNH 6885, have the characteristics of bilineatus. Two specimens are at BMNH and another at NMV. The remaining five specimens have not been located.

Arius andamanensis: Day also, did not state the number of specimens he used to describe this species. One specimen in Day's Collection, purchased by the AMS (number B.7931), claims to be the "type". With 49 free vertebrae, it belongs in bilineatus.

Arius serratus: a 128 mm SL specimen in Day's Collection at AMS is labelled "Type". AMS B.7971 has 46 free vertebral centra, and I refer it to "A". bilineatus.

Netuma osakae: the single type is at FMNH, number 59388, 390 mm SL. Although the vertebral count is unavailable, its characteristics are those of bilineatus.

Arius dayi: Dmitrenko nominated a holotype (Zool. Museum, Kiev; number TNPMAN Pi2/1-2) and several(?) paratypes, which are at the Zoology Museum, Odessa National University and Ardievniro in Kirsch. The lengths of these specimens and their vertebral count are unknown.

Condition of types: bilineatus: fair. Stuffed and mounted; varnished(?) eye replaced by glass; stitching and stuffing altered some morphology. All barbels broken off.

rhodonotus: type not identified.

andamanensis: sound. Belly slit to vent; LHS first gill arch removed; dorsal spine broken (no other information).

serratus: sound. Body eviscerated and belly shrunken; tips of caudal lobes broken off.

osakae: good, reasonably well-preserved and firm; strongly curved to the left. Skin on flanks with many abrasions which render a mottly and spotted appearance; dorsal spine broken but attached; left pectoral spine broken; tip of upper caudal lobe missing.

dayi: no information; none seen.

ETYMOLOGY

Latin, bi = two; lineatus = line. Valenciennes (1840: 434) chose this name in reference to slightly noticeable curving lines on the flanks above the ribs.

MATERIAL EXAMINED

NORTHERN P.N.G. - 1*, KFRS F.4384-01, Murik Lakes, 1982, coll. G.R. Allen 139 mm SL.

SOUTHERN P.N.G. - 2*, KFRS F0080, Daru Roads, 19 Jan. 1961, 137 & 186 mm SL; 1, KFRS F0585, same data, 109 mm SL; 1, KFRS F03055, NW of Yule Island, Feb 1970, 138 mm SL; 1*, KFRS F.4428-01, Yule Island, 22 Jan. 1971, coll. J. Tokios, 123.5 mm SL; 2*, KFRS unreg., 08°06'S, 144°30'E, 23 Feb. 1978, coll. S. Frusher, 222 & 242 mm SL; 12, unreg., western Torres Strait, Nov. 1987, coll. P. Kailola, 223-620 mm SL.

QUEENSLAND - 4*, MAMU F.152, Torres Strait, no date, 222-251.5 mm SL; 1*, QM I.17349, Torres Strai, 26 March 1974, coll. Qld Fish., 215.5 mm SL; 1*, QM I.16506, S of Caldbeck Reef, Torres Strait, 5 Dec. 1974, 148 mm SL; 2*, JCU TP162, off Townsville, no date, 120 & 163 mm SL; 1*, WAM P.26501-01 (in part), Gulf of Carpentaria, Oct. 1964, coll. R.W. George, 128 mm SL; 1*, CSIRO C.4073, 6 mi. N of NE Islet, Gulf of Carpentaria, 4 Sept. 1963, 192 mm SL.

NORTHERN TERRITORY - 1*, NTM S.10031-154, N of Smith's Point, Coburg Peninsular, 18 Oct. 1981, coll. H.K. Larson & N.R. Anson, 125 mm SL; 1*, WAM P.26500-001, 37 km N of Darwin, 9 Sept. 1965, coll. A. Baker, 124 mm SL; 3*, not kept, N of Darwin, mid-Aug. 1980, coll. A. Baker, 240-310 mm SL; 2*, AMS I.29289-001, Melville Island, 1980, coll. A. Baker, 124 & 128 mm SL; 1*, MNHN 1989-1081, same data, 109 mm SL; 1, NTM S.0409, N of Melville Island, Sept. 1982, 252 mm SL; 1, NTM S.11614-019, N of Cape Wessel, March 1985, 225 mm SL; 1, CAS 52520, off Arnhem Land at 12°08'S, 130°04.5'E, 24 Dec. 1972, 129 mm SL; 2, USNM 173567, NW Groote Eylandt, coll. R.R. Miller, May 1948, 250 & 345 mm SL; 1, NTM S.10943-013, N of Groote Eylandt, Feb. 1983, 250 mm SL; 1, NTM S.1113, Burns Shoals off Point Arrowsmith, Oct. 1975, 147 mm SL; 3, NTM S.11839-002, same data, 112-115 mm SL; 1, NTM S.10939-014, Groote Eylandt, March 1983, 156 mm SL; 5, NTM unreg., S of Orontes Reef, Aug. 1986, 103-121 mm SL; 1, AMS I.21830-017, Arafura Sea at 10°11'S, 132°03'E, Nov. 1980, 260 mm SL; 2, unreg., Arafura Sea, Nov. 1980, 150 & 157 mm SL; 2, MZUSP unreg., same data, 145 & 157 mm SL; 1, NTM S.0449, N of Coburg Peninsular, Sept. 1975, 112.5 mm SL; 1, NTM S.0451, Snake Bay, Melville Island, Sept. 1975, 115 mm SL; 1, NTM S.0646, same data, 112 mm SL; 1, NTM S.0647, same data, 128.5 mm SL; 1, NTM S.0648, same data, 122 mm SL; 1, NTM S.0453, same data, 105 mm SL; 1, NTM S.0454, same data, 122 mm SL; 1, NTM S.0455, same data, 122 mm SL; 1, NTM S.0456, same data, 120 mm SL; 1, NTM S.0457, same data, 117 mm SL; 1, NTM S.0458, same data, 124 mm SL; 1, NTM S.0459, same data, 118 mm SL; 1, NTM S.0460, same data, 110.5 mm SL; 1, NTM S.0839, N of Melville Island, Oct. 1975, 114 mm SL; 1, NTM S.0840, same data, 130 mm SL; 1, NTM S.0843, same data, 125 mm SL; 1, NTM S.0845, same data, 117 mm SL; 1, NTM S.0846, same data, 120.5 mm SL; 1, NTM S.0847, same data, 124 mm SL; 1, NTM S.0848, same data, 119 mm SL; 1, NTM S.0849, same data, 116 mm SL; 1, NTM S.0850, same data, 116 mm SL; 1, NTM S.0852, same data, 113 mm SL; 1, NTM S.0853, same data, 106 mm SL.

WESTERN AUSTRALIA - 1, not kept, Arafura Sea at 10°35'S, 137°03'E, March 1985, 230 mm SL; 1*, NTM S.12065-001, Bedout Island, 6 June 1985, coll. J. Beecroft, 433 mm SL; 1*, NTM S.11670-008, NW Australia at 19°03'S, 118°29'E, 1 June 1985, coll. Fish. Observ. Team, 435 mm SL; 1*, CSIRO C.3855, Ashburton River mouth, Sept. 1966, 110.5 mm SL; 1*, WAM P.19191-001, outside of Shark Bay entrance, 1 Aug. 1970, 476 mm SL; 1, not kept, Shark Bay, May 1985, 2.8 kg whole weight (photo only); 1*, WAM P.24230, Napier Broome Bay, July 1973, coll. W.A. Fish & Fauna Dept, 110 mm SL; 1*, WAM P.24131, same data, 115 mm SL; 3*, unreg., 19°44'S, 116°02'E, 2 Dec. 1979, coll. CSIRO, 427-485.5 mm SL; 3*, unreg., 19°46'S, 116°00'E, 3 Dec. 1979, coll. CSIRO, 289-461 mm SL; 1*, unreg., 19°43'S, 116°02'E, 3 Dec. 1979, coll. CSIRO, 358 mm SL; 1*, unreg., 20°20'S, 115°00'E, 26 May 1980, coll. CSIRO, 344 mm SL; 10*, unreg., 17°49'S, 120°18'E, 15 June 1980, coll. CSIRO, 213-353 mm SL; 5*, unreg., 18°09'S, 120°02'E, 15 June 1980, coll. CSIRO, 226-282 mm SL; 1, CSIRO C.4869, NW coast, 1960, coll.

<u>Umitaka Maru</u>, 345 mm SL; 1, CSIRO C.4870, same data, 360 mm SL; 1, CSIRO C.4871, same data, 340 mm SL; 1, CSIRO C.4872, same data, 460 mm SL; 1, QM I.26089, northwest Australia, 1980, coll. CSIRO, 43.2 mm SL.

INDONESIA - 8*, RMNH 6885 (in part), Indonesia, pre-1879, coll. P. Bleeker, 65-200 mm SL; 1, CAS(SU) 8001, Sumatra, no date, 264 mm SL; 1, ANSP 27298, same data, 248 mm SL; 3, CAS 36057, Java Sea at 05°51'S, 106°48'E, Dec. 1975, 88-120 mm SL; 2, MCZ 30802, Jakarta, 1909, 245 & 250 mm SL; 2, MCZ 30884, Pelabuhan Ratu, 1909, 91 & 134 mm SL; 1*, AMNH 15890, Batavia, 6 May 1941, 186 mm SL; 1*, AMNH 58710, Muarakarang, Jakarta, 4 Dec. 1980, coll. P. Kailola, 177 mm SL; 2*, unreg., same data, 225 & 255 mm SL; 1, unreg., SE of Lombok Island, Sept 1982, SL not noted; 1, unreg., Roti Island, Aug. 1981, SL not noted; 1, LPPL 202, 06°25'S, 105°34'E, April 1983, 283 mm SL; 4, not kept, Jimbarang, Bali, June 1983, SL's not noted; 2, not kept, Lombok Island, Aug. 1981, 230 & 240 mm SL; 2, unreg., Samodra Besar, Benoa, Bali, Aug. 1982, 170 & 183 mm SL.

BORNEO - 1, CAS 35822, off Kuching, Sarawak, Nov. 1975, 220 mm SL; 2, MCZ 57970, Sarawak, 1979, 59 & 65 mm SL.

PHILIPPINES - 2, CAS 63624, Philippines, no date, 126 & 140 mm SL; 1, CAS(SU) 20382, Philippines, no date, 78 mm SL; 3, CAS(SU) 69118, Manila Bay, no date, 132 & 204 mm SL; 3, CAS 20108, Cavite, no date, 132-220 mm SL; 2, CAS 38202, Philippines, no date, 136 & 222 mm SL; 2, ANSP 79414, Bataan, Luzon Island, May 1923, 109 & 112 mm SL; 1, USNM 160545, Monju Island, Feb. 1909, 320 mm SL; 1*, SMF 22007, Navotas market, Manila, 28 May 1986, coll. P. Kailola, 188 mm SL.

EAST CHINA SEA - 1*, ZUMT 51164, East China Sea, Jan. 1960, 270 mm SL; 2*, ZUMT unreg., same data, 325 & 390 mm SL.

CHINA - 1*, ASIZB 640941, no data supplied, 290 mm SL.

THAILAND - 1*, AMS I.26974-001, Paknam market at Samutprakan (from S Gulf of Thailand), 20 Nov. 1985, coll. K. Mochizuki, 225 mm SL; 1*, AMS I.26975-001, Songhkla market (from S Gulf of Thailand), 25 Nov. 1985, coll. K. Mochizuki, 228 mm SL; 4*, unreg., same data, 186-290 mm SL; 2, CAS 63618, Gulf of Thailand at 11°34'N, 99°52'E, no date, 160 & 207 mm SL; 1, CAS 63625, same data, 151 mm SL; 1, CAS 63637, same data, 175 mm SL; 5, CAS 63623, Rayong Bay at 12°30'N, 100°00'E, Dec. 1957, 156-229 mm SL; 1, CAS 63626, off Kas Rong at 10°41'N, 103°03'E, no date, 191 mm SL; 1, CAS 63834, Prachnap at 12°13'N, 100°18'E, Aug. 1960, 183 mm SL.

VIETNAM - 1, UMMZ unreg., Vietnam, May 1974, 201 mm SL; 1, UMMZ unreg., Vietnam, Sept. 1974, 122 mm SL.

BURMA - 1, CAS(SU) 39554, Moscos Islands, Nov. 1940, 166 mm SL.

INDIA - 1*, MNHN A.9344, Pondicherry, 240 mm SL (= COTYPE of _A. bilineatus_); 1*, AMS B.7931, Andaman Islands, coll. F. Day, purch. by AMS 1885, 192 mm SL (= TYPE of _Netuma thalassina andamanensis_); 2*, ZSI unreg., Kakinada, Andhra Pradesh, 20 Sept. 1979, coll. K.C. Jayaram, 306 & 330 mm SL; 1, CAS 30504, Chatrapur, no date, 183 mm SL; 1, ANSP 90524, Bombay, 1924, 207 mm SL.

SRI LANKA - 1, CAS(SU) 30155, Colombo market, April 1934, 245 mm SL.

PAKISTAN - 1*, AMS B.7971, Sind, coll. F. Day, purch. by AMS 1885, 128 mm SL (= TYPE of _Arius serratus_); 12, LACM 38129-94, near Paitani Creek mouth, Sind, April 1978, 86-181 mm SL.

PERSIAN GULF - 2, WAM P.25977-014, Bahrain, 1974, 58 & 62 mm SL; 4, CAS(SU) 69117, Ras et Tanura, Arabia, no date, 147-224 mm SL.

6.6.7.3

"*Arius*" (*Netuma*) *proximus* Ogilby

(Figures 154, 155, 156, 157; Tables 31, 32)

Arius proximus Ogilby, 1898: 280 (Port Darwin)

Arius (*Tachysurus*) *graeffei* (*non* Kner & Steindachner): Paradice & Whitley, 1927: 80

Tachysurus proximus: McCulloch, 1929: 59

Tachysurus (*Pararius*) *proximus*: Whitley, 1940: 409, fig. 16

Arius arafurensis Hardenberg, 1948: 409, figure (Dobo market, Aru Islands)

Hexanematichthys proximus: Munro, 1957: 39, fig. 279

Pararius proximus: Whitley, 1964: 36

Arius (*Hexanematichthys*) *proximus*: Kailola, 1974: 61

DEFINITION

Four groups of teeth across front of palate; outer, autogenous patches subtriangular, much larger than vomerine patches. Snout curved or acute, always with crescent-shaped depression between nostrils; dorsomedian head groove deep and distinct posteriorly; head shield moderately to very granular. No rakers along posterior face of first and second gill arches; swimbladder margin scalloped. Caudal lobes slender; adipose fin small-based and posteriorly situated. A 16-19; first arch gill rakers 10-13; total vertebrae 18-19+7-8+25-26. Fresh colouration dark blue to violet; adipose fin mostly black.

DESCRIPTION

D I,7. P I,10-11 (rarely 12). A 16-19. GR (first arch) 10-13 of which 4-6 on upper limb. GR (last arch) 9-12. Number of vertebrae 51-52 (44-45 free).

Body robust, moderately elongate. Predorsal profile slightly convex, more so at nape. Snout evenly curved to slightly acute; lips moderately thick, especially at corners of mouth, inner margins creased or scalloped. Mouth subterminal, gape moderately broad and curved; none or 1/4 of premaxillary tooth band visible when mouth closed. Nostrils ovate or rounded, anterior one slightly median to posterior nostril. Crescent-shaped depression or groove on dorsum of snout between nostrils (at all sizes); larger individuals may bear fine papilla-like structures scattered over snout. Eye ovate, dorsolateral, its margin free from head skin; mid-head length about opposite posterior eye margin. Lateral ethmoid slightly prominent before eye. Gill opening wide, membranes uniting ventrally in a deep concave arch, leaving broad, free margin.

Teeth in jaws conical, slender, sharp and depressible; partly embedded in fleshy tissue. Premaxillary band of 8-12 irregular series (in young), increasing to 12-16 series in larger fish. Teeth in lower jaw similar: 5-6 series in juveniles, 8-10 series in adults; and band interrupted at symphysis by edentulous space. Conical, sharp, non-depressible teeth arranged in 4 groups across front of palate. Smaller, vomerine pair rounded or square; outer pair pear-shaped or triangular, apex directed posteriorly; base of outer pair 2-3 times wider than that of inner pair. Tooth patches distinct in juveniles; margins indistinct with age as teeth become more numerous and patches coalesce, so forming one broad, laterally expanded band. Palate smooth, two low diagonal ridges occasionally present posteriorly just before branchial chambers.

Head shield often exposed through thin skin. Shield rugose in small fish, very granular in larger ones: granules numerous, extending forward to above eye, and posteriorly over supraoccipital process and predorsal plate. Dorsomedian head groove originates above eye and reaches base of supraoccipital process. Groove deep and narrow with distinct parallel edges. Process triangular, keeled, with straight sides. Sides of head moderately venulose. Humeral process triangular, granular and striate in juveniles to smooth or rugose in adults. Process moderately ossified anteroventrally; shaft acute and slightly oblique, reaching 1/3-1/2 along pectoral spine. Axillary pore small and ovate.

Barbels almost strap-like. Maxillary barbel reaches to opposite dorsal spine (juveniles) to preopercular or head margin in larger fish. Mandibulary barbel reaches from ventral head margin to pectoral base. Mental barbel reaches ventral head margin or to opposite hind eye margin. Chin barbel bases moderately staggered.

Gill rakers slender and robust, 2/3 as long as opposing filaments. Rakers absent from posterior face of first two arches, 9-11 along third. Pad of thickened epithelium posterodorsally on first two arches, better developed on second.

Fin spines moderately thick and slightly flattened; rugose, longitudinally striate. Anterior (leading) edge sharply granular and sharp antrorse serrae near tip. Posterior (trailing) dorsal spine margin with similar serrae along distal half; and pectoral spine with 12-20 sharp serrae along most of its length. Dorsal subequal to pectoral spine. Short filament on spine tips. Dorsal fin high, longest ray 2.4-3.9 longer than last ray. Pectoral reaches below or beyond dorsal base. Ventral fin in males moderately slender, failing to reach anal origin by distance of approximately one eye diameter; broader in females, reaching anal origin and up to 3rd ray. Large, thick pad of tissue on inner ventral rays in sexually mature females. Adipose fin convex, rather short-based and high, situated above posterior 2/3 of anal fin. Anal margin concave, longest ray 1.3-3.6 times last ray. Caudal lobes slender, acute; fin deeply forked.

Caudal peduncle moderately deep. Lateral line straight for most of its length, oblique below dorsal and turned dorsad at caudal base. Mass of short tubules surround anterior part of line and numerous short, oblique lines diverge from remainder of its length; vertical series of tiny pores extend over back.

Fresh colouration: Dark blue-grey, lilac or pale bluish grey above, silvery on sides, creamy white below. Iridescent or opalescent sheen over back and sides. Fins grey, very finely speckled black, outer 2/3 of adipose fin dark brown or black.

Colour in preservative: Silvery grey, black or dark brown above, brown on sides, grey, cream or dusky fawn below. Dorsal and caudal brown, black at tips and along distal margins. Upper aspect of pectoral and ventral fins and anterior 2/3 of anal stippled dark brown. Outer 2/3 of adipose fin black. Maxillary barbels black, others brown or pale. Peritoneum pale cream.

DISTRIBUTION

NEW GUINEA: south coast: Aru Islands, Gulf of Papua east to the Lakekamu River mouth (Kailola, 1974).

AUSTRALIA: north coast: Withnell Bay and Dampier to Darwin, Melville Island, (?Nourlangie Creek - see Discussion), Cape Arnhem (Taylor, 1964), Gulf of Carpentaria, Cape York, east Queensland coast, NSW coast to Newcastle.

BIOLOGY

Habitat: Near shore coastal waters and estuaries. [Bishop et al.'s (1980) record of "A". proximus from freshwater lagoons is doubtful.] Taylor's (1964) specimens were caught over sandy or rocky bottoms and in turbid water below jetties. Whitley (1940) remarked that "A". proximus is common on mudflats near the Broome jetty.

Maximum size: 410 mm SL. Haines (1979) recorded 510 mm FL (identification uncertain).

Diet: Probably omnivorous. Gut contents in my material includes prawns, crustacean fragments, gastropods, fish remains and very large, loose fish scales.

Breeding: Spawning in "A". proximus takes place between the end of the dry monsoon to the mid wet monsoon. I have examined mature males with gonad stage IV-VI caught in July and November; and Marshall (1941) captured a male incubating 14 juveniles (approx. 50-55 mm SL) in April. No other information is available.

DISCUSSION

Paradice and Whitley's (1927) Gulf of Carpentaria specimen (AMS IA.1484) of Arius graeffei Kner and Steindachner is a specimen of "A". proximus. Whitley (1940) and Taylor (1964) also realised this, although Whitley considered proximus a possible synonym of "A". graeffei. [Refer also to Kailola, 1983.]

Taylor (1964) and Kailola (1974) recognised that A. arafurensis Hardenberg is a synonym of "A". proximus.

Haines (pers. comm., 1978) recorded "A". proximus only from the Era River delta, where it was locally abundant. He noted that those specimens resembled Baimuru individuals of his "Grey Catfish", some of which I have examined. Most are referable to "*A*". *graeffei* Kner and Steindachner. As I have not seen Era River specimens of *proximus*, I suggest that the biological information on "Grey Catfish" presented by Haines (1979) is mostly from *graeffei*, not from *proximus*.

The small specimen (107 mm SL) from the East Alligator River tentatively determined as "*A*". *proximus* by Pollard (1974) is also a specimen of "*A*". *graeffei* (AMS I.16827-001).

I tentatively determined as *proximus*, a sample of distinct specimens of an "*Arius*" species collected from the Nourlangie Creek area of the Jabiru region (Bishop *et al*, 1980). In hindsight, I suspect these may have represented *graeffei*.

In the size and arrangement of palatal tooth patches, "*A*". *proximus* is similar to "*A*". *graeffei*. However, the two species can be separated on the lack of posterior rakers on the first two gill arches in *proximus* (present on all arches in *graeffei*), swimbladder form, and relative granulations and extent of the head shield. "*Arius*" species 6, the only other Australo-Papuan taxon which could be confused for "*A*". *proximus*, differs in having a larger adipose fin, smaller eye (fig. 158), as well as differently-shaped mouth, head shield and supraoccipital process (refer comparison under "*Arius*" species 6).

TYPES

A. *proximus*: This species is based on a single specimen, AMS I.25691-001, 338 mm SL (ex MAMU F.1174). Labelled "*A*. *australis*; Smaller Salmon Catfish". Ogilby (1898) recorded its (TL) length as 400 mm.

The type of *A*. *arafurensis*, said to be 320 mm SL, is not in the ZMA. Its whereabouts are unknown.

Condition of type: sound. Body firm, bent at caudal peduncle. Tear in skin of lower jaw near barbel bases; gill membranes cut through on LHS; belly slit medially. Fins tattered, tips of rays frayed, some twisted. Body colour lost.

ETYMOLOGY

Latin, *proximus* = near. "On account of its outward resemblance to *A. australis*" (Ogilby, 1898: 281) (= *graeffei* Kner & Steindachner).

MATERIAL EXAMINED

SOUTHERN P.N.G. - 1*, KFRS F.5521-01, off Kerema, June 1978, coll. S. Frusher, 169 mm SL; 2, KFRS F04092, off Oreke River mouth, May 1973, 156 & 179.5 mm SL; 1*, USNM 288555, Gulf of Papua, no date (1975?), coll. A.K. Haines, 192 mm SL; 1*, unreg., Gulf of Papua, no date (1975?), coll. A.K. Haines, 310 mm SL.

QUEENSLAND - 1, AMS I.15557-043, Gulf of Carpentaria at 16°46'S, 141°05'E, Nov. 1963, 140 mm SL; 1, CSIRO C.3797, Norman River at Karumba, 1969, 410 mm SL; 1, AMS IA.18304, same data, 300 mm SL; 1*, SAM F.6255, Moonkan River, 19 Nov. 1980, coll. D.B. Carter, 320 mm SL; 1*, AMS A.18307, Burdekin River, Aug. 1983, coll. A. Morton, 264 mm SL; 1*, QM I.8935, Queensland coast, 29 Oct. 1912, 153 mm SL; 1*, QM I.12427, Proserpine River, 17 July 1974, 209 mm SL; 4* + 10, QM I.7142, Bohle River N of Townsville, 4 April 1941, coll. G. Coates, 52-55 mm SL (from mouth of 380 mm TL adult); 1*, JCU 4188, Bohle River estuary, Cleveland Bay, no date, coll. M. Leet, 283 mm SL; 1*, JCU 4193, same data, 333 mm SL; 1*, JCU unreg., Cleveland Bay, 23 March 1980, coll. W. Dowd, 158 mm SL ; 1*, JCU4183, Cleveland Bay, 10 Nov. 1981, coll. N. Milward, 141 mm SL; 2, unreg., Cleveland Bay, March 1980, 73-80 mm SL; 3, ZMA 119.481, same data, 77-162.5 mm SL; 2, GCRL unreg., Deception Bay, 1984, 67 & 73 mm SL; 3*, QM I.12977, Mud Island, Moreton Bay, 5 Feb. 1975, 181-187 mm SL.

NORTHERN TERRITORY - 1*, AMS I.25691-001 (previously MAMU F.1174), Port Darwin, no date, coll. W. Macleay, 338 mm SL (= HOLOTYPE); 1, NTM S.10452-030, Caiman Creek, Port Essington, no date, 290 mm SL; 1, NTM S.10562-001, Vesty's Beach, Darwin, April 1982, 345 mm SL; 1, NTM S.11538-001, inlet at mouth of Elizabeth River, Darwin Harbour, Dec. 1984, SL not noted; 1, NTM S.11482-001, Fannie Bay, Darwin, Nov. 1984, 198 mm SL; 1, NTM S.471, East Point, Darwin, March 1977, 164 mm SL; 1, NTM S.472, same data, 161 mm SL; 1*, BMNH unreg., Camerson's Beach, Melville Island, 19 May 1976, coll. D. Grey, 70 mm SL; 1*, BMNH unreg., mouth of King Creek mouth, Shoal Bay, Melville Island, 24 Jan. 1974, 76 mm SL; 1*, NTM S.10060-003, Mickett's Creek in Shoal Bay, 28 March 1973, 84 mm SL; 1, USNM 173569, Melville Bay jetty, July 1948, 284 mm SL; 1, USNM 173570, same locality, Aug. 1948, SL not noted; 1*, AMS IA.1484, Pellew Islands, June 1923, coll. W. Paradice, 239 mm SL; 1, CSIRO CA2540, Arnarrama, Jan. 1981, 255 mm SL.

WESTERN AUSTRALIA - 1*, WAM P.5590, Broome, 4 Oct. 1971, 186 mm SL; 1, AMS I.13211, Broome, Aug. 1916, 280 mm SL; 1*, AMS I.26978-001, Withnell Bay, 16 July 1983, handlined, coll. S. Blaber, 375 mm SL; 1*, CSIRO 1681-01, Dampier, 12 July 1983, coll. M. Dunning, 345 mm SL; 1*, unreg., Dampier, July 1983, coll. M. Dunning, 310 mm SL; 1*, SMF 22006, Dampier, 9 July 1983, coll. M. Dunning, 258 mm SL.

NEW SOUTH WALES - 1*, AMS IB.3226, Newcastle, no date, coll. A. D'Ombrain, 288 mm SL.

6.6.8 Species Group A

In the Australo-Papuan region, this group contains three taxa: velutinus Weber, taylori Roberts and species 7. They have in common several homoplasies: vomerine tooth patches absent; autogenous palatal tooth patches absent (not in species 7); posterior dorsomedian fontanelle always open; and frontal broad or moderately narrow posteriorly, anterior arms narrow to moderate, with large frontal-lateral ethmoid space.

6.6.8.1

"Arius" velutinus (Weber)

New combination

(Figures 159, 160, 161, 162; Tables 33, 34)

Hemipimelodus velutinus Weber, 1908: 225 (in part), 551 (Lake Sentani, Tami River, Tarawin River)

Hemipimelodus papillifer Herre, 1935: 390 (Timbunke, Sepik River)

Hemipimelodus sp. Kailola, 1975: 40

Hemipimelodus crassilabris: Desoutter, 1977: 18 (partim)

Arius "sp.D" Allen and Boeseman, 1982: 74,99

Hemipimelodus sp. Allen and Boeseman, 1982: 75

DEFINITION

Palate usually naked, rarely with one or two oval patches of fine teeth; posterior aspect of first two gill arches with up to 7 short rakers on upper limb, many broad papillae (rarely rakers) on lower limb. A 17-21; total gill rakers (first arch) 13-18; total vertebrae 51-53, of which 6-7 are haemal. Eye 10-24 %HL; mouth gape 8-13 %SL; maxillary barbel 16-32 %SL; adipose fin base moderate, 7-14.5 %SL;

premaxillary tooth patch short and broad, 3-8.2 in its width. Dorsal head shield smooth, rugose in larger fish; vertical series of papillae along length of lateral line often conspicuous. Fresh colouration bluish to blue-grey; all fins with distinct, dark margins.

DESCRIPTION

D I,7. P I,10-12. A 17-24. GR (first arch) 13-18, of which 4-7 on upper limb. GR (last arch) 15-19. Number of vertebrae 51-53 (44-46 free).

Moderately elongate, heavy bodied fish. Predorsal profile straight, slightly convex posteriorly. Snout moderately fleshy or "rubbery", shape varies from blunt and turned ventrad to slightly acute; lips thick and fleshy, swollen and creased with age, inner margins scalloped and crenulate. Mouth subinferior; gape moderate, 1/4-1/2 of premaxillary tooth band exposed when mouth closed. Nostrils rounded to ovate, posterior one situated slightly lateral to anterior one. Small to moderately large eye more rounded than oval, orbital rim free from head skin. Eye dorsolateral, situated slightly before mid-head length. Gill opening moderately wide, gill membranes united ventrally in a broad curve or obtuse angle, leaving free margin.

Jaw teeth fine, depressible and sharp-tipped, embedded in spongy tissue. Premaxillary teeth increasing with age, in 6-15 irregular series, in contiguous broad, rectangular patches. Lower jaw teeth in 4-8 irregular series, separated at midline by edentulous space. Palate usually devoid of teeth, rarely (8% of my specimens, SL range 156-380 mm) with one or two small, oval patch(es) of fine teeth anteriorly. Palate skin usually smooth, sometimes papillose anteriorly; oblique ridge of skin posteriorly on each side of palate usually well-developed.

Thick skin usually obscures head shield. Shield almost smooth, larger fish with low granules around base of and over supraoccipital process and extending laterally to above gill opening. Dorsomedian head groove lanceolate, beginning short distance behind nostrils, ending about one eye diameter before process base. Head groove shallow, becoming deeper and narrow posteriorly. Supraoccipital process subtriangular, with straight sides. Broad, triangular humeral process almost smooth, thickened anteroventrally and forming flange over pectoral spine base. Shaft of process horizontal, blunt-tipped, reaching about 1/3 distance along pectoral spine. Axillary pore rounded and tiny.

Barbels moderately flattened, their length very variable. Maxillary barbel ends from about two eye diameters before head margin, to below first dorsal spine. Mandibulary barbel reaches from well short of head margin as far as pectoral base. Mental barbel ends opposite eye margin to halfway between eye and pectoral base. Chin barbel bases moderately staggered.

Gill rakers 1/2-2/3 length of opposing filaments. Upper, posterior limb of first gill arch has none to 7 short rakers; that of second arch has none to 6 rakers. Lower, posterior limb of first and especially second arch densely covered with small to larger, broad papillae, in up to four irregular series; 1-7 distinct rakers rarely present on posterior of second arch; 12-19 rakers along posterior face of third arch. Well-developed flap or cushy pad of epithelial tissue posterodorsally on first two arches, flap margin often scalloped.

Fin spines moderately long, slightly compressed; short filament at tip. Anterior margin of spines smooth to rugose; lateral margins smooth. Posterior spine margin with none to 4 low serrae distally on dorsal spine and 4-10 low, antrorse serrae along distal section of pectoral spine. Last dorsal ray 2.4-4.6 shorter than longest ray. Pectoral extends to below last dorsal ray or beyond and hind fin margin noticeably concave. Ventral narrow and fails to reach anal origin in males, or broad and extends as far as 4th ray in females. Sexually mature females develop broad pad of thick, spongy epithelial tissue along proximal 2/3 of 6th ventral ray. Adipose fin oblong, over middle of anal. Anal margin concave, longest ray 1.2-3.7 longer than last ray. Caudal lobes broad and tapered.

Caudal peduncle moderately compressed. Lateral line almost straight, sloping down from anterior body to turn dorsad at caudal base. Numerous short, oblique lines and 15-20 conspicuous vertical series of pores emanate from lateral line, extending to dorsal midline above and halfway down sides below.

Fresh colouration: Bluish or dark blue-grey above and pale silvery blue-grey on sides, white below. Dorsal, adipose, and upper surfaces of pectoral and ventral fins dusky grey, underside of fins, lower half of anal and most of caudal fin yellowish. Distinct brown or blackish margin on all fins, broadest on anal fin.

Colour in preservative: Dark grey, brown, mauve or reddish on upper 2/3 of body, clearly separated from fawn, creamy pink or dark-stippled undersides. Barbels dark brown, mandibular ones pale distally. Fins fawn to dark brown, ventral aspect of pectoral and ventral often pale; all fin margins dark brown. Sensory pores on sides dark brown. Peritoneum dusky.

DISTRIBUTION

NEW GUINEA: North-draining rivers. Lower Mamberamo River, Tarawin, Arso, Tami and Bewani Rivers, Lake Sentani (Weber, 1908; 1913), Sepik River system, Jimmi River (Whitley, 1956) and lower and middle Ramu River.

BIOLOGY

Habitat: Freshwater rivers and lakes. Coates, Osborne and Redding-Coates (1983) studied the hydrology of the lower Sepik River, which meanders through a very extensive floodplain of recent alluvium, and where seasonal fluctuations in water level affect nutrient value. Depth of the main river channel at Angoram (where there is some tidal influence) varies widely around 20 m. Water temperature during one year ranged from 27.5°C to 29.6°C, pH 6.2-7.4. The Sepik River is moderately turbid, especially during the early wet season.

Maximum size: 500 mm SL (D. Coates, pers. comm., 1983). "*A*". *velutinus* is the largest ariid after "*Arius*" species 7 in the Sepik River fishery.

Diet: "*A*". *velutinus* feeds mainly on small food items. In 27 stomachs from adult fish containing food, the relative fullness of various food items noted by D. Coates (pers. comm., 1983) were: aquatic macrophytes and other plant material (leaves, bark, seeds) (11%), fine detritus (32%), coarse detritus (6%), aquatic insect larvae and nymphs (36%), terrestrial insects (11%) and unidentified eggs (4%). Three of my small specimens (152 mm SL), had ingested plant material, detritus, and small insect larvae.

Breeding: The main spawning period takes place during the early wet season, but spawning continues throughout the year (D. Coates, pers.

comm.). First maturity occurs at about 250 mm SL, and fecundity ranges from 25-90 ova (Coates, pers. comm.). Some of my larger specimens have maturing gonads, capture date from August to November. The body cavity of maturing males contained large reserves of pale yellow fat.

DISCUSSION

The type series of "*A*". *velutinus* contains two species: *velutinus* and "*Arius*" species 2. The two species can however, be easily separated on the presence of palatal dentition (four patches in species 2), barbel length (16-32 %SL in *velutinus*, 28-50 %SL in species 2), head shape and shield rugosity, and premaxillary band shape (narrower in species 2; refer Table 38).

Weber either did not base his description of "*A*". *velutinus* on all of the syntypes or, he did not examine them carefully. For example:

(a) only one count for the anal(15) and the pectoral fins(10) is given, and frequently, only one ratio of body proportions. No specimens I examined have less than 17 (mean 20.9) anal rays; and Desoutter (1977) found 17-22 anal rays in many of the syntypes. The pectoral count ranges from 10 to 12 (including syntypes).

(b) some individuals of "*A*". *velutinus* develop one or two patches of teeth on the palate. Roberts (1978) located a patch of teeth on the palate in the 276 mm SL syntype in ZMA 112.654, and five specimens I examined have palatal teeth. Desoutter (1977: 12) observed "... certains specimens, possedant des plaques de dents sur le palais ..." and implied that there were more than the 5 examples of ZMA 112.655 and RMNH 8001 she particularly noted as having such. Yet Weber diagnosed *velutinus* as lacking palatal dentition.

(c) although omitting to mention the axillary pore in his 1908 description, Weber noted its absence in 1913 when discussing the relationships of another new species, *Hemipimelodus macrorhynchus* Weber. Smith (1945: 417) recounted that de Beaufort reexamined some typical specimens of "*A*". *velutinus* and found a "small slitlike pore in all of them." Weber (1913), Weber and de Beaufort (1913) and Munro (1967) overlooked the axillary pore. Herre (1935, 1936) and Whitley (1956) also overlooked the tiny axillary pore in their descriptions of *H. papillifer*. Every individual examined by Desoutter and I, possesses an axillary pore.

Portrayals of "*A*". *velutinus* by Weber (1913), Herre (1936) and Desoutter (1977) all accurately represent the species.

Desoutter (1977) stated that she examined all of Weber's syntypes, although her list of material examined contains only 15 syntypes (the other ZMA and BMNH material mentioned was listed by Weber, but not until 1913).

It is significant that those syntypes now recognised as belonging to another species ("*Arius*" species 2) were all collected in brackish water of the Tami River, a habitat not preferred by "*A*". *velutinus*.

Roberts (1978) remarked that *velutinus* differs from its congeners in having well-developed gill rakers on the lower limb of the posterior face of the second gill arch. His conclusion is based on two syntypes in ZMA 112.654 (specimens I have not seen) which, he stated, have 14 rakers on this limb. However, gill rakers in this position are present in only five specimens I examined, and then only through a range of one to 7. Many specimens I examined have well-developed papillae on the posterior face of the anterior gill arches instead. It is possible that raker and papillae development on the second gill arch has labile expression in this species. Roberts (1978: 40) also stated that the snout of "*A*". *velutinus* is "relatively truncate ...", a view I find difficult to accommodate on most of the material I have examined.

Herre (1935: 390) named his species in reference to the "conspicuous transverse rows of papillae" ... "extending downward one-half or three-fourths of the distance to the ventral surface". These papillae are apparent to a greater or lesser degree in preserved material, but are usually inconspicuous in fresh (large) material (D. Coates, pers. comm.) in which they are probably concealed by mucous.

Whitley (1956) was the first to recognise that *H. papillifer* Herre (and he supposed *H. bernhardi* also) is a synonym of "*A*". *velutinus*. Munro did not acknowledge this until 1967, even then referring to the species as *papillifer* instead of by the older name of *velutinus*.

Desoutter (1977) misidentified Whitley's specimen of "*A*". *velutinus* from the Jimmi River (AMS IB.3354) as *H. crassilabris* Ramsay and Ogilby.

Smith (1945) tentatively and erroneously included Fowler's (1935) *H. bicolor* from Bangkok in the synonymy of "*A*". *velutinus*. I have examined the type of *H. bicolor* Fowler (ANSP 60777): it has two patches of granular teeth posteriorly on the palate and may be referable to "*A*". *maculatus* Thunberg. Chevey (1932) included *velutinus* in a dichotomous key to the genus *Hemipimelodus*, and compared it with *H. daugueti* Chevey.

"*A*". *velutinus* has been collected at a higher elevation and further inland than has any other of the northern New Guinea species, so providing an ecological comparison with *A. latirostris* Macleay and "*A*". *taylori* Roberts of southern New Guinea.

"*A*". *velutinus* and "*A*". *taylori* are very similar taxa. "*A*". *taylori* is dark green to olive above, iridescent gold, with small golden spots in vertical series (*cf*. *velutinus*: uniform blue to dark grey above). Furthermore, *taylori* has 5 haemal vertebrae (6-7 in *velutinus*), lacks posterior rakers and papillae on the first two gill arches (up to 7 rakers in *velutinus*), has a slightly larger eye and more pointed snout.

The scattergrams and stepwise discriminant function analyses prepared for this species pair (using only two specimens of *taylori*) tentatively supported recognition of the two taxa (see for example, Tables 33, 34; figs 167, 168 of *taylori* *cf*. *latirostris*, and compare eye diameter). Further support comes from skull form. However, scattergrams did prove the synonymy of the nominal *papillifer* Herre with *velutinus*. Examination of more material should confirm these characters.

"*A*". *velutinus* is generally similar to "*Arius*" species 7 and "*A*". *macrorhynchus*. Characters such as palatal dentition (species 7) and lip development (*macrorhynchus*), eye size (species 7) and barbel length, are among the several which distinguish the three taxa.

TYPES

A. *velutinus*: There were 31 specimens in the type series, now located as follows: 21 specimens at ZMA, one at RMNH (= RMNH 8001), one at ZSI, two at NMW, one at AMNH; whereabouts of five unknown. Lot ZMA 112.654 contains 3 specimens, the complete series from Lake Sentani; ZMA 112.655 contains 6 specimens, from the Tami River mouth; ZMA 112.656 contains 12 specimens, all from the Tarawin River. RMNH 8001, the NMW and the ZSI types are four of the remaining 6 from the Tami River mouth;

and the AMNH specimen came from the Tarawin River. I have examined 3 paratypes.

H. papillifer: The type series consists of 3 specimens. The holotype from Timbunke and one paratype from Marienberg, are in the FMNH (FMNH 17211 and 17212); the other paratype is at the CAS, number CAS (SU)24453. I have examined the paratypes.

Condition of types: "*A*". *velutinus*: (on ZMA 112.656, 2 specimens). Good. Tail curved to LHS, slits on each side of dorsal fin; belly cut from pectoral girdle to anus; most fins and barbels intact; tip of dorsal and both caudal fin lobes twisted in larger specimen (147.5 mm SL), tear along ventral midline of gill membrane in small specimen (133 mm SL) and lower caudal lobe lost. RMNH 8001 is a specimen of "*Arius*" species 2.

H. papillifer (paratypes): Fair to good. Body slightly twisted, belly slit longitudinally from pectoral area; most fins and barbels intact but caudal fin tips lost (FMNH 17212). CAS (SU)24453 is a maturing female; mouth twisted and cut, LHS; pores on sides distinct.

ETYMOLOGY

Latin, *velutinus* = velvety. In lieu of a statement by Weber, I assume it refers to either the smooth to papillose palate or the thick, smooth body skin.

MATERIAL EXAMINED

NORTHERN IRIAN JAYA - 2*, ZMA 112.656 (in part), Tarawin River, 20 June 1903, coll. L.F. de Beaufort & H.A. Lorentz, 133 & 147.5 mm SL (= SYNTYPES); 3*, RMNH 28819, 11 km from Holtekang, Tami River, 18-21

Nov. 1954, coll. M. Boeseman, 232-310 mm SL; 1*, WAM P.27870-003, Danau Biru (= Lake Holmes), lower Mamberamo River, 22 Nov. 1982, coll. G.R. Allen, 260 mm SL; 6*, RMNH 28815, SE part of Lake Sentani near Poee, 13 Nov. 1954, coll. M. Boeseman, 215-290 mm SL; 3*+2, WAM P. 27856-002 (in part), market at Lake Sentani, 10 Nov. 1982, coll. G.R. Allen, 149-158 mm SL.

NORTHERN P.N.G. - 1*, FMNH 17212, Marienberg, Sepik River, 14 May 1929, coll. A.W. Herre, 224 mm SL (= PARATYPE of _H._ _papillifer_ Herre); 1, CAS (SU)24453, same data, 223 mm SL (= PARATYPE of _Hemipimelodus papillifer_ Herre); 1*, KFRS F0086, Angoram, Sepik River, Sept. 1960, coll. S. Bucknall, 155 mm SL; 1*, AMS IB.3354, Jimmi River, 20-27 July 1954, coll. E.le G. Troughton & N. Camps, 380 mm SL; 1*+8, WAM P.27847-009, Kwatit River at junction with Sepik River, 28 Oct. 1982, coll. G.R. Allen & D. Coates, 46-98 mm SL; 1*, KFRS F.5517-002, Keram River, 17 April 1980, coll. A. Richards, C. Brooks & K. Makeu, 235 mm SL; 1, QM I.26084, Angoram, Sepik River, Aug. 1981, 55 mm SL; 1*, AMS I.27410-001, market at Angoram, Sepik River, 1981, coll. D. Coates, 270 mm SL; 2*, NTM S.11911-001, same data, 303 & 375 mm SL; 1*, SMF 22005, same data, 268 mm SL; 1*, SAM F.6340, same data, 181 mm SL; 1*, QM I.25054, Sepik River, no other data, 375 mm SL; 5, WAM P.28216-001, Sepik River, no date, 182-415 mm SL; 1, unreg., May River, Nov. 1986, 176 mm SL; 1*, KFRS F02813, Aiome, Ramu River, 19 Dec. 1970, coll. G. West, 180 mm SL; 13*+10, USNM 217321 (in part), Ramu River near Mt.Otto, 11 Feb. 1976, coll. T.R. Roberts, 49-189 mm SL; 1, USNM 122822, Gusah & Ramu Rivers, no date, 150 mm SL.

6.6.8.2

"Arius" taylori (Roberts)

New combination

(Figures 163, 164, 165; Tables 33, 34)

Hemipimelodus taylori Roberts, 1978: 40, figs 19, 20h (Palmer River, 65 km N.E. of Kiunga).

Hemipimelodus macrorhynchus (in part): Haines, 1979: 52.

DEFINITION

No palatal teeth; jaw teeth in moderately broad bands. Head tapered, rounded from side-to-side; snout moderately acute; head shield rugose. No posterior rakers or papillae on first two gill arches. A 19-20; total gill rakers (first arch) 15; total vertebrae 49-50, of which 5 are haemal. Eye 13-14 %HL, mouth gape 11-12 %SL, maxillary barbel 25-26 %SL, adipose fin base 10-12 %SL. Fresh colouration green above, sides iridescent gold; small golden spots in numerous, vertical series on sides.

DESCRIPTION

D I,7. P I,11. A 19-20. GR (first arch) 15, of which 6 on upper limb. GR (last arch) 15-17. Number of vertebrae 49-50 (43-44 free).

Body robust, moderately slender. Anterior profile straight, slightly elevated at nape; head somewhat rounded from side to side. Snout prominent, well-curved and bluntly pointed, lips thick and fleshy, crenulate along inner border. Fine, papilla-like structures sometimes scattered over anterior of head in larger fish. Mouth moderately wide, subinferior, 1/2 of upper jaw tooth band exposed when mouth closed.

Nostrils elliptical or ovate, anterior one slightly median to posterior one. Eye ovate, free of head skin; situated dorsolaterally, just before mid-head length. Gill opening moderately wide, membranes shallowly concave across isthmus, with broad, free margin.

Jaw teeth sharp, pointed and curved, those in outer series somewhat peglike; depressible. Premaxillary teeth in broad band of 10-12 irregular series, lower jaw band with about 7 series; symphysis of lower jaw edentate. Palate smooth, lacking teeth; two low, thick epithelial ridges posteriorly before branchial chambers.

Head shield pattern largely obscured by thick skin; appears smooth or slightly rugose. Low striae flank dorsomedian head groove posteriorly and extend along supraoccipital process. Dorsomedian head groove flat, lanceolate, beginning between nostrils and almost reaching supraoccipital process base. Supraoccipital process triangular, with straight sides, keel-less. Sides of head slightly venulose, sometimes granular. Humeral process moderately rugose, well-ossified anteroventrally. Triangular shaft of process long and slightly oblique, extending more than 1/3 distance along pectoral spine. Axillary pore small.

Barbels slender, moderately long. Maxillary barbel extends to middle of pectoral spine. Mandibulary barbel reaches to beyond pectoral fin base. Mental barbel terminates at or beyond ventral gill membranes. Bases of chin barbels moderately staggered.

Gill rakers of first arch 2/3 length of opposing gill filaments. Posterior aspect of first and second arches raker-less, smooth or villose; 15-16 rakers along back of third arch. Thick, bisected fold or pad of epithelial tissue on posterodorsal face of first two gill arches, better developed on second arch.

Fin spines moderately compressed, sides patterned with fine, longitudinal striae. Short filament at tips. Each spine with anterior margin roughened; low serrae towards tip of posterior margin: 2-4 on dorsal, 4-7 on pectoral. Last dorsal ray 2.8 in longest ray. Pectoral fin extends to below end of dorsal fin. Ventral just reaches anal origin in male, to about third anal ray in female; and sexually mature females have a thick epithelial pad on inner of 6th ray. Moderately large adipose fin situated above middle of anal fin. Anal margin concave, anterior rays 2.8-2.9 longer than last ray. Caudal lobes moderately broad.

Caudal peduncle moderately deep. Lateral line almost straight, curving dorsad at tail base and below dorsal. Numerous short lines diverge from lateral line, especially extensive anteriorly; and vertical dense series of broad papillae extend from line over back.

Fresh colouration: Dark green to olive above, bluish green to fawn on sides, white below. Upper sides and back with golden sheen; small golden spots in vertical rows on sides. Fins dusky green, narrow black margin to dorsal and caudal; upper aspect of pectoral fin dark.

Colour in preservative: Brown above, dusky cream or tan below; snout and upper half of head dark grey. Fins mostly light brown, margins and filaments dark brown or blackish; outer half of anterior anal rays dusky brown. Barbels brown. Peritoneum grey.

DISTRIBUTION

NEW GUINEA: South-draining rivers. The upper Fly River headwaters (Palmer River is a major tributary), upper Strickland River, upper Purari River.

BIOLOGY

Habitat: Freshwater. Roberts' type series came from slightly turbid, moderately flowing water. "*A*". *taylori* also occurs in swiftly flowing rivers. P. Dwyer (pers. comm., 1989) found it by far the most abundant of the 6 ariid taxa collected in the middle-upper Strickland River, where it was restricted to the silt-laden river "where the water is *never* clear". This species inhabits higher altitudes than do other southern New Guinea ariids, except possibly "*A*". *latirostris*.

Maximum size: 353 mm SL.

Diet: The Palmer River specimens had fed on pulpy fruit and terrestrial insects, the Wabo one on pulpy fruit, ants, detritus and plant material. [Haines (1979) had confused this species with "*A*". *macrorhynchus* (Weber).]

Breeding: Probably occurs between November and January. The smaller paratype, caught early November, is a female with partly developed ventral fin pads; and the Wabo specimen caught in January, is a mature male, gonad stage V-VI.

DISCUSSION

"*A*". *taylori* tolerates rather swiftly flowing water and appears to be very sediment tolerant. For example, its numbers have increased in the upper Fly River and Ok Tedi since the onset of mining near the rivers' headwaters and the resulting higher sediment load in the water (K. Hortle, pers. comm., 1986).

This species can be confused with "*A*". *latirostris* Macleay (K. Hortle, pers. comm.), as it has a similar body shape and habitat preference. Stepwise discriminant function analysis showed that eye diameter as % of HL and SL + eye diameter/interorbital width ratio +

premaxillary tooth band length/HL ratio + snout length/eye diameter ratio + head height/head width ratio + longest barbel length/HL and /SL ratios + longest barbel length as % of HL and SL, always separated latirostris and taylori in a robust jackknife classification (Tables 33, 34 and 37, 38; figs 166, 167, 168, 169). These taxa also differ in other features such as head shape, gill opening width, and extent of the dorsomedian head groove.

From "A". macrorhynchus, taylori differs mostly in barbel length, snout shape and lip development and adipose fin size. Comparison with "A". velutinus has been made under the velutinus presentation. The body colouration of taylori is similar to that of "A". leptaspis, but the golden spots are less coarse, less widely-spaced (both vertically and horizontally) and not as bright golden.

Gwyther's (1984) and Haines' (1979) statements that "A". latirostris is unaffected by increased water situation, actually refer to "A". taylori.

TYPES

"A". taylori is based on the holotype and two paratypes. The type is AMS I.27087-001 (ex USNM 217076), 353 mm SL. The smaller paratype (325 mm SL) is USNM 217077, and the second paratype (350 mm SL, ex USNM 217077) is KFRS F.4682-01.

Condition of types: All in good condition.

ETYMOLOGY

Named for William R. Taylor (formerly staff of USNM Fish Division).

MATERIAL EXAMINED

SOUTHERN P.N.G. - 1*, USNM 217077, Palmer River, 65 km NE of Kiunga, 10-11 Nov. 1975, coll. T.R. Roberts, 325 mm SL (as 330 mm SL in Roberts, 1978) (= PARATYPE); 1, KFRS F.4682-01 (ex USNM 217077), Palmer River, 65 km NE of Kiunga, 10-11 Nov. 1975, 350 mm SL (= PARATYPE); 1, AMS I.27087-001 (ex USNM 217076), same data, 353 mm SL (= HOLOTYPE); 1*, QM I.25053, Wabo, Purari River, Jan. 1977, coll. A.K. Haines, 290 mm SL; 3, unreg., Gwaimasi village, upper Strickland River, Aug. 1986-Nov. 1987, coll. P. Dwyer and M. Minnegal (dried skulls only), 79, 108, 108 mm l. (ex specimens to 345 mm SL).

6.6.8.3

"*Arius*" species 7

(Figures 170, 171, 172, 173; Tables 33, 34)

Hexanematichthys sp: Kailola, 1975: 40

Hexanematichthys leptaspis: Kailola, 1975: 42 (in part)

DEFINITION

Body robust; snout broadly rounded; jaws strong. Teeth on single, oval autogenous tooth plates each side of palate; broad band of jaw teeth. Usually no posterior rakers on first two gill arches. Eye small, 8-11 %HL; barbels thin and short, 28-34 %HL. A 19-21; total gill rakers (first arch) 13-17; total vertebrae 20-21+5+30. Fresh colouration blue-grey to bronze, fin margins dark brown.

DESCRIPTION

D I,7. P I,10-12. A 19-21. GR (first arch) 13-17, of which 5-7 on upper limb of arch. GR (last arch) 15-17. Number of vertebrae 55-56 (48-49 free).

Body robust, thickset anteriorly; head broad and slightly depressed. Predorsal profile almost straight. Snout broad, well or slightly rounded; lips "rubbery", thicker at corners of mouth. Jaws strong; mouth subterminal, upper jaw projecting such that 1/3-1/2 premaxillary tooth band visible when mouth closed. Nostrils ovate, anterior one almost directly in front of posterior nostril. Eye small, ovate or rounded; margin free from head skin. Lateral ethmoid slightly prominent. Eye situated dorsolaterally, before mid-head length. Gill opening wide, membranes united below at an obtuse angle, leaving broad, free margin.

Teeth in jaws very small and slender, sharp-tipped; embedded in soft tissue; depressible. Premaxillary teeth in 8-14 irregular series; lower jaw teeth in 6-8 series, band divided at symphysis by edentulous space. Two widely separated oval patches of conical, sharp-tipped or blunt teeth anteriorly on palate. Palate smooth or with scattered, slender papillae (smaller specimens) and low oblique ridges of thick epithelial tissue before branchial chamber.

Head shield partly obscured by thick skin. Shield smooth anteriorly, rugose posteriorly; clusters of low granules along lateral margin of shield, around dorsomedian head groove and over supraoccipital process variably developed. Dorsomedian head groove lanceolate, narrow posteriorly, terminating well before supraoccipital process base. Process long, slightly triangular; with straight sides and low, granular median keel. Triangular humeral process smooth, heavily ossified anteroventrally. Process shaft oblique, extending 1/3 distance along pectoral spine. Axillary pore rounded and very small.

Barbels thin, wisp-like posteriorly. Maxillary barbel reaches to 1/2-1 1/2 eye diameter's behind eye. Mandibulary barbel reaches to below middle or hind margin of eye. Mental barbel fails to reach level of eye front margin. Chin barbels moderately staggered.

Gill rakers rigid and strong, 1/2-2/3 length of opposing filaments. No rakers along posterior face of first and usually second gill arches (one, and 2 small rakers on upper limb in two specimens); 12 to 17 well-developed rakers along posterior face of third gill arch. Low, thick pad of epithelial tissue posterodorsally on second arch.

Fin spines moderately compressed, fine longitudinal striae on sides of spine becoming granular in larger fish. Anterior spine margin with regular series of sharp, transverse ridges; posterior margin of dorsal with 3-12 low serrae, posterior margin of pectoral with 12-18 larger, forward-directed serrae. Short filament on spine tips at all sizes. Last dorsal ray 2.6-3.3 shorter than longest ray. Pectoral extends to below or beyond dorsal base. Ventral fin rather oblong, usually reaching anal fin origin. [No sexually mature females in my material.] Adipose fin oblong, wholly over anal. Anal margin slightly concave, longest ray 2.3-2.8 times last ray. Caudal lobes broad but well-tapered, subequal in length.

Caudal peduncle moderately compressed. Lateral line oblique anteriorly, thence straight, turned dorsad at caudal base. Short oblique lines and vertical series of pores diverge above and below length of lateral line.

Fresh colouration: Dark blue-grey, olive to bronze above, silvery white to cream below. Fins dusky grey to bluish.

Colour in preservative: Mottled brown or dark grey above; lower third of head and body pinkish white, grey or fawn; clusters of dark spots or freckles along lower jaw and breast. Fins tan; dorsal, anal and caudal fin margins dark brown; upper aspect of pectoral fin blackish brown. Barbels dark brown. Peritoneum pale grey.

DISTRIBUTION

NEW GUINEA: north-draining rivers. Lower and middle reaches of the Sepik and Ramu River systems.

BIOLOGY

Habitat: Fresh water. "*Arius*" species 7 inhabits the channels of the main river and its tributaries. The habitat of juveniles may be different (smallest specimen available is 237 mm SL); and D. Coates obtained adult fish only (1983 survey).

Maximum size: 660 mm SL (Coates, 1983)

Diet: Omnivorous. Food items recorded by D. Coates (1983 survey) from the stomachs of 37 specimens consisted mostly of crustacea, particularly small prawns (*Caridina* spp., less *Macrobrachium* spp.), aquatic plants and other plant material, fine and coarse detritus, aquatic insect larvae and nymphs, some worms, eggs and a few small fish. Most of my material had empty stomachs or stomach had been removed; but one contained anguillid and prawn fragments, plant and animal detritus.

Breeding: D. Coates (pers. comm.) found that spawning occurs throughout the year, with a peak during the early wet season. Fecundity ranges up to 170 ova (very large fish).

DISCUSSION

This is the largest ariid in northern New Guinea fresh waters.

"*Arius*" species 7 is phenotypically similar to "*A*". *augustus* of southern rivers, with which it shares the characters of small eye, short barbels, strong and robust head and jaws. Both species attain a large maximum size. However, "*A*". *augustus* has an even broader mouth (50-56 %HL) and wider space between nostrils (40-44 %HL *cf*. 29-31% in "*Arius*" species 7), more rakers (20-22) on the first gill arch, a truncate snout (tapered in "*Arius*" species 7), four patches of teeth on the palate and 51-52 free vertebral centra, of which 12 are trunk centra (*cf*. 13-14 trunk centra in species 7). The short barbels, single palatal tooth patches and small eye distinguish "*Arius*" species 7 from "*A*". *velutinus*, "*A*". *taylori*, and the sympatric "*Arius*" species 2.

It is possible that juveniles of this species have been mistaken for "*A*". *velutinus* in collections.

TYPES

No types have been nominated.

ETYMOLOGY

This species has not been named.

MATERIAL EXAMINED

NORTHERN P.N.G. - 1*, AMS I.25405-001, market at Angoram, Sepik River, Aug. 1982, coll. D. Coates, 270 mm SL; 1*, QM I.21673, same data, 375 mm SL; 4*, WAM P.28221-001, same locality, July 1982, coll. D. Coates, 290-390 mm SL; 1*, KFRS F04108, Zirken village, lower Ramu River, 27 Aug. 1972, coll. G. West, 242 mm SL; 1*, KFRS F03995, Kambaramba, Sepik River, May 1972, 237 mm SL (also as: AMS I.30112-001); 1*, AMS I.25405-002, same data as holotype, 450 mm SL.

6.6.9 Species Group B

The species group B in New Guinea and Australia contains three taxa: graeffei Kner & Steindachner; berneyi Whitley and species 3. They have in common several homoplasies: vomerine tooth patches unstable or absent; moderately wide gill opening; and rakers present on the trailing edge of all arches.

6.6.9.1

"Arius" graeffei Kner & Steindachner

(Figures 174, 175, 176, 177; Tables 35, 36)

Arius graeffei Kner & Steindachner, 1866: 383, fig. 12 (Samoa - locality doubtful; prob. northern Australia)

Arius australis Günther, 1867: 103, fig. (Ash Island, Hunter River, N.S.W.)

Arius curtisii Castelnau, 1878: 236 (Moreton Bay)

Galeichthys australis: Stead, 1906: 40,42

Tachysurus graeffei: McCulloch, 1929: 59

Neoarius curtisii: McCulloch, 1929: 60

Netuma australis: McCulloch, 1929: 60

Pararius graeffei: Whitley, 1964: 36

Neoarius australis: Whitley, 1964: 36

Arius species A: Allen & Boeseman, 1982: 74

Arius graffei: Grant, 1987: 67,68

DEFINITION

Palatal teeth villiform, in transverse series of four oval patches (very rarely less), outer patches considerably larger than vomerine patches. Head shield finely granular; dorsomedian head groove narrow and lanceolate. Eye moderate, 10-28 %HL. Maxillary barbel reaches opposite dorsal spine base, usually shorter. A 15-21; total first arch GR 16-23; posterior rakers absent along all gill arches; vertebrae 18-21+6-8+26-28. Fresh colouration dark brown, blue or fawn above, pale below; variable.

DESCRIPTION

D I,7. P I,9-12. A 15-21. GR (first arch) 16-23 of which 6-8 on upper limb. GR (last arch) 15-23. Number of vertebrae 52-54 (45-48 free).

Body robust, moderately elongate. Predorsal straight, slightly elevated before dorsal fin; interorbital flat. Snout rounded to slightly acute, often prominent; lips moderately thick and fleshy, crenulate along inner margin. Juveniles often with a shallow, crescentic groove on dorsum of snout between nostrils; fine, papilla-like structures scattered over anterior of head in many adults. Mouth subterminal to subinferior, gape broad, curved to slightly truncate; premaxillary tooth band not or up to 1/2 exposed when mouth closed. Nostrils ovate, posterior opening somewhat lateral. Eye rounded-oval, free of head skin; situated dorsolaterally and well to just before mid-head length. Gill opening moderately wide, membranes meeting over isthmus to form concave, free margin.

Jaw teeth in curved bands; teeth fine and sharp, depressible; in 6-9 irregular series in premaxillary band, 4-6 in lower jaw band; lower jaw band divided by narrow edentulous space at symphysis. Palate smooth or villose. Four patches of small, fine and sharp, non-depressible teeth in line across front of palate: vomerine patches ovate-rounded, much smaller than outer, oval to triangular patches. Patches may fuse into single unit on one or both sides of palate with increasing age, or all four may form one broad, transverse patch. Occasionally, one vomerine or outer tooth patch may be absent. Two fleshy or smooth oblique ridges of epithelial tissue on palate before branchial chambers.

Head shield finely and somewhat sharply granulated, granules extending from above eye over all of shield and supraoccipital process, arranged into striae on each side of dorsomedian head groove. Groove narrow, lanceolate, beginning between nostrils and reaching supraoccipital process base; flat anteriorly. Process somewhat triangular, with straight or convex sides and low or no median keel. Thick skin often obscures head shield (especially on fish caught from freshwater); sides of head smooth to slightly venulose. Triangular humeral process broad, rugose or granular, heavily ossified anteroventrally. Process horizontal to oblique, somewhat acute, extending 1/3 distance along pectoral spine. Axillary pore small.

Barbels thick and slightly flattened. Maxillary barbel reaches to below dorsal spine in juveniles, to head edge of pectoral base in larger fish. Mandibulary barbel usually reaches pectoral base. Mental barbel ends up to half-way between eye and pectoral fin base. Chin barbel bases moderately staggered.

Gill rakers half as long as opposing filaments. All arches smooth posteriorly, and all bear rakers: 12-20 on first arch, 15-23 on second arch, 15-21 on third arch. Arches thickened posterodorsally to form fleshy pad, best developed on second arch.

Fin spines moderately thick; sides patterned with longitudinal striae, anterior margin rough with low granules and 3-6 low serrae towards tip. Posterior margin with serrae: 4-6 along dorsal and 12-19 stouter, sharper ones along pectoral. Longest dorsal ray 2.5-3.5 times last ray. Short filament on spines in juveniles. Pectoral extends to below dorsal fin. Ventral fin in males narrow, usually ending well before anal fin origin; ventral in females broad and reaching to 4-6th anal ray. Sexually mature females have a thick pad of epithelial tissue dorsally on 5-6th rays. Adipose fin above middle of anal. Anal margin slightly concave, last ray 2.4-3.3 times shorter than longest ray. Caudal lobes moderately broad, pointed and tapered distally.

Caudal peduncle moderately deep and stout. Lateral line straight, elevated below dorsal and at tail base. Numerous short oblique lines emanate from length of lateral line.

<u>Fresh colouration</u>: Variable. Usually, fish from clear water dark brown, deep purple or blue above, silvery white below; fish from turbid water fawn or dark ochre-coloured above, yellowish, cream on undersides, frequently stippled brown. Sides and back often iridescent. Maxillary barbels black or dark brown, other barbels fawn. Fins uniform bluish charcoal or tan, margins variably pale or darker brown, undersides of pectoral and ventral fins cream. Some individuals from the Victoria and Daly Rivers "piebald" - blotched black and white, black patches extending into mouth and over fins.

<u>Colour in preservative</u>: Dark brown or tan above, paler below. Fins dusky, usually a dark margin to unpaired fins. Barbels brown. Peritoneum pale, with scattered faint brown dots.

DISTRIBUTION

NEW GUINEA: South-draining rivers and associated coasts. Jamoer Lake, Bensbach River, Purari River delta, Gulf of Papua, Hall Sound, Goldie River.

AUSTRALIA: North, west and east-draining rivers and associated coasts. Widespread. Abrolhos Islands, Ashburton, Fortescue, Maitland, Fitzroy, King and Ord Rivers, Dampier; Daly, Victoria, McKinlay, Alligator Rivers, Mary River, Roper River system, Arnhem Land, Melville Island; Flinders River, Bynoe, Fitzroy, Burdekin, Chapman, Mitchell, Archer, Dawson, Boyne, Brisbane Rivers, Townsville, Moreton Bay; Richmond, Clarence, Macleay and Hunter Rivers.

BIOLOGY

Habitat: Coastal draining rivers and streams, lakes and billabongs from above tidal influence, to estuaries and adjacent coastal waters. Bishop *et al*. (1980; 1986) and Midgley (1980, 1981, 1983, 1984) found that "*A*". *graeffei* prefers sandy and rock/gravel substrate to mud or clay. The species inhabits still to swiftly flowing water, from clear to turbid. Quality in *graeffei*-inhabiting waters of the Victoria, Daly and Arnhem Land rivers was 23-32°C surface temperature, pH 7-8.7 (Midgley, 1980-84); and in similar waters of the Alligator Rivers region, quality was 27-31°C surface temperature, dissolved oxygen 4.4-6.5 mg/l (surface) and 0.6-4.9 mg/l (bottom), pH 6.1-7 (Bishop *et al*., 1980; 1986). Considerable movement along waterways and between estuaries by this species has been observed (e.g. Kowarsky and Ross, 1981), to some extent, although breeding individuals are usually found only in fresh water.

Maximum size: Approx. 500 mm SL. 550 mm TL, 1.6 kg (Lake and Midgley, 1970). Larger sizes are stated in literature, although the identification of the fish has not been verified: Ogilby (1918) estimated a specimen from the Burnett River as 700 mm SL, 925 mm TL (identification doubtful); Grant (1987) gave maximum length as 690 mm TL, 3.9 kg.

Diet: Omnivorous and opportunistic, dietary items varying with season. Stomachs of my material contained detritus, gravel, plant material (sticks, leaves), fruit, *Macrobrachium* and prawn fragments, loose fish scales, beetle fragments, some loose fish rays. In 38 food-containing stomachs analysed by Bishop *et al*. (1980), were fish scales and few fish (23%), terrestrial plants (22%), macrocrustacea (19%), aquatic insects (9%), and terrestrial insects, bivalves, detritus and inorganic material comprising the remainder.

Breeding: In Australia, spawning occurs between the late dry and the end of the wet season. Rimmer (1985, 1985a) presented detailed information on the reproduction and early development of "*A*". *graeffei* in the Clarence River system. Rimmer (1985b) reported the size at first maturity as approx. 250 mm SL. Fecundity varies with size of the parents; and Lake and Midgley (1970) recorded 123 ova averaging 14 mm diameter from one large brooding male. T. Davis (pers. comm., 1981) collected small juveniles (44-50 mm SL) from creeks associated with mangrove areas in January, water salinity +/- 6ppt.

DISCUSSION

Lake's (1978) discussion on "*A. leptaspis*" refers largely to "*A*". *graeffei*; and *graeffei* is included in Pollard's (1974) information on "*A. leptaspis*", as is "*A*". *midgleyi*. Lake and Midgley's (1970) specimen of "*Hexanematichthys leptaspis*" is referable to *graeffei*. One of Macleay's (1884) syntypes of *Arius latirostris*, AMS I.9127, is a specimen of "*A*". *graeffei*.

"*A*". *graeffei* was described approximately 7 months before its synonym "*A*". *australis* (Kailola, 1983). Günther (1867; 1909) executed fine drawings of the type of both species, but failed to recognise their conspecificity. The real and imagined affinities of the species included "*A*". *proximus* Ogilby, "*A*". *gagorides* (Valenciennes), "*A*". *sona* (Hamilton-Buchanan) and "*A*". *trachipomus* Valenciennes (Whitley, 1940; Kner and Steindachner, 1866; Fowler, 1928). A history of the name changes is given in Kailola, 1983.

"*A*". *graeffei* is most similar to "*A*". *berneyi* Whitley, especially as juveniles. Eye shape and diameter (fig. 178) (10-28 %HL in *graeffei*; 16-32 %HL in *berneyi*), maxillary barbel length (fig. 179) (17-41 %SL in *graeffei*; 33-48 %SL in *berneyi*) and relative size and development of palatal tooth patches (figs 176A, 187A-C) best distinguish the taxa. In addition, *graeffei* has a somewhat broader mouth with thinner lips, slightly narrower bands of jaw teeth (e.g. 6-9 premaxillary series *cf*. 8-11 series in *berneyi*), broader caudal lobes (slender in *berneyi*), slightly shorter fin spines (Table 35; fig. 180), a generally paler body colour (dark in *berneyi*), flatter interorbital, less developed epithelial flaps on upper gill arches and palate (large, crenulate pads in *berneyi*), and a few more vertebrae (52-54 *cf*. 49-51 in *berneyi*). "*A*". *graeffei* tolerates a wide range of water types, whereas "*A*". *berneyi* is usually only in fresh water.

Statistical analyses revealed a discriminant function which always separated all individuals of *graeffei* + *berneyi* accurately in the robust jackknife classification, using the characters of:

supraoccipital process length + anal ray count (fig. 181) + total number of first arch gill rakers (fig. 182) + palatal tooth pattern + caudal peduncle depth/peduncle length ratio + head height as %HL + snout length as %HL (fig. 183) + eye diameter as %SL (fig. 184) + maxillary barbel length as %SL + dorsal fin base length as %SL + adipose fin base length as %SL (Z function: Appendix C).

From "*Arius*" species 3, "*A*". *graeffei* is distinguished by (usually) having four palatal tooth patches (2 in species 3), smaller pectoral spine serrae, different mouth shape and width, eye size and caudal fin colouration. All other members of "*Arius*" have no or few posterior rakers on the first two gill arches (except "*Arius*" species 4, which has more gill rakers and other characters).

TYPES

Arius graeffei. Based on a single specimen, NMW 67152, 253 mm SL.

Arius australis. There are three specimens in the type series, all at BMNH. I have seen two, BMNH 1866.6.19: 7 (380 mm SL) and 1866.2.13: 4 (275 mm SL). The other type is BMNH 1866.6.19: 8.

Arius curtisii. Castelnau had "several paratypes, but all badly preserved" (1978: 237). The largest was nearly 15 inches long, others about 6 inches. One syntype is in the MNHN, number B.693 (144 mm SL, 178 mm TL). I have not located the remaining Castelnau specimens.

Condition of types: *Arius graeffei*: good. Mouth cut along LHS corner to below eye; belly cut on RHS adjacent to ventral fins; base of dorsal spine broken across (and note, one mandibulary barbel is forked).

Arius australis (on two syntypes): good. 275 mm SL specimen has belly slightly bloated; end of caudal lobe broken off. 380 mm SL specimen has belly slit open; pectoral and caudal fins torn.

Arius curtisii: poor; eviscerated. Brittle and rigid, orange-coloured (from rust?); LHS of head smashed, including mouth and palate; skin torn under head; RHS pectoral spine broken; tips of caudal fin lost.

ETYMOLOGY

Named for Dr Ed. Graeffe of the Godeffroy Museum in recognition of his work in the field of zoology.

MATERIAL EXAMINED

UNKNOWN LOCALITY - 1*, NMW 67 152, "Samoa" - locality erroneous, don. Steindachner, 253 mm SL (= HOLOTYPE) (original number 2103, Godeffroy Museum).

SOUTHERN IRIAN JAYA - 2*, RMNH 28811, near Kampong Gariau, Jamoer Lake, 7-13 Dec. 1954, coll. M. Boeseman, 261 & 333 mm SL;

SOUTHERN P.N.G. - 1*, AMNH 13994, Wurio, W. Papua, Oct.-Nov. 1933, coll. A.L. Rand & R. Archbold, 205 mm SL; 1*, AMNH 14001, same data, 166 mm SL; 2*, WAM P.27819-008, Bensbach River, 15 km downstream of Balamuk, 30 Sept. 1982, coll. G.R. Allen & J. Paska, 55 & 82 mm SL; 1*, QM unreg., Ihu market, Purari River delta area, 29 Nov.1974, coll. A.K. Haines, 285 mm SL; 1*, unreg., same data, 265 mm SL; 1*, LACM 44927-1, Papua (no other data), 1974-75, coll. A.K. Haines, 228 mm SL; 1*, unreg., same data, 268 mm SL; 1*, UMMZ 214015, Morowan, 28 Jan. 1976, coll. A.K. Haines, 157 mm SL; 1*, unreg., Morowan, 15 May 1975, coll. A.K. Haines, 253 mm SL; 1*, unreg., Arehava, 8-9 Sept.

1974, coll. A.K. Haines, 208 mm SL; 1, KFRS F.5622-04, Arehava, April 1975, SL not noted; 1*, KFRS F0079, NW of Hall Sound, 7 June 1961, 166 mm SL; 3, KFRS F.4302-03, Galley Reach, Feb. 1972, SL's not noted; 7, unreg., Koki market, Port Moresby (from Waigani Swamp), Jan. 1983, 212-295 mm SL; 1*, AMS I.9127, Goldie River, no data, coll. W. Macleay, 138 mm SL (= SYNTYPE of A. latirostris Macleay).

NEW SOUTH WALES - 1*, BMNH 1866.6.19.7, near Ash Island, Hunter River, no date, coll. Scott, 380 mm SL (= SYNTYPE of A. australis Günther); 1*, BMNH 1866.2.13: 4, same data, 275 mm SL (= SYNTYPE of A. australis); 3*, MMS F.154, Richmond River, no date, 197-207 mm SL; 1*, UMMZ 215078, Clarence River, 10 Feb. 1981, coll. M. Rimmer, 139 mm SL; 12*, unreg., same data, 148-400 mm SL; 1*, unreg., Clarence River, 11 Feb. 1981, coll. M. Rimmer, 228 mm SL; 9*, unreg., Clarence River, 16 Feb. 1981, coll. M. Rimmer, 155-305 mm SL; 5*, unreg., Clarence River, 24 Feb. 1981, coll. M. Rimmer, 260-327 mm SL; 2*, unreg., Clarence River, 27 Feb. 1981, coll. M. Rimmer, 292 & 336 mm SL; 3, AMS I.19341-007, Clarence River, Oct. 1976, 49-52 mm SL; 1, AMS I.14473, Clarence River, July 1918, approx. 410 mm SL; 1, CSIRO A.816, Ulmarra, Clarence River, Feb. 1940 (from mouth of parent), 44 mm SL; 1, CSIRO A.817, same data, 40 mm SL.

QUEENSLAND - 1*, MNHN B.693, Moreton Bay, no date, coll. Curtis, 144 mm SL (= SYNTYPE of A. curtisii); 1*, QM I.12001, Moreton Bay, 11 Nov. 1950, 237 mm SL; 1*, QM I.403, Brisbane River, no date, 258 mm SL; 1*, QM I.8924, Brisbane River, 1951, 48 mm SL; 1*, QM I.8925, same data, 46.5 mm SL; 1*, QM I.3674, Breakfast Creek, 1921, 270 mm SL; 1*, QM I.9835, Toowong Reach, trib. of Brisbane River, 2 Nov. 1969, 176.5 mm SL; 1*, QM I.9836, same data, 272.5 mm SL; 1*, QM I.9839, same data, 216 mm SL; 1*, QM I.7155, Oxley Creek, trib.

of Brisbane River, 21 April 1941, 165 mm SL; 1*, QM I.8944, same data, 173 mm SL; 1*, QM I.8606, Dawson River, 19 May 1965, 171 mm SL; 1, AMS I.17982-006, Dawson River, March 1967, 80 mm SL; 1, QM I.15502, Dawson River at Delusion Creek junction, Feb. 1979, SL not noted; 1, CSIRO A.4121, Orange Weir, Dawson River, no date, 97 mm SL; 15, QM I.15484, Mackenzie River at Bedford Weir, Feb. 1979, SL's not noted; 3, AMS I.10091, Gayndah, no date, 210-224 mm SL; 1, AMS I.10090, Wide Bay, no date, 218 mm SL; 1, QM I.16452, Isaac River above Connor's River junction, Feb. 1979, SL not noted; 1, QM unreg., Yabba Creek at Imbil, 1987, 353 mm SL; 4*, QM I.16734, Boyne River below Awoonga Dam, June 1976, coll. H. Midgley, 80-117 mm SL; 3*, QM I.16740, Boyne River above Awoonga Dam, coll. H. Midgley, 297 & 325 mm SL, plus one head: 170.5 mm (SL not stated); 1*, JCU 4181, Bogie & Burdekin Rivers junction, 12 July 1980, coll. T. Orr, 243 mm SL; 1, QM I.16442, Fitzroy River, 20 km upstream from Yamba, April 1979, SL not noted; 2, AMS I.17961-002, Saxby River at Taldora Station, 1967-1971, 61 & 73 mm SL; 1, AMS I.10094, Burdekin River, 1882, 287 mm SL; 1, AMS A.18305, Burdekin River, Aug. 1883, 350 mm SL; 1, AMS A.18306, same data, 375 mm SL; 1, AMS A.18308, same data, 330 mm SL; 1, AMS A.18309, same data, 305 mm SL; 1, AMS A.18310, same data, 305 mm SL; 1, AMS I.12185, Eidsvold, Burnett River, Nov. 1911, 88 mm SL; 1, MCZ 33093, Burnett River, 1932, 53 mm SL; 1, MCZ 33095, Burnett River near Mundubber, March 1932, 340 mm SL; 1, AMS I.12184, same data, 370 mm SL; 1*, QM I.12758, Flinders River near Maxwellton, 340 mm SL; 1*, QM I.16733, Flinders River, coll. H. & M. Midgley, 340 mm SL; 1*, CSIRO A.3687, Walker's Bend Crossing, Flinders River, 19 Oct. 1972, coll. I. Munro, 99.5 mm SL; 1*, unreg., Moonkan River, 24 Nov. 1980, coll. D.B. Carter, 223 mm SL; 1*, unreg., Malamon River, 19 March 1981, coll. D.B. Carter, 300 mm SL; 2*, unreg., Chapman River, 20 March 1981, coll. D.B. Carter, 225 & 236 mm SL; 1, ZMH 7859, Chapman River, 8-20 March 1981, coll. D.B. Carter, 187 mm SL; 5, unreg., Chapman River, 8-20 March 1981, 207-385 mm TL; 1, CSIRO C.4251, saltwater hole in Bynoe River at Normanton-Burketown road crossing, Nov. 1971, 240 mm SL; 1, CSIRO C.4252, same data, 280 mm SL.

NORTHERN TERRITORY - 1*, QM I.16732, Roper River, 14 Sept.1979, coll. H. & M. Midgley, head only: 88 mm HL; 1*, QM I.16739, same data, 280 mm SL; 2, QM I.16746, Wilton River, Sept. 1979, upper jaws only, SL not stated; 1*, unreg., same data, head only: 106.5 mm HL; 1*+1, AMNH 57300, muddy lagoon into Jim Jim crossing, 12 May 1969, coll. G. Nelson, D. Rosen & H. Butler, 112 & 193 mm SL; 2, unreg., Ludmilla Creek, Darwin, Dec. 1984, 280 & 390 mm SL; 1, NTM S.11850-003, mouth of Leader's Creek, Gunn Point, May 1986, 225 mm SL; 2, NTM S.11699-001, Wood's Inlet, May 1985, 180 & 260 mm SL; 1*, SAM F.1080, Melville Island, 13 Nov. 1928, coll. W.D. Dodd, 195 mm SL; 1*, NTM S.10706-001, Palmer's Creek, Adelaide River, 20 June 1972, 99 mm SL; 1*, not kept, Baroalba Crossing, South Alligator River, May 1979, coll. K. Bishop, 78 mm SL; 1*, unreg., Jabiru (Deaf Adder Creek), Oct. 1978, coll. K. Bishop, 236 mm SL; 4*, unreg., Nourlangie Creek, South Alligator River, 6 May 1979, coll. K. Bishop, 178-176 mm SL; 3*, AMS I.27419-001, same data, 178-184 mm SL; 1*, WAM P.30029-001, Jabiru, June-July 1980, coll. B. Rooney, 91 mm SL; 3*, unreg., Long Harry's Billabong, Jabiru, 13 May 1980, coll. B. Rooney, 176.5-323 mm SL; 6, not kept, Long Harry's Billabong, Jabiru, May 1980, 99-320 mm SL; 23, CSIRO & BMNH unreg., Sampan Creek (15 km from coast), Jan. 1980, 43-50 mm SL; 7, AMNH 51641, South Alligator River at Oenpelli-Darwin Road crossing, May 1969, 73-94 mm SL; 5, AMNH 51642, isolated pools in Soda Creek at

Oenpelli-Darwin Road crossing, May 1969, 86-106 mm SL; 18, AMNH 51643, main bed of Soda Creek, May 1969, 79-93 mm SL; 16, AMNH 51640, South Alligator River on Pie Creek-Oenpelli Road, May 1969, 86-150 mm SL; 2*, AMNH 57302(SW), lower Daly River near police station, 14-15 May 1969, coll. G. Nelson, D. Rosen & H. Butler, 86 & 93.5 mm SL; 1, NTM S.1244, Cooper's Creek, Mt Borrodaile area, no date, 97 mm SL; 1, AMS I.16827-001, Cahill's Crossing of East Alligator River, July 1972, 107 mm SL; 1*, MZUSP unreg., Katherine River at Maude Creek junction, 17 km ENE of Katherine, Aug.-Sept. 1980, coll. H. & M. Midgley, 300 mm SL, head only kept; 3*, NTM S.12087-002, Katherine River, few km below Limestone Creek junction, 55 km WSW of Katherine, Aug.-Sept. 1980, coll. H. & M. Midgley, 360-370 mm SL, heads only kept (104, 109 & 114 mm HL); 19, AMNH 51639, Katherine River, 8 mi. downstream from Katherine, May 1969, 95-133 mm SL; 1*, NTM S.11800-002, Daly River on Florina Station, 62 km W of Katherine, 25-26 Aug. 1980, coll. H. & M. Midgley, 310 mm SL; 5*, NTM S.12138-001, lower Daly River, 110 km W of Pine Creek, Aug.-Sept. 1980, coll. H. & M. Midgley, 83-96 mm SL; 4, AMS I.20847-003, upstream from Daly River crossing, June 1978, 130-214 mm SL; 3, AMS I.20857-001, Victoria River district, June 1978, 215-305 mm SL; 83, AMNH 51644, Big Horse Creek junction with Victoria River, May 1969, 45-108 mm SL; 5, AMS I.20858-004, Wickham Gorge, Victoria River, June 1978, 173-295 mm SL.

WESTERN AUSTRALIA - 2*+14, AMNH 57296, Cave River, 9mi. from mouth, 6 April 1969, coll. G. Nelson, D. Rosen & H. Butler, 84-98 mm SL; 5*+5, AMNH 51637, pool in streambed of Ashburton River, 9mi. upstream from Minderoo Station, 6 April 1969, coll. G. Nelson, D. Rosen & H. Butler, 79-291.5 mm SL; 3*, AMNH 57298, pool in streambed of Fortescue River, 1 mi. downstream from coastal highway, 7 April 1969, coll. G. Nelson, D. Rosen & H. Butler, 148-169 mm SL; 1*, WAM P.5807-001, Millstream, Fortescue River, 20 July 1958, date?, 376 mm SL; 1*, WAM P.22876-001, salt ponds at Dampier, March 1973, coll. D. Hombre, 358 mm SL; 4*, AMS I.18217-006 (in part), Maitland River, 22 Nov. 1974, coll. G.R. Allen & Sumadiharga, 77-88 mm SL; 1*, AMS I.7035, Abrolhos Islands, coll. W.A. Museum, reg. Jan, 1905, 220 mm SL; 7*+9, AMNH 51638, isolated pools in Yeeda Creek bed, 4 mi. downstream from Yeeda Homestead, 19 April 1969, coll. G. Nelson, D. Rosen & H. Butler, 79-143.5 mm SL; 4*+12, AMNH 57297, Hann River at Moll Gorge, 15mi. NE Mt House Station, 28 April 1969, coll. G. Nelson, D. Rosen & H. Butler, 123-205 mm SL; 3*+5, AMNH 57299, King River, 6 May 1969, coll. G. Nelson, D. Rosen & H. Butler, 64-119 mm SL; 10, not kept, Lake Argyle, early 1982, 170-350 mm SL; 2*+9, AMNH 57301, Ord River main stream, below Great Western Highway crossing, May 1969, coll. G. Nelson, D. Rosen & H. Butler, 86-183.5 mm SL; 1*, WAM P.25417-002, Carson River, 14 Aug. 1975, coll. J.B. Hutchins, 181 mm SL; 1*, WAM P.25418-002, Carson River, 14 Aug. 1975, coll. J.B. Hutchins, 184 mm SL; 1*, WAM P.25023-003, Plain Creek at Beverley Springs Station (trib. of Isdell River), 11 Aug. 1974, 202 mm SL; 1*, WAM P.25597-002, Fitzroy River, June 1974, 328.5 mm SL; 1*, SAM F.4242, Carlton Hill Crossing of Ord River, E of Wyndham, 17 May 1973, coll. T. & C. Houston, 93 mm SL.

6.6.9.2

"*Arius*" *berneyi* (Whitley)

(Figures 185, 186, 187, 188; Tables 35, 36)

Tachysurus (*Pararius*) *berneyi* Whitley, 1941: 9, fig. 8, no. 5
(in part) (pools of Flinders River near Hughenden & Richmond)

Hexanematichthys *berneyi*: Munro, 1957: 40, fig. 280

Pararius *berneyi*: Whitley, 1964: 36

Arius *cleptolepis* Roberts, 1978: 37, fig. 15, 20e (Elevala River, 17 km
east of Kiunga, Papua)

Arius *berneyi*: Allen and Boeseman, 1982: 98

Arius *armiger* (*non* De Vis): Grant, 1987: 68

DEFINITION

Palatal teeth slender, in transverse series of four patches, outer pair twice as large as oblique vomerine patches which usually unite and expand with age to form one large, median vomerine patch. Snout rounded, with shallow groove between nostrils; lips crenulate and moderately thick. Head shield finely granular. Eye large, 16-32 %HL. Maxillary barbel reaches dorsal spine base, often further. A 16-19; total first arch GR 15-20; posterior rakers present along all gill arches; vertebrae 17-19+5-6+25-27. Fresh colouration bluish black to violet brown above, white below.

DESCRIPTION

D I,7. P I,9-11. A 16-19. GR (first arch) 15-20 of which 4-7 on upper limb. GR (last arch) 14-20. Number of vertebrae 49-51 (43-44 free).

Body sleek, trunk section somewhat rounded. Head moderately small and narrow; predorsal profile straight. Snout slightly and evenly rounded, turned ventrad; lips closely creased and crenulate (less so in New Guinea material), moderately thick. Shallow crescent-shaped groove on dorsum of snout between nostrils, present in fish of all ages; very fine papilla-like structures scattered over snout in larger fish. Mouth subterminal, gape moderately narrow; none of premaxillary tooth band exposed when mouth closed. Anterior nostril ovate, directly before or slightly median to posterior one. Eyes large and rounded; orbit free of head skin; situated dorsolaterally, slightly before mid-head length. (Lateral ethmoid somewhat prominent in New Guinea specimens.) Gill opening wide, membranes meeting ventrally in an obtuse angle, leaving broad, free border.

Teeth in both jaws depressible, fine and sharp, frequently tipped dark brown. Teeth mostly concealed by spongy tissue, arranged in 8-11 irregular series in premaxillary band and 5-9 series in lower jaw; edentulous space at symphysis of lower jaw. Teeth on palate slender, conical and pointed (more stout in New Guinea material) and non-depressible: in 4 groups arranged in band across front of palate; vomerine pair rounded or oval, obliquely inclined, half as wide as outer patches. Patches well-separated in juveniles; vomerine patches expanded, often forming one large, undivided tooth patch in larger fish (possession of a single median tooth patch is more prevalent in New Guinea material of various sizes). Palate smooth, with two large, moderately thin epithelial flaps posteriorly before branchial chambers.

Head shield with numerous granules, beginning above eye and extending over supraoccipital process. Dorsomedian head groove lanceolate, reaching base of supraoccipital process; moderately shallow anteriorly, deeper and narrow posteriorly. Process more or less triangular, frequently concave near its base; sharply keeled. Sides of head smooth or venulose. Humeral process rugose to granular, heavily ossified anteroventrally; shaft of process triangular, acute, extending 1/4-1/3 distance along pectoral spine. Ovate axillary pore conspicuous.

Barbels long, usually flat. Maxillary barbel reaches at least to base of dorsal spine, often past dorsal fin to opposite ventral fin origin. Mandibulary barbel reaches pectoral base or beyond. Mental barbel attains ventral edge of gill membranes, often to below pectoral base. Chin barbel bases moderately staggered.

Gill rakers short, half as long as opposing filaments. Rakers along posterior face of all arches: 15-23 on first, 16-21 on second, 14-20 on third. Large, narrow flaps ("pads") of epithelial tissue posterodorsally on first 3 arches, that on second largest. Flaps dimpled, with crenulate edges.

Spines moderately thick or slender, pectoral spine flatter than dorsal. Fine, longitudinal striae along lateral face of each spine; anterior spine margin with many small, sharp granules and few antrorse serrae near tip. Low serrae extend along dorsal half of posterior edge of dorsal spine; 10-26 sharp serrae (larger and fewer in juveniles) extend along inner edge of pectoral. Dorsal often tipped with filament. Last dorsal ray 2.9-3.8 shorter than longest ray. Pectoral reaches at least one eye diameter beyond dorsal base. Ventral narrow in males, reaching anal origin; broader in females and slightly longer. Sexually mature fish develop an elongate, scalloped, cushy pad of epithelial tissue along upper surface of 5th-6th rays. Adipose fin moderately large, opposite middle of anal fin. Anal margin concave, anterior rays elevated, 1.4-3.5 length of last ray. Caudal lobes slender and pointed, upper lobe longer than lower.

Caudal peduncle moderately compressed. Lateral line almost straight, elevated anteriorly and turned dorsad at tail base. Numerous short lines and vertical series of pores branch from main line along its length.

Fresh colouration: Bluish black to violet brown above, fawn or brown on sides; undersides of head and body silvery white or cream. Barbels blackish-brown to fawn. Fins dusky to dark brown, pectoral and ventral fins paler below.

Colour in preservative: Dark brown, charcoal or bluish grey above, grey to orangey below. Snout tip pale. Dorsal, adipose and caudal fins brown, darker towards margins, dark brown anteriorly on anal, pectoral and ventral fins. Barbels brown. Peritoneum grey or fawn.

DISTRIBUTION

NEW GUINEA: South-draining rivers: upper and middle sections of the Fly River (including Strickland R. and Lake Murray).

AUSTRALIA: Rivers draining northwards into the Gulf of Carpentaria, e.g. Roper River system (Limmen Bight, Hodgson and Wilton Rivers), Gregory, O'Shannassy, Leichhardt, Alexandra, Saxby, Flinders, Smithburne, Mitchell and Coen Rivers (Midgley, 1982; 1983; 1984); Norman and Staaten Rivers (H. Midgley, pers. comm.).

BIOLOGY

Habitat: Freshwater rivers, streams, lakes and waterholes. Almost always above tidal influence. Water slow to moderately fast-flowing; quality clear and dark (black, reddish, brown), pH 6.1-8.2 and warm (24-31.7 °C) (Roberts, 1978); more rarely, "*A*". *berneyi* occurs in slightly turbid to swampy waters. Midgley (1979) noted water conditions in the Roper River system where "*A*". *berneyi* was obtained as clear to turbid, alkaline (pH 7.7-8.2) and with surface temperature of 26-29°C. "*A*". *berneyi* was the most common ariid species at Kiunga (Fly River) (Maunsell and partners, 1982) and is overall well-dispersed along the Fly River between about 400 and 900 km from its mouth. Ecologically, it succeeds "*A*". *latirostris* downstream along the Fly (*ibid*.).

Maximum size: 480 mm SL (Maunsell and partners, 1982); 375 mm SL (paratype).

Diet: Lake's (1978) claim that "*A*". *berneyi* is carnivorous, is not substantiated by the work of others. "*A*". *berneyi* is instead omnivorous (Roberts, 1978; Maunsell and partners, 1982). Most of Roberts' (large) specimens had swallowed quantities of large fish scales (see also Chapter 4, Character 86), as well as prawns, terrestrial insects and mud (no fish). Maunsell and partners (1982) also observed that *berneyi* individuals had consumed large fish scales (probably picked up from bottom sediment), terrestrial insects (mostly grasshoppers), aquatic insects, worms, molluscs, macrocrustacea, fish and some vertebrates. The gut contents of specimens I have examined included plant material, loose fish scales, small and slender fish (few; clupeiform or atheriniform), detritus and mud.

Breeding: "*A*". *berneyi* undertakes a long spawning period, extending over several months. Midgley's (1979) 240 mm SL mature female (gonad stage V-VI) from the Wilton River was caught at the end of September. Roberts' 309 mm SL type of *A*. *cleptolepis* is a mature female, caught on 20 October. In the Fly, Maunsell and partners (1982) recorded large females (up to 570 mm TL) with developing or mature ovaries in the middle section of the river in July, but no mature males. Small fish (to 64 mm SL) were caught only at Kiunga (in June). I have no information on fecundity.

DISCUSSION

Differences between New Guinea and Australian material have been noted in the species description. However, they (expression of tooth size, extent of tooth patches, lip shape and prominence of the lateral ethmoid) may be a function of size. Recognition of two distinct taxa (*cleptolepis* Roberts, *berneyi* Whitley) was not substantiated in scattergrams, e.g. HL/SL ratio; eye diameter/HL ratio (figs 189, 190). Lack of sufficient material from New Guinea has hampered any effective investigation into these differences.

Roberts (1978) characterised *cleptolepis* on palatal dentition and presence of a snout groove. However, examination of a series of specimens and several growth stadia, showed that the tooth patches change in shape with increase in fish size. Roberts' types are all larger than 141 mm SL, a size from which the vomerine tooth patches tend to expand and fuse (although not always; *cf*. "*A*". *solidus* Herre). Furthermore, presence of a transverse snout groove is not a character unique to this taxon (see for example, "*A*". *proximus* Ogilby and "*A*". *mastersi* Ogilby).

Maunsell and partners (1982) and Allen and Boeseman (1982) correctly placed *A*. *cleptolepis* Roberts following my advice.

This species is most similar to "*A*". *graeffei*. Characters distinguishing these taxa are noted under the "*A*". *graeffei* discussion.

Whitley (1941) misidentified 12 small specimens of "*A*". *mastersi* Ogilby from Mapoon in Qld., nominating them as paratypes of *A*. *berneyi*. I have examined these specimens (AMS I.8077-8088, 79-116 mm SL).

Contrary to the distribution of other bidomicilic ariids in this region, "*A*". *berneyi* has not been collected from rivers adjacent to the Fly-Strickland in New Guinea and the Gulf of Carpentaria drainage in Australia.

TYPES

Tachysurus (*Pararius*) *berneyi* is based on 14 specimens, although as noted above, only the holotype and the largest paratype represent the taxon. These specimens are AMS I.13076 (holotype, 140.5 mm SL) and AMS I.13075 (paratype, 255 mm SL).

Arius cleptolepis is based on 9 specimens, 141-375 mm SL. These types are: AMS I.27092-001, 309 mm SL (ex USNM 217069) (HOLOTYPE); USNM 217070, 218 mm SL; KFRS F.4618-01, 2 specimen, SL not noted (ex USNM 217071); USNM 217071, 3 specimens, 141, 353 and 375 mm SL; USNM 217072, 225 mm SL; and a final paratype ex USNM 217071 sent to BMNH (register number unknown).

Condition of types: *Arius berneyi*: holotype fair. Body firm, dimpled, with scattered small "pimples". Mouth cut to below eye on RHS, head cut through on LHS, snout tip pushed upward. All fins tattered or rays crushed, notably those of anal, ventral and caudal; tips of caudal lobes lost. Paratype in fair condition. Body firm but scattered with small blisters. Both caudal lobes broken off.

Arius cleptolepis: all types in good condition. Underside of head cut on RHS through gill cover and branchiostegals as far as hyoid arch in some specimens; belly slit on RHS; some fin membranes torn or detached from spines.

ETYMOLOGY

This species is named for Mr Frederick L. Berney, ornithologist, in acknowledgement of his collections of Queensland fishes.

MATERIAL EXAMINED

SOUTHERN P.N.G. - 1*, USNM 217070, trib. of upper Fly River, 1-2 mi. upstream from Elevala River, 26 Oct. 1975, coll. T.R. Roberts, 218 mm SL (= PARATYPE of *A. cleptolepis*); 1, USNM 217071, oxbow lake, 4 km downstream from Kiunga, Oct.-Nov. 1975, coll. T.R. Roberts, 353 mm SL (= PARATYPE of *A. cleptolepis*); 2*, KFRS F03770, swamp at Kiunga, 26 Sept. 1973, coll. J. Timothy & J. Koaia, 122 & 152 mm SL; 3, KFRS F.4980-01, Kiunga, June 1982, 27.5-63.5 mm SL; 2*, KFRS F02816, Lake Murray, June 1970, 156 & 183 mm SL; 2, KFRS F03003, Lake Murray, May 1967, 146 & 171.5 mm SL; 1, KFRS F02864, Lake Murray, June 1970, 113 mm SL; 4, KFRS F02820, Lake Murray, June 1970, 129-161 mm SL; 2, KFRS F03066, Lake Murray, June 1970, 143 & 148 mm SL; 2*, RMNH 30321, Fly River at Lake Bosset, 19 Sept. 1986, coll. K. Hortle, 165 & 184 mm SL; 1*, ZMB 31876, same data, 230 mm SL; 1*, CSIRO H 1684-01, same data, 154 mm SL; 1*, CSIRO H1684-02, same data, 280 mm SL; 4*, unreg., same data, 122, 182, 205, 238 mm SL.

QUEENSLAND - 1*, AMS I.13076, pools of Flinders River near Hughenden & Richmond, coll. F.L. Berney, pres. July 1914, 140.5 mm SL (= HOLOTYPE); 1*, AMS I.13075, same data, 255 mm SL (= PARATYPE); 1*, CSIRO C.4592, O'Shannessy River, 20 May 1969, coll. J.S. Lake, 170 mm SL; 1*, CSIRO C.4593, same data, 144 mm SL; 7, AMS I.17990-009, junction of O'Shannessy & Gregory Rivers, May 1967, 147-290 mm SL; 1*, AMS I.17969-003, O'Shannessy River near Riversleigh station, 20 May 1969, coll. J.S. Lake, 165 mm SL; 12, CSIRO numbers A.3684, A.3685, A.3686, A.3687, A.3688, A.3689, A.3796, A.3797, A.3798, A.3799, A.3800, A.3801, all Walkers' Bend Crossing, Flinders River, Oct. 1972, SL's not noted; 1*, QM I.10422, junction of Mitchell River & Desaille Creek, Mt. Carbine, 12 May 1973, coll. R.J. McKay, 177 mm SL; 1*, QM I.14412, Leichhardt River, Oct. 1977, 200.5 mm SL; 1*, CSIRO A.4116, Saxby River, May 1970, coll. J.S. Lake, 108 mm SL; 1*, QM I.9183, Saxby River, 16 Oct. 1967, 65.7 mm SL; 1*, QM I.9184, same data, 119 mm SL; 1*, QM I.9185, same data, 127 mm SL; 1*, QM I.9186, same data, 58 mm SL; 1*, QM I.9187, same data, 113.5 mm SL; 1*, QM I.9188, same data, 111 mm SL; 1*, QM I.9189, same data, 139 mm SL; 1*, QM I.9190, same data, 161 mm SL; 2*+2, AMS I.17942-005 (in part), Saxby River, 28 Sept. 1967, coll. J.S. Lake, 69 & 70, 129 & 182 mm SL; 1, CSIRO A.4115, Saxby River, May 1970, 71 mm SL; 1*, QM I.10748, Dunbar station, Mitchell River, Oct. 1947, 137 mm SL; 1*, AMS IB.2223, Dunbar station, Mitchell River, 25 Oct. 1947, pres. J.L. Wassell, 137 mm SL; 1, AMS IB.2224, same locality, Oct. 1971, 67 mm SL; 1, AMS IB.2350, Coen River, no date, coll. R.McKay, SL not noted; 1, CSIRO C.3759, no collection data, 1969, 280 mm SL.

NORTHERN TERRITORY - 1*, QM I.16736, Limmen Bight River, 1 Sept. 1979, coll. H. & M. Midgley, 224 mm SL; 1*, NTM S.12072-001, Limmen Bight River, 1 Sept. 1979, coll. H. & M. Midgley, 209 mm SL; 5*, NTM S.12078-001 (in part), Hodgson River, 17 Sept. 1979, coll. H. & M. Midgley, 60-78 mm SL; 1*, unreg., flood channel lagoon, Wilton River, 27 Sept. 1979, coll. H. & M. Midgley, 102 mm SL; 2*, QM I.26082, flood channel lagoon, Wilton River, 27 Sept. 1979, coll. H. & M. Midgley, 95 & 118 mm SL; 1*, MNHN 1989.1082, same data, 84 mm SL; 2*, unreg., same data, 97 & 181 mm SL; 2, NTM S.11907-001 (in part), Hodgson River, Sept. 1979, 66 & 69 mm SL; 2, ZMH 7860, flood channel lagoon, Wilton River, Sept. 1979, 75 & 83 mm SL; 2, LACM 44931-1, same data, 78.5 & 158 mm SL; 1, MZUSP unreg., same data, 113 mm SL; 3*, KFRS F.5524-01, same data, 75-240 mm SL; 3*, AMNH 51648, Red Lily Lagoon, 9 mi. NE of Elsey Homestead, 7 Oct. 1969, coll. G. Nelson, H. Butler & D. Rosen, 132-172 mm SL.

6.6.9.3

"Arius" species 3

(Figures 191, 192, 193; Tables 35, 36)

DEFINITION

Palatal teeth conical, in two oblique, oval patches; one each side of palate, well-separated. Snout acute; lips fleshy and crenulate; mouth transverse. Head shield finely granular; dorsomedian head groove lanceolate, narrow distally. Eye large, 19-28 %HL. Large, flattened serrae along inner margin of pectoral spine; caudal lobes slender, acute. A 17-22; total first arch GR 15-20; posterior rakers present along all gill arches; vertebrae 18+6+27. Distinct, blackish margin on dorsal, pectoral and inner caudal fin.

DESCRIPTION

D I,7. P I,8-11. A 17-22. GR (first arch) 15-20, of which 5-7 on upper limb. GR (last arch) 14-18. Number of vertebrae 51 (44 free).

Body moderately slender. Predorsal profile straight. Snout moderately to slightly acute; lips fleshy and crenulate; short, transverse crescent often present on dorsum of snout between nostrils. Mouth subinferior, gape moderately large; upper jaw somewhat acute medially, lower jaw almost transverse; half of premaxillary tooth band exposed when mouth closed. Nostrils ovate, anterior nostril slightly medial to posterior one. Eye ovate to rounded, large, border free from head skin. Eye dorsolateral, slightly before mid-head length. Gill opening moderately wide, concave at isthmus; moderately broad margin.

Teeth in jaws fine and sharp, depressible, forming 7-8 irregular series in upper jaw and 4-6 series in lower jaw. Teeth form two elongate lateral bands on premaxillary, meeting at midline; patches on lower jaw separated by median narrow, edentulous space. A large, oval patch of conical, blunt teeth on each side of palate anteriorly, obliquely situated and well-separated. Palate smooth or slightly papillose; two oblique, low to moderately well-developed epithelial ridges posteriorly on palate before branchial chambers.

Head shield finely granular. Dorsomedian head groove originates between nostrils and reaches supraoccipital process base. Groove flat and lanceolate anteriorly, narrow and straight posteriorly. Supraoccipital process triangular, straight-sided and with median keel. Sides of head moderately venulose. Triangular humeral process rugose, well-ossified anteroventrally; its shaft oblique, extending 1/3 along pectoral spine. Axillary pore small.

Barbels flattened, moderately thick and fleshy. Maxillary barbel extends slightly beyond dorsal fin in juveniles, to humeral process in adults. Mandibulary barbel usually reaches pectoral spine base. Mental barbel reaches ventral head margin. Chin barbels slightly staggered.

Gill rakers short, 1/3-1/2 length of opposing filaments. Rakers present along posterior aspect of all arches: 6-7 (upper limb only) to 11-14 (total) on first arch; 13-18 along second; 11-16 along third. Often some papillae on first two arches. Fleshy, scalloped epithelial folds moderately developed posterodorsally on first two arches.

Fin spines strong, moderately long, slightly curved; sides with fine, longitudinal striae. Short filament on tip of spines. Anterior spine margin finely rugose with several sharp, antrorse serrae near tip; posterior (trailing) margin with low (dorsal) or large and flattened (pectoral) serrae: 8-11 along dorsal, 12-13 along pectoral. Last dorsal ray 2.9-3.4 shorter than longest ray. Pectoral fin extends to below posterior dorsal rays. Ventral in males narrow, failing to reach anal origin by distance of 1/2 eye diameter; in females, broad-based, reaching to 4th anal ray. Inner ventral rays thickened to form a pad in sexually mature fish. Adipose fin rectangular, situated above middle of anal. Anal margin slightly concave, last ray 2.5-3 shorter than longest ray. Caudal lobes slender and tapered, acute, upper lobe slightly the longer.

Caudal peduncle moderately stout. Lateral line straight along sides, oblique below dorsal and turned dorsad at tail base. Fine, short lines diverge off length of lateral line.

Fresh colouration: Unknown.

Colour in preservative: Dusky fawn to charcoal above, creamy below; colours well-separated. Maxillary barbel usually dark. Unpaired fins and dorsal aspect of pectoral and ventral fins dusky or charcoal; distinct charcoal or black margin to inner caudal, dorsal and pectoral fins. Peritoneum pale, occasionally with scattered, dark stipples.

DISTRIBUTION

NEW GUINEA: Port Moresby-Kempwelch River area.

AUSTRALIA: Darwin (harbour and Ludmilla Creek) to Karumba and Chapman River.

BIOLOGY

Habitat: Coastal waters, estuaries and rivers within tidal influence; among mangroves.

Maximum size: 310 mm SL.

Diet: Probable omnivorous. Gut contents of my material included loose scales, plant material, water nymphs and other insect fragments, beetles.

Breeding: "*Arius*" species 3 probably spawns at the end of the dry season-early wet season. Although no fully mature females were examined, the 226 mm SL specimen collected in December has developed ovaries (approximately stage IV). Juveniles less than 100 mm SL were collected in August, October, December and March. I have no information on fecundity.

DISCUSSION

There are no literature records of this species, which has probably been confused in the field and earlier reports for "*Arius*" *berneyi* or "*A*". *graeffei*.

"*Arius*" species 3 can be distinguished from other taxa in group B (*berneyi*, *graeffei*) by its snout shape, palatal dentition, strong pectoral spine serrae and caudal fin colouration. It differs from other taxa with similar palatal dentition (*Cinetodus froggatti*, "*Arius* species 7) by its wide gill opening and head shield form (*cf*. *froggatti*) and moderately long barbels and large eye (*cf*. species 7).

TYPES

There are no nominated types.

ETYMOLOGY

This species has not been named.

MATERIAL EXAMINED

SOUTHERN P.N.G. - 6, unreg., Koki market (from Kempwelch River), Feb. 1988, 280-310 mm SL.

QUEENSLAND - 1*, AMS I.27415-001, Chapman River, 21 Dec. 1980, coll. D.B. Carter, 226 mm SL; 1*, unreg., Chapman River, 16 Nov. 1980, coll. D.B. Carter, 121 mm SL; 1*, unreg., Chapman River, 5 March 1981, coll. D.B. Carter, 127 mm SL; 1*, unreg., several km. upstream from mouth of Chapman River, 14 March 1981, coll. D.B. Carter, 80 mm SL;
1*, CSIRO A.3608, Norman River above Karumba, 22 October 1972, coll. I.S.R. Munro, 112 mm SL; 1*, CSIRO A.3609, same data as A.3608, 117 mm SL; 1*, CSIRO A.3610, same data, 116 mm SL.

NORTHERN TERRITORY - 1*, QM I.14917, Darwin Harbour, Nov. 1972, 105 mm SL; 2*, NTM S.10254-001, Mickett Creek, Shoal Bay, Melville Island, 16 Dec. 1976, coll. D. Grey, 94.5 & 101 mm SL;
1*, NTM S.10319-003, Shoal Bay, Melville Island, 19 Oct. 1972, coll. D. Grey, 56 mm SL; 1*, NTM S.10235-001, Shoal Bay, Melville Island, 1 Aug. 1973, coll. D. Grey, 90 mm SL; 1*, NTM S.11507-004, Ludmilla Creek, Darwin, 19 Dec. 1984, coll. G. Cole & A. Howard, 145 mm SL.

The remaining species in "*Arius*" did not form consistent groupings on the cladograms.

6.6.10

"*Arius*" *armiger* De Vis

(Figures 194, 195, 196; Tables 29, 30)

Arius armiger De Vis, 1884: 454 (New Britain - locality doubtful; probably northern Australia)

Arius stirlingi Ogilby, 1898a: 281 (estuary of Adelaide River, N.T.)

Nemapteryx stirlingi: Ogilby, 1908: 10

Tachysurus armiger: Fowler, 1928: 62

Tachysurus stirlingi: Fowler, 1928: 2

Hexanematichthys stirlingi: Munro, 1967: 81

Hexanamatichthys stirlingi: Munro, 1967: 84 (misspelling)

DEFINITION

Palatal teeth small and sharp, in transverse series of four oval patches (2 vomerine, 2 autogenous). Mouth subterminal, symphysis of jaws elevated. No rakers on posterior of first 2 gill arches (rarely 1-4 on second arch), these arches posterodorsally with thick, fleshy pads. Barbels long, maxillary 30-56 %SL. Dorsomedian head groove posteriorly deep and elliptical. Fin spines slender, dorsal longer than pectoral; short filament on fin spines at all ages. A 22-25. Fresh colouration golden brown to greyish pink above; fin margins and fin filaments dark brown or black.

DESCRIPTION

D I,7. P I,9-11. A 22-25. GR (first arch) 16-22, of which 6-9 on upper limb. GR (last arch) 16-22. Number of vertebrae 52 (45-46 free).

Body robust yet slender, tapered anteriorly. Predorsal profile straight, slightly convex at nape. Snout rounded to slightly acute, prominent; lips thick and firm. Jaws very strong; mouth subterminal, gape moderately broad and curved; symphysis of both jaws elevated (especially lower jaw); anterior 1/3-1/2 premaxillary tooth band exposed when mouth closed. Nostrils moderately large and ovate, anterior nostril slightly median to posterior one. Eye small, ovate-oblong, its border largely free of head skin. Eye dorsolateral, visible from above; situated slightly before mid-head length. Gill opening wide, membranes meeting at slightly acute angle at isthmus, leaving broad, free margin.

Teeth in jaws villiform, slender and sharp, slightly depressible; in 5-9 irregular series in premaxillary band, 4-6 series in mandibulary band. Narrow, edentulous space separates each side of mandibulary tooth band. Palate teeth small, sharp and stout or conical and bluntly-pointed. Teeth form four patches across front of palate: vomerine patch rounded, always well-separated at midline; outer patches larger and elongate oval, contiguous with or adjacent to vomerine patches. Palate smooth with two short oblique ridges of epithelial tissue posteriorly.

Head shield smooth anteriorly, posteriorly and laterally feebly granulated, with striate ridges adjacent to dorsomedian head groove and radiating over supraoccipital process. Groove lanceolate, beginning between nostrils and terminating at supraoccipital process base; narrow anteriorly, deep and elliptical posteriorly. Margin of groove and anterolateral arms of head shield pronounced. Process triangular, narrow, with straight sides and sharp, median keel. Sides of head smooth and venulose. Triangular humeral process short, heavily ossified anteroventrally; smooth and rugose. Process shaft oblique, acute, extending 1/4 distance along pectoral spine. Axillary pore moderately large.

Barbels slender, flattened. Maxillary barbel always reaches dorsal fin, often to ventral origin. Mandibulary barbel extends to opposite supraoccipital process or further. Mental barbel reaches pectoral base. Chin barbels well-staggered.

Gill rakers somewhat club-shaped, 1/4-1/2 length of opposing filaments. Arches smooth; no rakers on posterior aspect of first arch, none (rarely 1-4 on upper limb) on posterior of second arch; 16-21 on third. Thick epithelial tissue posterodorsally on first two arches, fleshy and better developed on second.

Fin spines long and slender, smooth to finely striate on sides. Anterior (leading) edge smooth to rough with 5-9 low serrae distally. Posterior margin with 14-19 low, sharp serrae (dorsal spine), 17-22 stout, short serrae (pectoral). Short to moderately long filament on spine tips at all ages. Longest dorsal ray 2.5-4.4 longer than last ray. Pectoral extends to below or beyond dorsal base. Ventral narrow in males, fin scarcely reaching anal origin; broad-based in females, reaching opposite 3rd-8th anal ray. Sexually mature females with fleshy epithelial pad on inner fin rays, pad often with short, lateral process. Adipose fin above posterior 2/3 of anal. Anal moderately elevated, longest ray 2.2-4.2 times last ray. Caudal lobes broad, then slender and tapered.

Caudal peduncle moderately deep. Straight lateral line oblique anteriorly and turned dorsad at tail base. Numerous short lines diverge from length of lateral line, especially dense and extensive around anterior third.

Fresh colouration: Coppery, golden brown, bronze or greyish pink on head and upper sides, shading to creamy yellow below. Juveniles grey on back. Fins dusky yellow, pinkish or pale orange and finely stippled grey, with charcoal margins and filaments; underside of paired fins cream. Barbels brown.

Colour in preservative: Tan to dusky grey above, grey to yellowish below. Fins dusky yellow. Peritoneum pale grey or white.

DISTRIBUTION

NEW GUINEA: south coast. Vogelkopf Peninsular to lower Digoel River (Hardenberg, 1941) and Lorentz River system (Weber, 1913); Daru and Fly River entrances, Gulf of Papua, to off Yule Island and Oreke.

AUSTRALIA: north coast. The King River, lower Victoria River, Adelaide and Alligator Rivers, Edward River system to eastern Gulf of Carpentaria.

BIOLOGY

Habitat: Coastal waters and estuaries, river deltas and rivers within tidal influence. *Nypa* palm and mangrove habitats (Haines, 1979). It is abundant in prawning areas of the Gulfs.

Maximum size: 295 mm SL (Adelaide River specimen).

Diet: Haines (1979) recognised "*A.*" *armiger* as an important prawn predator in the lower mangrove areas of the Purari River delta. Of 9 food-containing stomachs, he found prawns in 5, crab fragments, fish, aquatic insects, and plant material in one. Stomachs of my specimens contained crustacean fragments, loose fish scales, spines and grit (in specimens less that 100 mm SL) and prawns (200-285 mm SL specimens).

Breeding: In Australia, "*A.*" *armiger* spawns from about September to January (i.e. early wet season) in the lower deltas and estuaries. T. Davis (pers. comm.) collected numerous small *armiger* (24-80 mm SL) from swamps, streams and channels associated with Murganella Creek and East Alligator River between October 1978 and May 1979 (surface water temperature 26-31.9°C, salinity 0-3 ppt [December] to 29 ppt [May]). Brooding males have been caught in October. A 243 mm SL female of maturity stage V (my material) has 17-20 ova in each gonad, 0.8-1 cm diameter. Adelaide River specimens larger than 240 mm SL collected mid-July to early August 1989 were in early-mid maturity stages.

DISCUSSION

Maunsell and partners (1982) confused "*A.*" *armiger* with "*Arius*" species 1; and Roberts (1978) compared these two species, using one of Weber's (1913) specimens of *stirlingi* (= *armiger*). However, "*A.*" *armiger* can be distinguished from species 1 by its longer barbels, more anal rays, more first gill arch rakers (Tables 29, 30), colouration and number of thoracic vertebrae (11 in *armiger*, 14-15 in species 1).

Fowler (1928: 62) suggested that "*A.*" *armiger* is "possibly related to, if not synonymous with, *Tachysurus* *caelatus* (Val.)".

The only other Australo-Papuan ariids with long barbels which could be mistaken for "*A.*" *armiger* are *leptaspis* and *berneyi*. However, "*A.*" *leptaspis* has fewer anal rays (16-22, *cf*. 22-25 in *armiger*), a shallow dorsomedian head groove posteriorly, and fresh body colouration of vertical series of golden spots (*armiger* has a uniform golden brown body). "*A.*" *berneyi* has rakers along the back of all gill arches (absent from first two in *armiger*), fewer anal rays, a larger eye (16-32 %HL, *cf*. 10-17 %HL in *armiger*) and dark blue body colouration.

The validity of the stated type locality of New Britain for "*Arius*" *armiger* is doubtful because 1) the nominal species was known only from the types, 2) there are no other records of ariid catfishes inhabiting New Britain coastal waters, even over the past 15 years when surveys have been more regular; indeed these fishes have not been reliably recorded east of the main New Guinea island, 3) the short, fast-flowing rivers on New Britain do not form the preferred ariid habitat of extensive estuaries.

De Vis (1884) obtained the material described in his paper from personnel sailing between several Western Pacific islands (Kailola, 1983), and it is probable that collection information was confused. His armiger specimens more likely came from a northern Queensland or Papuan locality.

TYPES

Arius armiger: This species is based on two syntypes: QM I.3088, 148 mm SL and QM I.3089, 134 mm SL.

Arius stirlingi: This species is based on a 270 mm SL specimen, apparently lost. A search was made for the specimen, although Roberts (1978) had been unable to trace it in two Australian museums. The type is not in the NMV, nor in the collections of the MAMU and the SAM. Although Ogilby (1989a) stated that the specimen was sent to him by the South Australian Museum authorities, the only specimens of armiger in the SAM of appropriate size from the Adelaide River were collected in 1928 (Kailola, 1983).

Condition of types: fair. The skin is shrivelled, belly shrunken; all colour lost; both curved to the RHS. Dorsal spine is broken off completely in one specimen, half broken in the other. Mouth corners torn; the fins are tattered, especially the caudal which lacks most of the upper and lower lobes.

ETYMOLOGY

De Vis gave no indication of the name source, which I am unable to trace.

MATERIAL EXAMINED

UNKNOWN LOCALITY - 1*, QM I.3088, 148 mm SL; 1, QM I.3089, 134 mm SL (= SYNTYPES).

SOUTHERN IRIAN JAYA - 1, WAM P.29951-009, Bintuni Bay, 17 March 1989, coll. G.R. Allen, 180 mm SL; 2, WAM P.29972-001, mouth of Ritui River, Bintuni Bay, 2 April 1989, coll. G.R. Allen, 110 & 158 mm SL; 1, WAM P.29962-008, same locality, 26 March 1989, coll. G.R. Allen, 223 mm SL; 1, WAM P.29976-001, Kasuri River, 10 April 1989, coll. G.R. Allen, 140 mm SL.

SOUTHERN P.N.G. - 2, KFRS F.5626-02, Sagero, north bank, Daru Island, Sept. 1988, 180 & 185 mm SL; 1, AMS I.24639-007, Fly River delta, 1981, 96 mm SL; 1*, CSIRO A.3043, Kerema Bay, 4 April 1955, coll. A.M. Rapson, 92.5 mm SL; 1*, MNHN 1988-800, off Kerema, June 1978, coll. S. Frusher, 155 mm SL; 5, KFRS F.5541-01, off Oreke River mouth, May 1973, SL's not noted; 5, KFRS F02902, off Oreke River mouth, May 1973, 113-136 mm SL; 2, KFRS F.5274-01, Gulf of Papua, Oct. 1970, SL's not noted; 1*, LACM 44929-1, Baimuru, 12-14 Sept. 1974, coll. A.K. Haines, 256.5 mm SL; 1*, unreg., same data, 142 mm SL; 1*+2, CAS 60485, Moinamu, 10 Aug. 1976, coll. A.K. Haines, 129-164.5 mm SL; 1, unreg., Morowan, Ini Island, May 1975, 152 mm SL; 1, LACM 44930-1, Baimuru, Oct. 1974, 161 mm SL; 1*, AMS I.26972-001, Kubiri Creek, 3 Dec. 1974, coll. A.K. Haines, 150 mm SL; 1*, SAM F.6341, Ravikoupara, Oct.-Nov. 1978, coll. J. Opnai, 243 mm SL; 3, unreg., same data, 165.5-235 mm SL; 1, MNHN 1988-801, same data, 145 mm SL; 1, USNM 288558, same data, 166 mm SL; 1*, WAM P.30030-001, Purari River delta area, 1974-75, coll. A.K. Haines, 176 mm SL; 1*, unreg., Kaivu, 17 May 1975, coll. A.K. Haines, 195 mm SL; 1*, unreg., Purari River delta area, 1974-75, coll. A.K. Haines, 234 mm SL; 1*, RMNH 30318, Purari River delta area, 1974-75, coll. A.K. Haines, 146 mm SL.

QUEENSLAND - 1*, CSIRO C.3800, Norman River at Karumba, 1969, coll. D.J. Turner, 161 mm SL; 1*, CSIRO C.4378, same locality, 1971, coll. I. Munro, 188 mm SL; 2*, QM I.11789, Karumba, 24 Sept. 1953, 105 & 111 mm SL; 2*, QM I.11632, Bynoe River, 24 Sept. 1953, coll. T.C. Marshall, 79 & 89 mm SL; 1*, AMNH 17717, Queensland, 178 mm SL; 1, AMS I.23668-002, Karumba, no date, 98 mm SL; 2, AMS I.15557-042, Gulf of Carpentaria at 17°29'S, 140°48'E, Nov. 1963, coll. I. Munro, 111 & 184 mm SL; 11, CSIRO B.1107, Norman River at Karumba, 1971, 40-48 mm SL; 1, AMS IB.3694, "Queensland", no date, 90 mm SL; 1, QM I.23362, van Diemens' Inlet, Gulf of Carpentaria, June 1987, coll. D. Tuma, 273 mm SL; 1*, QM I.867, "Queensland coast", 29 Oct. 1912, 215 mm SL; 2*, unreg., Moonkan River, 16 Nov. 1980, coll. D.B. Carter, 273 & 285 mm SL; 1*, unreg., Moonkhan River, 19 Nov. 1980, coll. D.B. Carter, 255 mm SL.

NORTHERN TERRITORY - 1*, BMNH unreg., Murganella Creek, 28 Nov. 1978, coll. T. Davis, 110.5 mm SL; 3, NTM S.12598-001, same data, 24-24 mm SL; 1*, AMS I.27418-001, same locality, 23 May 1979, coll. T. Davis, 102 mm SL; 1*, BMNH unreg., mouth of East Alligator River, 27 Nov. 1978, coll. T. Davis, 74 mm SL; 1, unreg., 5 km upstream in South Alligator River, Nov. 1978, 57 mm SL; 74, CSIRO unreg., East Alligator River-Cooper's Creek-Murganella region, Oct. 1978-May 1979, 39-93 mm SL; 1*, SAM F.1094, Adelaide River, 16 Nov. 1928, 221 mm SL; 1*, SAM F.1095, Adelaide River, 16 Nov. 1928, 280.5 mm SL; 28, unreg., Adelaide River (Marakai Creek), July-Aug. 1989, coll. T. Coleman, 150-295 mm SL; 2, NTM S.11850-001, mouth of Leader's Creek, Gunn Point, no date, 180 & 185 mm SL; 1*, AMNH unreg., Victoria River, 8 May 1969, coll. G. Nelson, D. Rosen & H. Butler, 87 mm SL; 24, unreg., Victoria River (5-25 km downstream from Timber Creek), 1-6 July 1989, coll. T. Coleman, 105-290 mm SL.

WESTERN AUSTRALIA - 1*, unreg., King River at Wyndham, 17 July 1981, coll. L. Turner, 260 mm SL; 1*, ANSP 164918, same data, 184.5 mm SL; 1*, ZMA 119.482 , same data, 201.5 mm SL; 2*, RMNH unreg., same data, 173.5 & 236.5 mm SL.

6.6.11

"Arius" augustus Roberts

(Figures 197, 198, 199; Tables 27, 28)

Arius augustus Roberts, 1978: 36, fig. 14, 20d (mouth of Binge River, middle Fly River, 06°2.5'S., 140°5.0'E.)

Hexanematichthys acrocephalus (in part): Kailola, 1975: 41

Hexanematichthys latirostris: Liem & Haines, 1977: 25

DEFINITION

Jaw teeth strong and small, slightly depressible. Four patches of teeth across palate, vomerine ones smaller and always separated medially. Snout blunt or truncate; jaws strong, elevated at symphysis; mouth terminal. Eye small, 10-13 %HL; head broad, width 71-78 %HL. Barbels thin and short, 10-12 %SL; chin barbel bases well separated. No posterior rakers on first two gill arches; gill opening very wide. Adipose base as long as dorsal base; fin spines thick and rugose. A 21-22; total gill rakers (first arch) 20-22; total vertebrae 19+6+33. Fresh colouration olive to vivid blue, white below.

DESCRIPTION

D I,7. P I,10-11. A 20-22. GR (first arch) 20-22, of which 6-7 on upper limb. GR (last arch) 18-20. Number of vertebrae 55-58 (48-52 free).

Heavy-bodied fish, noticeably depressed anteriorly, compressed posteriorly. Head broad; predorsal profile straight to dorsal origin and not elevated at nape. Snout blunt, almost truncate. Mouth terminal, curved and broad, jaws strong, elevated slightly at symphyses. Lips thin along jaws, moderately developed at mouth corners; teeth entirely concealed when mouth closed. Nostrils small and rounded, anterior one directly in front of posterior one. Eye ovate and small, free from head skin, dorsolateral, situated short distance before mid-head length. Gill opening wide; broad, free margin to gill membranes.

Teeth small and sharp, strong, conical or needle-like, those on jaws slightly depressible. Premaxillary band of 5-6 irregular series, mandibulary band of 4-5 series, divided by edentulous space at symphysis. Teeth on palate arranged into transverse row of 4 oval, contiguous patches: inner (vomerine) pair separated by median space, half width of outer patches. Outer palatal tooth patches often develop backward extension in very large individuals. Palate completely smooth anteriorly, creased posteriorly with pair of long, thin ridges of epithelial tissue posteriorly above gill arches.

Head smooth anteriorly; exposed head shield striate and rugose, granular posteriorly. Dorsomedian head groove ends before supraoccipital process base; groove lanceolate, broader anteriorly, flanked posteriorly by striae. Supraoccipital process triangular, straight-sided, with low median keel. Humeral process smooth, long-based and heavily ossified anteroventrally; triangular shaft of process horizontal, extending 1/4-1/3 along pectoral spine. Axillary pore rounded and very small.

Short barbels very thin and wisp-like. Maxillary barbel extends 1-2 eye diameter's beyond eye, never as far as preopercular ridge; mandibulary barbel extends almost as far; mental barbel attains mid or hind eye margin. Chin barbel bases strongly staggered.

Gill rakers slightly shorter than gill filaments. Posterior face of first and second arches completely smooth, lacking rakers and papillae; 17-19 rakers along back of third arch. Low fleshy epithelial pad on posterodorsal aspect of 2nd arch.

Fin spines moderately stout, subequal, patterned with fine, longitudinal striae. Anterior spine margin granular with 3-4 low serrae towards tip; posterior margin with 8-9 low serrae (dorsal spine) and 15-18 stout serrae on pectoral spine. Short filament at tip of each spine. Longest dorsal ray 1.6-3 longer than last ray. Pectoral fin extends to below posterior of dorsal. Anal hind margin straight or slightly concave, longest ray 3-3.2 longer than last ray. Adipose fin moderately large, oblong or convex in outline, above middle of anal. Ventral narrow and failing to reach anal origin in males, broader-based and extending to about 4th ray in females; inner ventral rays in sexually mature females thickened, with fleshy pad. Caudal lobes well-tapered and narrow.

Caudal peduncle slender. Lateral line straight along most of its length, slightly arched anteriorly and curved dorsad at tail base. Vertical series of fine pores ascend from line over sides whilst short, diagonal, thin lines extend over lower sides.

Fresh colouration: Deep olive or vivid violet-blue above, cream to milky-white below; colours distinctly separated. Fins bluish charcoal grey, unpaired fins with narrow blackish margin. Maxillary barbels brown, other barbels cream.

Colour in preservative: Head and body dusky to dark brown above, dusky cream or ochre-coloured below. Fins mostly light brown; pectoral dark brown on upper surface; dorsal and caudal stippled dark brown; anterior anal rays and median ventral fin dark brown. Barbels brown; peritoneum pale.

DISTRIBUTION

NEW GUINEA: south-draining rivers. Upper, middle and lower Fly River (Roberts, 1978; Maunsell and partners, 1982), Lake Murray, upper Strickland River (Bebelubi) (D. Gwyther, 1984), Aramia River (Kyle and Ghani, 1982), Kikori River, Era, Wame, Purari and Vailala Rivers (Haines, 1979; pers. comm.).

BIOLOGY

Habitat: freshwater. Common to abundant in larger rivers (Haines, 1979; Maunsell and partners, 1982), extending into the lower rivers and rarely into the upper estuarine sections of deltas. Inhabits flooded creeks, lagoons, mainstream of rivers; in swift and still water. Water quality in some areas inhabited by "*A.*" *augustus* noted by Roberts (1978) was: pH 6.7-7.5, clear to turbid, blackish to brown or grey. In the Fly River, Maunsell and partners (1982) obtained "*A.*" *augustus* between about 230 and 850 km from Toro Pass, river elevation 0-40 m. P. Dwyer (pers. comm., 1989) found *augustus* restricted to the silt-laden sections of the middle-upper Strickland River.

Maximum size: 940 mm FL (Haines, 1979); achieves a weight of 16-20 kg. Maunsell and partners (1982) caught a 900 mm SL (1090 mm TL) specimen, and suspected the existence of larger fish because bent fish hooks were retrieved in areas where large "*A.*" *augustus* had been sighted.

Diet: A predaceous fish feeding mostly on fish and prawns. Maunsell and partners (1982), and Haines (pers. comm.) considered it one of the top fish carnivores in the Fly and Gulf rivers and deltas. Of 25 stomachs containing food, Haines recognised prawns in 9, crabs in 5, fish in 7, insects in 2 and mud, algae and detritus in 2 (size range of fish 5-94 cm FL). Roberts (1978) found only fish remains in 4 stomachs: of *Clupeoides papuensis*, *Nematalosa cf. papuensis* (= *N. flyensis*, in part), *Ambassis agrammus* and *Melanotaenia nigrans*. In 32 fish 475-1090 mm TL examined by Maunsell and partners (1982), 66.2% of stomachs contained fish, 22.3% macro-crustaceans (e.g. *Macrobrachium* spp.) and 10.6% aquatic insects and larvae (larvae only in smaller fish). In all but one of my specimens the stomach was empty: it contained fish and *Macrobrachium* fragments, aquatic insects and larvae.

Breeding: Haines (1979) recorded the minimum size at first maturity as 450 mm FL. Sexually mature individuals were caught in the Purari River system between October and January, and spawning probably continues into February. Males with mouth young were caught in the Era River in December (Haines, pers. comm.). During his Gulf rivers survey, Haines (1979) found that breeding individuals and juveniles were ubiquitous throughout the Purari River system, from mangroves to the Wabo-Kibi Creek area. Maunsell and partners (1982) suspected that breeding occurs locally in the middle Fly River because they caught mature and developing females (in July) but no incubating males and juveniles. These authors recorded ripe ovaries containing mature ova 10.4 mm diameter.

DISCUSSION

Haines (1979) and Kyle and Ghani (1982) misidentified this species as "*Hexanematichthys latirostris*".

"*A.*" *augustus* is most similar to "*A.*" species 7. Both taxa attain a large maximum size, have a small eye, short barbels and heavy head and body. However, they differ in head shape, mouth size, gill raker number and other characters (refer "*A.*" species 7 Discussion; Tables 27, 28, 33, 34). Other ariids which share the characters of no posterior rakers and 4 palatal tooth patches are "*A.*" *leptaspis* and "*A.*" *latirostris*. However, these taxa can be distinguished by the combination of colouration, barbel length, snout shape, eye size and predorsal profile.

"*A.*" *augustus* and "*A.*" *armiger* have in common characters such as barely depressible jaw teeth, large mandibulary pores and well-staggered chin barbels. However, relative barbel length, internostril width, dorsal spine length and thickness (Tables 27-30), fin filament length, and colouration readily separate these taxa.

TYPES

A. augustus is based on six types. The holotype is AMS I.27090-002 (ex USNM 217065). Three paratypes at the USNM are USNM 217067 (one specimen, 412 mm SL) and 217068 (2 specimens, 91 & 102 mm SL). The remaining paratypes are KFRS F.4681-01 (288 mm SL, ex USNM 217066) and AMS I.22460-001 (308 mm SL, ex USNM 217066) (wrongly labelled 288 mm).

Condition of types: I have examined all types, which are in good condition.

ETYMOLOGY

Latin, augustus = abbreviated, short. Refers to this species' very short barbels.

MATERIAL EXAMINED

SOUTHERN P.N.G. - 1, AMS I.27090-001 (ex USNM 217065), mouth of Binge River, 23 Nov. 1975, coll. T.R. Roberts, 342 mm SL (= HOLOTYPE); 1*, AMS I.22460-001 (ex USNM 217066), same data, 308 mm SL (= PARATYPE); 1, KFRS F.4681-01 (ex USNM 217066), 288 mm SL (= PARATYPE); 2, USNM 217068, near Massey Bakers Junction, Strickland River, Dec. 1975, 90 & 102 mm SL (= PARATYPES); 1, USNM 217067, ox-bow lake, 4 km downstream from Kiunga, coll. T.R. Roberts, 27 Oct.-19 Nov. 1975, 412 mm SL (= PARATYPE); 1*, AMS I.25997-001, billabong, mid Purari River, 5 May 1975, coll. A.K. Haines, 250 mm SL; 1*, NTM S. 12352-001, same data, 185 mm SL; 1, KFRS F.5624-01, Purari River, 1975, SL not noted; 1*, QM I.22652, Pie River, 7 Dec. 1974, coll. A.K. Haines, 188 mm SL; 1*, RMNH 30314, Era River, 9 Dec. 1975, coll. A.K. Haines, 224 mm SL; 1*, unreg., Wame River, 6 March 1975, coll. A.K. Haines, 232 mm SL; 3, unreg., Gwaimasi village, upper Strickland River, Aug. 1986-Nov. 1987, coll. P. Dwyer and M. Minnegal (dried skulls only), 160-186 mm length (ex specimens 490-570 mm SL).

6.6.12

"Arius" latirostris Macleay

(Figures 200, 201, 202, 203; Tables 37, 38)

Arius latirostris Macleay, 1884: 277, fig. (Goldie River, Papua) (in part)

Arius acrocephalus Weber, 1913: 543, 608, figs 20,21 (Sande [= Bibis] River; Regen Island and Alkmaar on Lorentz River; other Lorentz River locations)

Tachysurus acrocephalus: Fowler, 1928: 62

Tachysurus latirostris: Fowler, 1928: 62

Arius digulensis Hardenberg, 1936: 369 (middle Digoel River)

Hexanematichthys acrocephalus: Munro, 1958: 123

Hexanematichthys digulensis: Munro, 1958: 123

Hexanematichthys latirostris: Munro, 1958: 123

Hexanematichthys leptaspis: Boyden, Brown, Drucker and Tuft, 1975: 26

DEFINITION

Snout rounded to acute; interorbital flat or slightly concave; head shield margins often raised. Four patches of teeth across front of palate; with age, vomerine ones larger and gaps between patches reduced. No posterior rakers on first two arches (rarely up to 4 on second); arches with fleshy, crenulate epithelial pad posterodorsally (always on second). A 19-24; total gill rakers (first arch) 14-21; vertebrae 18-20+5-7+33-35. Eye moderate, 13-27 %HL. Maxillary barbel reaches pectoral base. Fresh colouration yellowish to dark green, iridescent bronze on sides; fin margins brown.

DESCRIPTION

D I,7. P I,10-12. A 19-24. GR (first arch) 14-21, of which 4-7 on upper limb. GR (last arch) 14-21. Number of vertebrae 53-54 (45-48 free).

Robust, moderately heavy-bodied fish with broad head. Predorsal profile straight except for slight depression at level of flat to concave interorbital (more pronounced in larger individuals); nape slightly elevated. Snout broadly rounded to acute, blunt and fleshy in juveniles. Mouth broad and slightly curved, subinferior (inferior in juveniles); 1/4 to 3/4 of premaxillary tooth band exposed when mouth closed. Nostrils ovate, anterior nostril directly before posterior opening. Eye rounded or ovate, free of head skin, lateral ethmoid slightly prominent. Eye dorsolateral, slightly before mid-head length. Gill opening wide, membranes united at moderately acute angle; free posterior margin broad.

Teeth small, sharp and conical, slightly depressible; embedded in spongy tissue. Premaxillary band with 9-10 series of teeth, increasing to 14-15 series with age; mandibulary band with 5-9 series of teeth, band divided at symphysis by narrow, edentulous space. Teeth on palate in four groups arranged transversely. In juveniles, patches well-separated, vomerine groups rounded and about half size of elongate outer groups; in adults, all patches about equal in size (or outer patches larger), rounded or square, gap between them reduced or absent. Palate smooth with two short, oblique ridges of epithelial tissue posteriorly before branchial chambers.

Head smooth anteriorly. Granules on head shield fine and close together, arranged in whorls laterally, replaced by rough striae medially. Shield rough or almost smooth in juveniles; anterolateral arms moderately pronounced. Dorsomedian head groove lanceolate, flat, narrow posteriorly and not reaching supraoccipital process base. Process triangular, basally very broad or narrow, straight sided, midline without definite keel. Rugose humeral process broad-based, triangular, moderately ossified anteroventrally. Process shaft blunt, nearly horizontal, extending 1/3 along pectoral spine. Axillary pore a small slit. Often a large oval depression apparent in body, approximating position of swimbladder.

Barbels moderately flat. Maxillary barbel reaches to above pectoral base or not as far. Mandibulary barbel extends to head margin. Mental barbel reaches to opposite hind eye margin. Chin barbels slightly staggered.

Gill rakers 1/2-2/3 length of opposing filaments. Rakers absent from posterior face of first arch, 0-4 on upper part of posterior face of second arch, 15-21 rakers on back of third arch. Low, fleshy, often medially excavated pad of tissue posteriorly on upper limb of first arch and large, thick, fleshy pad or lobe with crenulate margin, on upper limb of second arch.

Fin spines moderately thick, with fine longitudinal striae. Anterior margin rough to granular; few antrorse serrae near tip of dorsal. Low retrorse serrae extend halfway along posterior (trailing) edge of dorsal, and from 6-7 (juveniles) to 25 (adult) short, stronger serrae line inner pectoral spine margin. Spines tipped with short filament. Last ray of dorsal 2.6-3.3 shorter than longest ray. Pectoral fin extends to below last dorsal rays. Ventral narrow-based in males, scarcely reaching anal origin; broad-based in females, reaching 2nd-6th anal ray. Sexually mature females have thick pad of epithelial tissue on upper aspect of 5th and 6th rays. Adipose fin well-rounded, opposite middle to posterior half of anal. Anal margin concave, last ray 2.6-3.5 shorter than longest ray. Caudal fin broad at base, lobes moderately broad, upper slightly the longer.

Caudal peduncle moderately stout. Lateral line oblique anteriorly and turned dorsad at caudal base. Short lines and vertical series of pores diverge from lateral line along its length.

Fresh colouration: Uniform dark green, yellowish green to purplish grey above, sides and belly creamy white; head, back and upper sides with bronze sheen. Fins green-brown; brown margin to dorsal and caudal fins, ventral and pectoral fins dusky green above.

Colour in preservative: Dark brown above, dusky or brown on sides, cream to dusky yellow-orange below. Fins tan or brown; dark margin to dorsal and caudal; upper aspect of pectoral, ventral, anterior anal and all of adipose fins, dark brown. Barbels dark brown. Peritoneum pale or light grey.

DISTRIBUTION

NEW GUINEA: south draining rivers. Kamundan River (Vogelkopf Peninsula), upper Lorentz River system (Sande, Lorentz), middle Digoel River, upper and middle Fly River system (Ok Tedi, Fly, Palmer, Binge), upper Strickland River (Bebelubi, Igibira), upper Purari River system, upper Vailala River (Lohiki, Ororo), Kubuna River, Laloki River system (Goldie, Brown, Laloki).

BIOLOGY

Habitat: "*A.*" *latirostris* and "*A.*" *taylori* Roberts are the only ariids present and abundant in highland and upper reaches of rivers in New Guinea. The fresh waters in these tributaries, streams and rivers are fast-flowing and often turbulent, turbid or clear in quality. Maunsell and partners (1982) recorded "*A.*" *latirostris* at elevations between 25 to 300 m and from 750 to 1,000 km from Toro Pass. P. Dwyer (pers. comm., 1989) found *latirostris* more frequent in large, clear streams draining back-swamps (upper Strickland River).

Maximum size: 447 mm SL (Roberts, 1978); 620 mm TL (Maunsell and partners, 1982). "*A.*" *latirostris* usually attains only 3 kg weight (Gwyther, 1984).

Diet: "*A.*" *latirostris* is omnivorous. Roberts (1979) noted that stomachs were often crammed with a variety of food, terrestrial arthropods, aquatic insects, higher plants and debris predominating. Maunsell and partners (1982) reported that the diet included fruit (*Ficus* spp.), crustacea (*Macrobrachium*, *Potamon* spp.), worms, terrestrial and aquatic insects and terrestrial plants (*Ficus*, *Pandanus* spp. being most common). Haines (1979) found that "*A.*" *latirostris* occupied the trophic niches of frugivore and insectivore (part omnivore) in the upper Purari system: of 30 stomachs he examined which contained food, prawns were in 4, crabs in 1, insects in 13, fruit in 24, mud, algae and detritus in 2, plant material in 8. *Ficus* fruits had been consumed in great quantity by individuals Haines captured in the upper Vailala River. Stomach contents of my specimens contained similar material to that noted above.

Breeding: In the Purari system, breeding occurs in January (late dry season). The smallest sexually mature individual obtained by Haines (1979) was 330 mm FL. Maunsell and partners (1982) caught juveniles and females with ripe ova in the Ok Ma (Ok Tedi tributary) in late June. Based on this and my material, it appears that breeding takes place from the end of the dry well into the wet seasons (although the west Papua and Gulf seasons are not concurrent). No information on fecundity is available.

As with some other Australo-Papuan ariids, problems in species recognition are reflected in paucity of accurate spawning information.

DISCUSSION

Although I did not examine the type of "*A.*" *digulensis* Hardenberg, I follow Roberts'(1978) who examined types of both nominal species and concluded that this species is a synonym of "*A.*" *acrocephalus*.

There are five specimens in the Australian Museum labelled "*Arius latirostris*", 4 of them as "syntype": AMS I.9072, I.9073, I.9074 and I.9127. The fifth specimen (AMS I.13398) was also collected by Goldie but not included in the type series. I have examined all specimens, and find that the I.9127 syntype (139 mm SL) is a specimen of "*Arius*" *graeffei* Kner & Steindachner. Macleay's four large specimens are clearly conspecific with *acrocephalus* and *digulensis*. The head shape is similar and meristics agree although the expanded supraoccipital process base of one of the syntypes is beyond the size exhibited by all other material I have seen.

Further evidence that *latirostris* is the correct name for this species is based on their size, *viz*.: only "*A.*" *acrocephalus* but no smaller *latirostris sensu* Macleay have ever been collected, even from the type locality. Thus, Berra *et al*.'s (1975) specimens of "*latirostris*" redetermined as "*acrocephalus*" by Roberts (1978) were correctly named. The regular position of types (both names) on scattergrams also supported the proposed synonymy (e.g. figs 166, 167, 168, 169).

Contra Roberts' (1978) description, I do not recognise a "pronounced nuchal hump" in my material and rakers are occasionally present on the posterior upper limb of the second gill arch.

"*A.*" *latirostris* is replaced downstream by "*A.*" *leptaspis* (Bleeker) (Roberts, 1978; Haines, 1979) and "*A.*" *berneyi* Whitley

(Maunsell and partners, 1982). Nevertheless, "*A.*" *latirostris* appears to have a patchy distribution. It is rare in middle sections of the Fly River and in the Purari River, yet common and the only ariid caught by Haines in the Vailala.

All of Haines' (1979) "*Hexanematichthys latirostris*" material is referable to "*A.*" *augustus* Roberts, as are Kyle and Ghani's (1982) from Lake Murray and the Aramia River. Kailola's (1975) specimens of "*A.*" *acrocephalus* are of "*A.*" *graeffei* (KFRS F0085) and "*A.*" *augustus* (KFRS F03768), but the "*H.* *leptaspis*" material from Kiunga and Ningerum (Kailola, 1975: 42) are specimens of "*A.*" *latirostris*. Hardenberg's (1941) 33 cm TL specimen of *Arius latirostris* from the lower course of the Digoel River (which I have not seen) probably does not belong to that species because of the stated locality, lower anal count, shorter barbels and small eye. It could refer to "*A.*" *leptaspis*.

Munro's (1964) listing of the species is partly erroneous, as he indicated that it inhabits fresh, salt and brackish water.

"*A.*" *latirostris* is most similar to "*A.*" *taylori* and "*A.*" *leptaspis*. Comparison with *taylori* has been discussed under the *taylori* presentation. A stepwise discriminant function analysis revealed functions which together always enabled separation of *latirostris* and *leptaspis* in the robust jackknife classification. These are: GR count (first arch) + supraoccipital process base width/process length ratio + dorsal spine/HL ratio + predorsal length as %SL + maxillary barbel length/SL ratio (fig. 204) + head width as %SL (fig. 205) + anal base length as %SL + caudal peduncle length as %SL (fig. 206) (Z function: Appendix C). "*A.*" *latirostris* also has a shorter head than does *leptaspis* (fig. 207), a larger eye (fig. 208), smaller mouth gape (fig. 209) and longer adipose fin base length (fig. 210). The head shape (especially prominent snout, depressed interorbital and exposed jaw teeth), broader palatal tooth patches, and fresh colouration also distinguish latirostris from leptaspis.

Other Australo-Papuan ariids similar to latirostris are "A." species 2 and "A." midgleyi. Although they have a comparable number of gill rakers (fig. 211), species 2 can be distinguished from latirostris by its larger eye, wider mouth, longer barbels and head shield form; and midgleyi can best be distinguished on anal count (fig. 212), mouth width, eye size and maxillary barbel length.

TYPES

Arius latirostris was based on four specimens. One of these belongs to "A." graeffei (see Discussion). The remainder are: AMS I.9072 (450 mm SL); AMS I.9073 (445 mm SL); AMS I.9074 (435 mm SL). Macleay's stated length of "20 inches" must have refered to TL for one of these specimens (or the largest) but there is no indication of which.

Arius acrocephalus was based on 7 cotypes. They are: ZMA 111.087 (1 specimen, 96 mm SL, 117 mm TL); ZMA 111.088 (2 specimens, 75 and 91 mm SL); ZMA 111.089 (1 specimen, 226 mm SL, 275 mm TL); ZMA 111.090 (1 specimen, 193 mm SL, 235 mm TL); and AMNH 9514 (120.3 mm SL, 148 mm TL). I have no number and SL for the MZB syntype.

Arius digulensis is based on one specimen, ZMA 110.781 (520 mm TL).

Condition of types: The AMNH specimen of acrocephalus is in fair condition, most fins intact.

The AMS specimens of latirostris are dark brown, rigid, and somewhat shrunken. All are eviscerated, the belly slit from pectoral girdle to ventrals. I.9072 is bent from its mid-length and the upper caudal lobe is snapped across, part lost; and I.9073 has lost 2/3 of both caudal lobes.

ETYMOLOGY

Latin, latus = side; rostrum = snout. Refers to the prominent, broadly triangular snout.

MATERIAL EXAMINED

SOUTHERN IRIAN JAYA - 1*, AMNH 9514, Lorentz River, 1909, 120 mm SL (= SYNTYPE of A. acrocephalus Weber); 1*, AMNH 9532, Lorentz (Noord) River, 16 Sept. 1909, coll. H.A. Lorentz, 189 mm SL;
2*, WAM P.27869-003, trib. of Kamundan River, Vogelkop Peninsular, 18 Nov. 1982, coll. G.R. Allen & W. Tins, 63 & 63.3 mm SL.
SOUTHERN P.N.G. - 1*, AMS I.9072, Goldie River, coll. W. Goldie, 1883, (approx.) 450 mm SL (= SYNTYPE); 1*, AMS I.9073, same data, (approx.) 440 mm SL (= SYNTYPE); 1*, AMS I.9074, same data, (approx.) 435 mm SL (= SYNTYPE); 1*, AMS I.13398, Goldie River, coll. W. Goldie, no date, pres. to AMS by MAMU in 1914, 312 mm SL; 2*+2, AMS I.17077-001 (in part), Laloki River, 15 mi. N of Port Moresby, 20 June 1970, coll. B.B. Collette, 76-88 mm SL; 1*, AMNH 14011, Kubuna River, central Papua, Dec. 1933, coll. A.L. Rand & R. Archbold, 146 mm SL;
1*, AMNH 14003, Kubuna River, Dec. 1933, coll. A.L. Rand & R. Archbold, 234 mm SL; 1*, AMNH 13995, Kubuna River, Dec. 1933, coll. A.L. Rand & R. Archbold, 280 mm SL; 2*, KFRS F.4213-06, Ningerum, Ok Tedi, Aug. 1974, coll. C.R. Boyden, B.E. Brown, R.F. Drucker & S.J. Tuft, 74 & 119 mm SL (119 mm specimen also as: AMS I.30114-001);
5*, AMS I.22459-001 (ex USNM 217060), side-channel of Ok Tedi mainstream

7 km NNE of Ningerum, 4 Nov. 1975, coll. T.R. Roberts, 100-150 mm SL; 1*, KFRS F.4333-01, Laloki River, Papua, 27 March 1973, coll. J. Timothy, 90 mm SL (also as: AMS I.30113-001); 1*, QM I.22651, billabong, mid-Purari River, 10 May 1975, coll. A.K. Haines, 287 mm SL; 1*, KFRS F.5520-01, Kibi Creek, Wabo damsite, 18 Jan. 1977, coll. A.K. Haines, 272 mm SL; 1*, AMS I.25991-001, Kuku Creek near Bevan Rapids, 12 May 1975, coll. A.K. Haines, 385 mm SL; 1*, NTM S.11912-001, Lohiki Creek, upper Vailala River, 23 April 1975, coll. A.K. Haines, 290 mm SL; 6*, unreg., Ok Tedi at Ningerum, 13 Oct. 1986, coll. K. Hortle, 99-155 mm SL; 2*, UMMZ 214016, Ok Tedi at Ningerum, 5 Aug. 1986, coll. K. Hortle, 88.5 & 113 mm SL; 12, AMNH 58712, same data, SL not noted; 20, RMNH 30323, same data, SL not noted; 30, CSIRO H1682-01, same data, 61-113 mm SL; 4, MZUSP unreg., same data, 69-89 mm SL; 5, KFRS F.4616-01 (ex USNM 217060), Ok Tedi near Ningerum, Nov. 1975, SL's not noted; 3, KFRS 0.4973-05, Ok Ma, June 1981, SL's not noted; 3, unreg., Gwaimasi village, upper Strickland River, Aug. 1986-Nov. 1987, coll. P. Dwyer & M. Minnegal, (dried skulls) 68-155 mm SL (no stated SL).

6.6.13

"Arius" leptaspis (Bleeker)

(Figures 213, 214, 215, 216; Tables 39, 40)

Hexanematichthys leptaspis Bleeker, 1862: 27, pl. 65, fig. 2 (Southwest New Guinea)

Hexanematichthys leptocassis (non Bleeker, 1861): Bleeker, 1863: 72. Error.

Arius leptaspis: Weber, 1913: 544 (in part)

Tachysurus leptaspis: Fowler, 1928: 62 (in part)

Arius australis (non Günther): Taylor, 1964: 80,81

DEFINITION

Fine teeth in four patches across front of palate, outer patches slightly larger. Mouth broad, 35-58 %HL, head broad, 67-83 %HL. Head shield granular, very extensive; dorsomedian head groove ends well before supraoccipital process base. Eye small, lateral, 10-23 %HL. No posterior rakers on first two gill arches; gill openings wide; barbels moderately long, maxillary barbel reaches level of supraoccipital process at least, 23-51 %SL. A 16-22; total gill rakers (first arch) 13-22; vertebrae 20-22+4-6+26-28. Fresh colouration blue to grey to bronze with vertical series of golden spots along body.

DESCRIPTION

D I,7. P I,9-11. A 16-22. GR (first arch) 13-22, of which 4-7 on upper limb. GR (last arch) 13-23. Number of vertebrae 53-56 (47-49 free).

Body robust, often stocky and thick anteriorly, slender and tapered posteriorly. Predorsal straight, slightly convex at level of operculum and before dorsal; interorbital flat. Snout broad and curved, sometimes slightly truncate; lips thin to moderately thick, especially at mouth corners. Shallow, crescentic groove often prsent on dorsum of snout between nostrils (juveniles); anterior of head (often to breast, shoulder) scattered with numerous fine papilla-like structures in larger fish. Jaws strong, often slightly elevated at symphysis; mouth subterminal, gape very broad and strongly curved or more transverse; teeth not visible when mouth closed. Nostrils rounded, posterior nostril slightly lateral. Eye small and rounded, free of head skin; situated dorsolaterally, (well) before mid-head length; just visible from above. Gill opening wide, membranes meeting ventrally at moderately acute angle; free posterior margin broad.

Teeth in jaws very fine and sharp, depressible; embedded in spongy tissue. Premaxillary teeth in broad band of 5-9 irregular series; lower jaw band of 4-6 series, band divided at symphysis by narrow, edentulous space. Teeth on palate stronger, more conical, non-depressible; in four oval-rounded patches in line across front of palate. Vomerine patches separated at midline by narrow space (all ages); outer patches slightly larger than inner patches. Palate smooth, two low ridges (more developed in juveniles) of epithelial tissue posteriorly before branchial chambers.

Head shield often concealed by thick skin; very extensive, rugose to very granular. Granules broad and low; striae border dorsomedian head groove posteriorly, granules before supraoccipital process slightly raised. Dorsomedian head groove shallow to moderately deep, lanceolate, as narrow slit posteriorly. Groove fails to reach process base by approximately one eye diameter in juveniles, ends long before base in adults: to opposite eye hind margin or preoperculum. Supraoccipital process not keeled in adults, sides straight to slightly convex. Triangular humeral process smooth to moderately granular, heavily ossified anteroventrally. Process shaft oblique, acute, reaching 1/3 distance along pectoral spine. Axillary pore very small and rounded.

Barbels more or less flattened. Maxillary barbel can extend beyond dorsal base (juveniles), usually to opposite supraoccipital process. Mandibulary barbel reaches to or beyond pectoral base. Mental barbel reaches from just past eye (adults) to pectoral base (juveniles). Chin barbels moderately staggered.

Gill rakers slender, 1/2-2/3 length of opposing filaments. No rakers along posterior face of first two arches; 13-20 along third arch. Low to moderately developed, crenulate pad of epithelial tissue posterodorsally on second arch.

Fin spines moderately stout, not long. Anterior spine margins smooth to rugose, serrate distally; posterior margin with very low, short serrae: 6-11 along dorsal margin; 8-20 along pectoral. Longest dorsal ray 1.3-3.2 longer than last ray. Pectoral extends to below dorsal fin. Ventral in males slender, usually failing to reach anal fin origin. Ventral in females broader, attaining anal origin up to 8th anal ray; inner rays thickened to form broad pad in sexually mature fish. Adipose fin moderately high, above middle of anal. Anal margin concave, last ray 2.4-3.7 shorter than longest ray. Caudal lobes short and broad, tapered posteriorly.

Caudal peduncle moderately deep. Lateral line straight, elevated anteriorly and at tail base. Fine oblique lines emanate from line along its length (more dense anteriorly); and vertical series of pores cross upper sides.

Fresh colouration: Body dark bluish, green or grey, dark brownish grey, sides and back burnished bronze or coppery above; white, light grey or golden below; colours clearly separated. Series of vertical rows of iridescent, widely-spaced, bright golden spots along body from head to tail base. Fins dusky; caudal charcoal, sometimes with distinct, white posterior margin.

Colour in preservative: Blackish, charcoal, brown, dusky tan or ochre-coloured above, yellow, fawn, creamy to white, sometimes stippled dusky below. Fins dusky or dark grey, upper aspect of pectoral and ventral brown; caudal charcoal or dark brown, with white margin (in Australian material). Barbels brown or dusky. Peritoneum pale.

DISTRIBUTION

NEW GUINEA: south-draining rivers and coastal waters; widespread. Aru Islands; Lorentz River, Digoel (Hardenberg, 1941), middle-lower Fly River, middle-upper Strickland River (Gwyther, 1984), Aird, Newbury and Kikori Rivers, Purari River delta to Bevan Rapids, Gulf of Papua, Vailala River; associated coasts.

AUSTRALIA: north-draining rivers and coastal waters; widespread. Most river systems along northern Australia including Wyndham and King River, Finniss, Mary, Alligator Rivers, Roper River system, Wearyan and Foelsche Rivers, McArthur, Flinders, Gilbert, Mitchell, Fitzroy River system, Edward, Chapman and Archer Rivers.

BIOLOGY

Habitat: Rivers, lakes, lagoons and tributaries; inshore, turbid coastal waters; saline to freshwater. Haines (1979) found this species abundant in the lower mangrove areas of main rivers and branches, and common in the freshwater/tidal zones. Roberts (1978) collected specimens from sluggish, swampy streams, clear to turbid water, pH 6.1-7.4, 31.7°C, and tidal water. P. Dwyer (pers. comm., 1989) reported *leptaspis* far more common in large, clear water streams draining swampy areas (middle-uppper Strickland). Midgley (1979-84) recorded water quality from areas where "*A.*" *leptaspis* was collected as clear to slightly turbid, surface temperature 18.5-29°C, pH 6.2-8.4, still to moderately flowing. Dissolved oxygen ranged from 0.1-9.7 mg/l in surface waters and 0.2-7.4 in bottom waters (Bishop *et al.*, 1980; 1986); pH at surface from 4.8-9.1, turbidity from very clear to very turbid and preferred bottom substrate of mud and clay, then sand substrate.

Maximum size: 710 mm TL (Maunsell and partners, 1982); 640 mm SL; 8.45 kg (P. Dwyer, pers. comm.); more than 10 kg (D. Gwyther, pers. comm.).

Diet: Omnivorous and opportunistic (Bishop *et al*., 1980), food items including insects, *Pandanus* fruit, crustacea, mud and detritus, terrestrial and aquatic insects, fish, bivalves, plants (leaves, twigs, grass, figs), prawns, loose scales (often in large proportions). Bishop *et al*. (1980) observed that the relative importance of dietary items fluctuated with the seasons and therefore food availability. Stomachs of my specimens contained loose scales, few small fish, seeds, beetles, mud and detritus, fruit, worms, prawn fragments. Haines (1979) recorded the following items from 124 food-containing stomachs: prawns in 40, crabs in 48, fish in 5, insects in 13, fruit in 32, other plant material in 7, mud, algae and detritus in 10, parts of a rat, crustacea, reptile egg and a snake in 5.

Breeding: Mature females and brooding males aggregate at mouths of backwaters and lagoons (Maunsell and partners, 1982; K. Hortle, pers. comm., 1986), with a general movement into estuaries for spawning (Haines, 1979). T. Davis (pers. comm, 1981) collected 38-46 mm SL juveniles from low salinity water near estuaries in May. Midgley (pers. comm.) has collected spawning and brooding *leptaspis* in "freshwater of the Fitzroy River system many hundreds of km inland". They appear to spawn all year round (in New Guinea), Haines having collected brooding males and mouth young in November, December, January and May; although the peak breeding period is between October and December. The spawning period in Australia is shorter, between the mid-late dry season to mid-wet. Numbers of young being brooded ranged from 10-50 in the Purari and Kikori regions, and fecundity of northern Australian fish ranged from 26-70, average of 42 per ovary (Bishop *et al.*, 1980). Size at first maturity is 260-270 mm FL (Haines, 1979; Bishop *et al.*, 1980). These authors estimated that fish at the end of their second year may be ready to spawn. The sex ratio of mature fish is between F3-4: M1.

DISCUSSION

Bleeker (1863) compared "*A.*" *leptaspis* with Richardson's (1845) *vertagus* and *venaticus*. Taylor's (1964) specimens of *australis* Günther (USNM 173571) are all referable to *leptaspis*. Two of his specimens of "*A. leptaspis*" (USNM 173565) are of *midgleyi* Kailola and Pierce. Some of Pollard's (1974) specimens of "*A. leptaspis*" are specimens of *graeffei* (e.g. AMS I.16827-001). The maximum size of more than 1m and 10 kg Pollard recorded for this species refers instead to "*A.*" *midgleyi*. Lake (1971) was influenced by Taylor (1964), and grouped all northern Australian riverine ariids except *berneyi* under the name "*Hexanematichthys leptaspis*". Kailola (1975) misidentified two specimens of *leptaspis* from Baimuru as *digulensis* Hardenberg.

Herre (1953) recorded *A. leptaspis* from Borneo. W.N. Eschmeyer (CAS) kindly sent me Herre's specimens (CAS(SU) 32709) from the Tawao River in north Borneo, which all belong to *A. sagor* (Hamilton-Buchanan).

Haines (1979) and Roberts (1978) observed that "*A.*" *leptaspis* replaces "*A.*" *latirostris* Macleay downstream, and that the two species appear to occupy the same ecological niche.

There is some morphological distinction between *leptaspis* populations of New Guinea and Australia. The former have longer barbels (fig. 217), larger eye (fig. 218), more exposed head shield and darker body colouring *cf.* fish of comparable size from Australia - which also have a stockier body and white caudal margin. Some meristic difference is also revealed in the spread of frequencies (figs 219, 220). More formal recognition of these differences (e.g. as subspecies), would require many more specimens and study with techniques not used here. Moreover, the influence of environmental factors on the phenotype is unknown.

"*A.*" *leptaspis* is similar to "*A.*" *midgleyi*, "*A.*" *latirostris*, and "*A.*" species 2. Comparison with these taxa is given under their respective presentations (and in Tables 37-40, figs 204-210, 224-227, 234-237). These four taxa can all be distinguished from the morphologically similar "*A.*" *graeffei* and "*A.*" *berneyi* largely on the absence/presence of posterior gill rakers.

TYPES

Hexanematichthys leptaspis: This species is based on one specimen, RMNH 3060, 204 mm SL (260 mm TL: Bleeker, 1863).

Condition of type: fair. Body soft. Short slit along middle of abdomen; skin sloughed off along body sides, part of branchiostegal and gill cover damaged on RHS. All fin spines broken; dorsal spine broken away from dorsal buckler; all fin rays undamaged, upper caudal lobe bent.

ETYMOLOGY

Greek, *leptos* = slender, fine, thin, peeled. Bleeker gave no indication why he chose this name.

MATERIAL EXAMINED

SOUTHERN IRIAN JAYA - 1*, RMNH 3060, SW of New Guinea, coll. H. Müller, 204 mm SL (= HOLOTYPE); 1*, RMNH 28809, Digoel River N of Tanah Merah,

Juveniles of these two taxa appear almost identical. However, although caudal peduncle length and head length are very similar in *leptaspis* and *latirostris*, characters such as head width, eye diameter, size of palatal tooth patches and particularly head shape, consistently distinguish these taxa at all growth stadia.

13 April 1955, coll. M. Boeseman, 350 mm SL; 2*, ZMA 115.066 (in part), lower course of Lorentz (Noord) River, 5-17 Sept. 1909, coll. H.A. Lorentz, 181 & 237 mm SL; 2*, RMNH 28808, Digoel River betw. Tanah Merah & Tjantang Okiba, 14 April 1955, coll. M. Boeseman, 370 & 438 mm SL; 1*, RMNH 28813, Digoel River betw. Tanah Merah & Tjantang Okiba, 13 April 1955, coll. M. Boeseman, 307 mm SL; 2*, RMNH 28810, same locality, 14 April 1955, coll. M. Boeseman, 372 & 375 mm SL; 1*, RMNH 28812, Digoel River at Tanah Tinggi, 10-11 March 1956, coll. M. Boeseman, 350 mm SL; 1, MZB 106, south New Guinea, 1907, 215 mm SL; 5, WAM P.29978-001, Kali Tujuh, Bintuni, 13 April 1989, coll. G.R. Allen, 60-123 mm SL; 2, WAM P.29973-006, Bintuni River, 5 April 1989, coll. G.R. Allen, 45 & 71 mm SL; 1, WAM P.29951-001, Bintuni Bay, 17 March 1989, coll. G.R. Allen, 220 mm SL.

SOUTHERN P.N.G. - 1*, AMS I.22458-001 (ex USNM 217051), oxbow lake off upper Fly River 4 km from Kiunga, 27 Oct.-19 Nov. 1975, coll. T.R. Roberts, 435 mm SL; 1*, AMS I.22462-001 (ex USNM 217052), Agu River mouth, middle Fly River, 25 Nov. 1975, coll. T.R. Roberts, 324 mm SL; 1*, AMS IB.7034, Mawa, Lake Murray, 12 Nov. 1963, coll. H. Cogger, 205 mm SL; 1, AMS IB.7033, Mawa, Lake Murray, Nov. 1963, 190.5 mm SL; 2, KFRS F.5606-01, Tureture village, W. Papua, 1971, SL not noted; 2, KFRS F.5626-04, Sagero, N bank of Daru Island, Sept. 1988, 105 & 180 mm SL; 1, unreg., W. Tirere village, Daru Island, April 1988, 380 mm SL; 1, ZMA 119.483, Balimo area, June 1976, 83 mm SL; 1*, unreg., Mira Point, Purari R. delta, 6 Dec. 1974, coll. A.K. Haines, 129 mm SL; 1*, UMMZ 214017, same data, 129 mm SL; 1*, LACM 44932-1, Era River, Dec. 1975, coll. A.K. Haines, 185 mm SL; 1*, RMNH 30319, Kuku Creek, Bevan Rapids, Purari River, 12 May 1975, coll. A.K. Haines, 280 mm SL; 1*, USNM 288550, Gulf of Papua, May 1975, coll. A.K. Haines, 127 mm SL; 1*, unreg., Aird Hills, 10 Dec. 1974, coll. A.K. Haines, 270 mm SL; 1*, KFRS F01106, Balimo area, Nov. 1967, 115 mm SL; 1*, AMS IA.7277, upper Fly River, no date, coll. S. Campbell, 295 mm SL; 1*, KFRS F.4303-44 (in part), Galley Reach, 27 July 1972, coll. L.F. Reynolds, 171 mm SL; 1*, WAM P.27815-016, 30 km upstream of Oriomo River mouth, 27 Sept. 1982, coll. G.R. Allen & J. Paska, 97 mm SL; 1*+2, KFRS F.5523-01, Baimuru, 30 March 1974, coll. L.F. Reynolds & K. La'a, 71-105 mm SL; 3*+2, unreg., Akoma (Baimuru area), Aug. 1975, coll. A.K. Haines, 99-320 mm SL; 1*, QM I.23773, Purari River delta, 1975, coll. A.K. Haines, 235 mm SL; 1*, LACM 44928-1, Ihu market, 20 Nov. 1974, coll. A.K. Haines, 275 mm SL; 1*, unreg., Ravikoupara, 20 Jan. 1975, coll. A.K. Haines, 104 mm SL; 3, KFRS F04098, Matupe River at Murua, Oct. 1971, 179-257 mm SL; 1, KFRS F04101, Tauri River SE of Malalaua, Oct. 1971, 270 mm SL; 1, KFRS F04100, billabong on Varoi River, Oct. 1971, 248 mm SL; 1, KFRS F0988, Kempwelch River at Kapogere, Sept. 1967, 270 mm SL; 2, KFRS F03318, mouth of Kempwelch River, Nov. 1970, 196 & 244 mm SL; 3*, unreg., Gwaimasi village, upper Strickland River, Aug.1986-Nov. 1987, coll. P. Dwyer & M. Minnegal (dry skulls only), 78-162 mm (max. SL not stated).

QUEENSLAND - 1*, QM I.14919, Peach Creek, Archer River system, 26 May 1973, 144 mm SL; 1*, QM I.10423, lagoon 10 mi. W of Rokeby, 5 June 1973, 126 mm SL; 1*+1, AMS I.17969-002, O'Shannessy River near Riversleigh Station, 20 May 1969, coll. J.S. Lake, 146 & 147 mm SL; 1, AMS I.21869-003, Wenlock River at Moreton, Sept. 1972, 238 mm SL; 1*, unreg., Edward River township, Chapman River, 12 Dec. 1980, coll. D.B. Carter, 220 mm SL; 1*, unreg., upstream of Chapman River mouth, 18 Nov. 1980, coll. D.B. Carter, 280 mm SL; 1*, NHRM A88/190428.4229, Chapman River, Oct. 1980, coll. D.B. Carter, 198 mm SL.

NORTHERN TERRITORY - 1, AMNH 51646, Mary River at Pine Creek-Oenpelli Road crossing, May 1969, 172 mm SL; 3*, NTM S.12355-001, Jaja billabong, Jabiru, Jan. 1979, coll. R. Tait, 67-69 mm SL; 1*, UMMZ 215076, Jabiru, Jan. 1979, coll. R. Tait, 131 mm SL; 1*, not kept, Alligator Rivers region, May 1979, coll. K. Bishop, 115 mm SL; 12, USNM 173565, East Alligator River, Oct. 1948, 137-395 mm SL; 2*, NTM S.12356-001, Magela Creek, East Alligator River, 6-8 May 1979, coll. K. Bishop, 137 & 137 mm SL; 3*, not kept, same data, 112-133 mm SL; 1*, SAM F.3865, Magela Creek, 4 June 1973, coll. J. Glover & M. Giles, 121 mm SL; 1*, AMS I.26970-001, Magela Creek, East Alligator River, 9 Aug. 1978, coll. K. Bishop, 256 mm SL; 3, AMS I.18089-010, Magela Creek, Sept. 1972, 90-100 mm SL; 4, AMS I.16826-002, Indium Billabong off Magela Creek, June 1973, 125-172 mm SL; 32, NTM S.11405-004, Police Water Hole, Sept. 1980, 80-210 mm SL; 1, AMS I.2000-007, Finniss River, May 1974, 310 mm SL; 2, AMS I.20007-006, Finniss River, May 1974, 300 & 330 mm SL; 1*+1, AMS I.20003-002, Finniss River, 28 May 1974, coll. N. Williams, 400-285 mm SL; 1*, unreg., McArthur River, 5 Aug. 1975, coll. H. & M. Midgley, 159 mm SL; 1, QM I.16742, McArthur River, June 1975, head only: 112 mm HL; 1, AMS I.26854-006, Georgetown Billabong, June-July 1972, 385 mm SL; 1*, AMS I.27420-001, Long Harry's Billabong, Jabiru, 14 May 1980, coll. B. Rooney, 174 mm SL; 2*, NTM S.12354-001, Long Harry's Billabong, Jabiru, 13 May 1980, coll. B. Rooney, 325 & 345 mm SL; 3*, not kept, same data, 194-430 mm FL; 2*, NTM S.10425-013, Scotts Creek, Adelaide River distr., 21 April 1982, coll. H. Larson & party, 183 & 184 mm SL; 11, CSIRO unreg., Mining Hut Creek, Kapolga, March 1978, 38-87 mm SL; 1, NTM S.11698-001, Scott's Creek, May 1985, 170 mm SL; 1, NMV 7703, Abraham's Lagoon, July 1911, 116 mm SL; 1, NMV 7704, same data, 131 mm SL; 1, NMV 7705, same data, 127 mm SL; 1, NMV 7706, same data, 112 mm SL; 1, not kept, Cooinda, Oct. 1985, 440 mm SL (det. on photo, details supplied);

2, NTM S.12597-001, Canon Hill, Nov. 1979, 37.4 & 37.7 mm SL (mouth juveniles); 1, QM I.16747, Limmen Bight River, Sept. 1979, upper jaw only, SL not stated; 1, NTM S.11153-002, Mainoru River, Sept. 1979, head only: 113 mm HL, SL not stated; 2, QM I.16731, Roper River, Sept. 1979, heads only: 94 & 96 mm HL; 12, USNM 173571, Arnhem Land, Oct. 1948, 187-415 mm SL.

WESTERN AUSTRALIA - 1*, AMNH 51645, King River, 6 May 1969, coll. J. Nelson, H. Butler & D. Rosen, 170 mm SL; 1*, WAM P.25707-001, Goosehill Creek, Ord River area, 3 June 1973, coll. W.A. Dept. Fish & Fauna, 218 mm SL; 1*, CAS 60488, King River, 15 km from Wyndham, 15 July 1981, coll. L. Turner, 182 mm SL.

6.6.14

"Arius" midgleyi Kailola & Pierce

(Figures 221, 222, 223, 229; Tables 37, 38)

Arius leptaspis: Taylor, 1964: 81 (in part)

Arius species 1: Allen, 1982: 30,31

Arius midgleyi Kailola & Pierce, 1988: 75, figs 1-8 (Wickham Gorge, Victoria River)

DEFINITION

Sleek body; jaws strong, upturned slightly at symphyses, mouth broad; snout truncate in profile; head oblong, its width averaging 66% HL. Supraoccipital process narrow with parallel margins. Numerous fine, sharp teeth on palate in transverse band of four oblong groups.

No rakers on posterior aspect of gill arches; total gill rakers (first arch) 10-17. A 16-19; vertebrae 20+7-8+28-29. Barbels thin and short, rarely reaching beyond pectoral base; less than 25% SL.

Two subspecies of "A". midgleyi are recognised: a western and an eastern form. They are distinguished from each other by gill raker number and eye size. As other morphological features examined do not differ between these taxa, one description is presented here.

DESCRIPTION

D I,7. P I,9-11. A 16-19. GR (first arch) 10-17 of which 3-6 on upper limb. GR (last arch) 11-19. Number of vertebrae 55-56 (47-50 free).

Body robust, moderately compressed; lateral head profile triangular and narrow. Predorsal profile straight. Snout broad and almost truncate, slightly projecting in juveniles; lips "rubbery", thicker at mouth corners. Short, crescentic groove between nostrils in juveniles; and large specimens often with numerous fine, papilla-like structures often scattered over anterior 2/3 of head and sometimes breast. Jaws strong, elevated at symphysis; mouth subterminal in adults, broad and curved; premaxillary tooth band partly visible laterally when mouth closed. Nostrils ovate, posterior one slightly lateral to anterior nostril. Eye rounded-ovate, free from head skin; situated dorsolaterally and visible from above, just or well before mid-head length. Lateral ethmoid somewhat prominent. Gill opening wide, free membranes broad and meeting over isthmus at a right angle.

Jaw teeth numerous, small, sharp and depressible, embedded in fleshy tissue. Premaxillary band with 16-24 irregular series, lower jaw with 10-15 series; edentulous space divides lower jaw band at symphysis. Stouter teeth in four transversely arranged oval patches on palate: always distinct, not contiguous; vomerine pair more rounded and about 2/3 width of outer pair. Palate smooth, two low ridges of epithelial tissue sometimes present before branchial chambers.

Head shield usually concealed by skin and mucus in juveniles and larger fish. When exposed, shield very granular, granules extending forward to above eye and over supraoccipital process. Dorsomedian head groove long and lanceolate, beginning at level of nostrils and tapering posteriorly almost to supraoccipital process base. Process oblong, straight-sided, sometimes with low median keel. Sides of head venulose. Triangular humeral process smooth to rugose with oblique and acute shaft; moderately ossified anteroventrally; reaching 2/3 distance along pectoral spine. Axillary process tiny.

Barbels thin and tapered. Maxillary barbel reaches from preopercular margin almost to pectoral base. Mandibulary barbel reaches or falls well short of, ventral head margin. Mental barbel extends to below middle of eye or hind border. Chin barbels moderately staggered.

Gill rakers rigid and rather sharp-tipped, as long as opposing filaments. Rakers absent from posterior face of first and usually second arches; 11-17 (mean 15.2) rakers along posterior aspect of third arch. Epithelial tissue forms low, thick pad on posterodorsal aspect of second arch.

Fin spines moderately to very thick, compressed, with fine longitudinal striae along sides. Anterior (leading) margin with low dentae and rugae, few low serrae towards tip; posterior (trailing) margin with few serrae extending proximally from apex (dorsal spine) or up to 20 saw-like, short serrae (pectoral spine). Tip of spines with short filaments (juveniles). Longest dorsal ray 2-3.5 longer than last ray. Pectoral fin extends to below posterior of dorsal fin. Ventral narrow in males, not reaching or well short of anal origin; fin broad in females, extending to anal origin or up to 4th anal ray, mature fish with thick pad of epithelial tissue proximally on 5th and 6th rays. Adipose fin oblong, opposite mid anal fin. Anal margin concave, longest ray 1.9-3.5 longer than last ray. Caudal lobes basally broad, thence slender and tapered.

Caudal peduncle moderately deep and compressed. Lateral line oblique anteriorly, thence straight, turned slightly dorsad at tail base. Distinct vertical series of pores extend from line over sides; and short, oblique lines diverge along length of lateral line, more dense anteriorly.

Fresh colouration: Highly variable. Some specimens ochre-coloured, brownish above, creamy below; fins orange, barbels pale. Other specimens countershaded olive brown, "smokey" blue to dark blue above, white below; dorsal, adipose and caudal fins brown to dark bluish brown, pectoral and ventral fins dark (blue) above, cream below; anal fin brown or bluish brown, anterior and posterior of fin cream; maxillary barbels blue, others white. Some individuals with "piebald" colouration: body greyish brown with small and large irregular cream or black blotches over anterior 2/3 of body, especially around mouth and head. Midgley (pers. comm., 1989) noted that juveniles from the Alligator Rivers have a black margin to the caudal fin.

Colour in preservative: Variable, from brown above and fawn below to blackish or dark charcoal-blue above, fawn, orangey, cream or white below, or blotched. Fins and barbels as when fresh, but blue becomes dark brown. Peritoneum pale grey or pinkish.

DISTRIBUTION

AUSTRALIA: Common and widespread in river systems of northwestern and northern Australia: (subspecies A): Fitzroy River, Ord and Victoria systems (including Armstrong, Camfield, Humbert, Wickham, East Baines, West Baines Rivers, Neave and Waterloo Creeks), rare in the Keep River, Daly, Katherine, Flora, Fergusson, Fish and Douglas Rivers, McKinlay, Mary, South Alligator, East Alligator Rivers; (subspecies B): Roper River system (Limmen Bight, Roper, Hodgson, Wilton and Mainoru Rivers), McArthur River, Tooganginie Creek, rare in the Robertson and Calvert River systems, southeasterly to the Flinders River, Gilbert, Staaten and Edward River systems (Strathgorden Lagoon) on Cape Yorke Peninsula (Midgley, 1979; 1980; 1981; 1982; 1983; 1984; pers. comm.).

There is a clear disjunction in range of the two subspecies: the one distributed in the west of the species' range, including the Victoria, Katherine, Daly, Ord, other Kimberley and northern river systems; the other distributed in the east, present in the Roper and Flinders River systems and all other rivers draining into the Gulf of Carpentaria.

BIOLOGY

Habitat: Fresh water, few records from within upper tidal limits. Found in fast-flowing main rivers, billabongs, creeks, deep pools and drying-out waterholes. Water quality varies considerably from turbid to very clear, still or moderately fast-flowing; pH range 7-8.7; surface temperature 22.5-35°C (Allen, 1982; Midgley, 1979-83). Larger fish inhabit the middle-upper water column, moving in large schools (Kailola and Pierce, 1987).

Maximum size: to about 28 kg whole weight (S. Sharpe, pers. comm.); approximately 1.3 m TL (R.J. McKay, pers. comm., S. Sharpe, pers. comm.).

Diet: mostly predatory, becoming a facultative omnivore during the dry season. Gut contents are: fish, aquatic and terrestrial insects and insect larvae, beetles and crustacean fragments and aquatic weed. Bony bream (*Nematalosa erebi* [Günther]) are the fish consumed almost entirely by Lake Argyle *midgleyi*. Midgley (1981) recorded gut contents of prawns, aquatic and terrestrial beetles, grasshoppers (August-September survey). Kailola and Pierce (1987) noted change in the diet of Lake Argyle *midgleyi* with growth, smaller fish eating bottom-dwelling organisms, aquatic plants and detritus, larger fish (>2 kg weight) eating almost exclusively fish. These authors drew a strong comparison between mouth width and prey size.

Breeding: "*A.*" *midgleyi* breeds only in fresh water, with no recorded spawning migrations. Spawning takes place in the early wet season (Roper River and Lake Argyle material). In Lake Argyle, spawning probably commences as early as July and continues through to late February (S. Sharpe, pers. comm., Kailola and Pierce, 1987), and first maturity is at approximately 50 cm FL. Kailola and Pierce found firm evidence of a second spawning in larger, well-conditioned individuals. Fecundity ranges from 40-240, spawned ova diameter 17-22 mm. Age at first maturity is probably 2 years, size approx. 30 cm SL. Newly hatched juveniles are approx. 75 mm SL.

DISCUSSION

The known biology of this species is reviewed in Kailola and Pierce (1987; 1988). "*A.*" *midgleyi* is the basis of a significant commercial fishery in Lake Argyle, and it displays a rapid growth rate (to 700 mm over two years).

"*A.*" *midgleyi* is possibly replaced in downstream river reaches by one or both of the other common ariids in northern Australia: "*A.*" *leptaspis* and "*A.*" *graeffei*.

"*A.*" *midgleyi* is immediately recognisable in the field because of its rather oblong, "square" snout and broad mouth. It is most similar to "*A.*" *leptaspis*, and some of Taylor's (1964) specimens of "*leptaspis*" from near the Roper River Mission belong to this species (Kailola and Pierce, 1988). The two species may best be separated on the relative length of the maxillary barbels: 16-25% SL in *midgleyi* *cf*. 22-51% in *leptaspis* (fig. 224). The maxillary barbels rarely reach as far posteriorly as the head margin in *midgleyi*, but reaches and exceeds the pectoral spine base in *leptaspis*. Additional characters which distinguish these species are: the combination of head width (56-76% 632 *cf*. 66-83% HL in *leptaspis*) (fig. 225); snout shape; the total number of rakers along the face of the first gill arch (10-17 [combined subspecies] *cf*. 13-22 in *leptaspis*) (fig. 226); and the number of haemal vertebrae (7-8 in *midgleyi*, *cf*. 4-6 in *leptaspis*). The shape of the occipital process and extent of the granular head shield also differ, *leptaspis* having a broader process (fig. 227) and more extensive head shield, the dorsomedian head groove terminating a considerable distance before the base of the occipital process. Finally, "*A.*" *leptaspis* is only known to a maximum body size of 64 cm FL. Statistical analysis revealed a discriminant function which always separated all individuals of *midgleyi* + *leptaspis* accurately in the robust jackknife classification using the characters of: maxillary barbel length as %SL + dorsal spine/HL ratio + total GR count (first arch) + head width as %HL + snout length as %HL (Z function: Appendix C).

"A." midgleyi is also similar to "A." latirostris, a Papuan species. However, anal ray count (fig. 212) easily distinguishes these two taxa.

"A." midgleyi consists of two ~~allopatric~~ subspecies which can be distinguished by (figs. 226, 228):

SUBSPECIES	A (western)	B (eastern)
Number of gill rakers on first arch	15-17	10-11
Number of gill rakers on third arch	16-19	11-14
Eye diameter as % HL	13-22, mean 17	9-15, mean 11

No other meristic of morphometric characters I have identified distinguish these subspecies, although juvenile colouration may be important. Other techniques (e.g. electrophoresis) would very likely support this classification.

TYPES

This species is based on a holotype and 30 paratypes from the Fitzroy River to the Mitchell River. Type material of the subspecies has not been designated.

Condition of type: good. Short slit along belly; membrane on all fins split; tip of upper caudal lobe lost.

ETYMOLOGY

Named for Hamar and Mary Midgley of Nambour, Queensland.

The subspecies are unnamed.

MATERIAL EXAMINED

Eastern subspecies (B)

QUEENSLAND - 2, QM I.16741, McArthur River, June 1975, heads only, SL not stated: 123.5 & 131 mm HL; 1*, QM I.12910, Flinders River near Maxwellton, 14 Oct. 1974, coll. H. & M. Midgley, 326 mm SL (= PARATYPE); 1*, QM I.12757, same data, 310 mm SL (= PARATYPE); 2*, QM I.16730, Flinders River near Maxwellton, Oct. 1974, coll. H. & M. Midgley, 315 & 329 mm SL (= PARATYPES); 1*, QM I.11364, Forest Home Station, Gilbert River, 24 Sept. 1953, coll. T.C. Marshall, 205 mm SL (= PARATYPE); 1*, AMS I.25315-001 (prev. IB.3159/2882), same data, 171 mm SL (= PARATYPE); 1*, QM I.11990, Mitchell River, 8 Sept. 1959, 145.5 mm SL (= PARATYPE).

NORTHERN TERRITORY - 1, NTM S.12077-001, Roper River, Sept. 1979, head only, SL not stated: 107.5 mm HL; 1, NTM S.11153-001, Mainoru River, Sept. 1979, head only, SL not stated: 110 mm HL; 2, QM I.16744, same data, upper jaws only, SL not stated; 2, QM I.16745, same data, upper jaws only, SL not stated; 1, QM I.16743, Hodgson River, Sept. 1979, upper jaw only, SL not stated; 1*, QM I.16735, Hodgson River, 17 Sept. 1979, coll. H. & M. Midgley, 240 mm SL (= PARATYPE); 2*, QM I.16738, Mannaburoo Hole, Limmen Bight River, 29-30 Aug. 1979, 327 mm SL & 151.5 mm HL (= PARATYPES); 2*, NTM S.12070-001, same locality, 298 & 315 mm SL (= PARATYPES); 1*, QM I.16737, same locality, Limmen Bight River, 1 Sept. 1979, 310 mm SL (= PARATYPE); 1*, NTM S.12083-001, Wilton River, 25-27 Sept. 1979, coll. H. & M. Midgley, 1979, 331 mm SL (= PARATYPE); 1*, CAM F.35, Wollogorang Station, 15 June 1974, coll. D. Howe, 257 mm SL (= PARATYPE); 1*, CAM F.36, same data, 273 mm SL (= PARATYPE).

Western subspecies (A)

NORTHERN TERRITORY - 1*, AMS I.20858-006, Wickham Gorge, Victoria River, 7 June 1978, coll. D.F. Hoese, 270 mm SL (= HOLOTYPE); 1*, AMNH 57454 (ex AMNH 51649), junction of Big Horse Creek & Victoria River, 8 May 1969, coll. G. Nelson, D. Rosen & H. Butler, 98.5 mm SL (= PARATYPE); 2*+1, AMNH 57454SW (in part) (ex AMNH 51649), same data, 103 & 114 mm SL (106 mm specimen = PARATYPE); 2, AMNH 51649 (in part), same data, 104 & 122 mm SL; 8, AMS I.20858-005, Wickham Gorge, Victoria River, June 1978, 255-320 mm SL; 1, AMS I.20848-010, Jasper Gorge, Victoria River, June 1978, 87 mm SL; 2, AMS I.20856-004, Bullo River Station, Victoria River, June 1978, 212 & 225 mm SL; 1, AMS I.20857-002, Victoria River district, June 1978, 240 mm SL; 1, AMS I.20847-008, upstream from Daly River crossing, June 1978, 240 mm SL; 1*, NTM S.11800-001, Daly River on Florina Station, 25-26 Aug. 1980, coll. H. & M. Midgley, 325 mm SL (= PARATYPE); 3, NTM S.12087-001, Katherine River near Limestone Creek junction, Aug. 1980, 355-385 mm SL (only heads seen: 112-117 mm HL); 3, AMS I.16838-007, same data, 127-151 mm SL; 1, AMNH 51650, Katherine River, 8mi. downstream from Katherine, May 1969, 125 mm SL;
1, AMS I.20453-001, McKinlay River, Aug. 1978, 250 mm SL;
1, AMS I.20848-010, Mary River, Sept. 1978, 310 mm SL; 16, AMNH 51651, South Alligator River at Pine Creek-Oenpelli Road crossing, May 1969, 118-224 mm SL;
WESTERN AUSTRALIA - 1*, WAM P.25597-001, Fitzroy River, June 1973, coll. R. Emiliani, 348 mm SL (= PARATYPE); 1*, WAM P.25708-001, Forbes Yard, Traine River, 18 June 1973, coll. J.B. Hutchins, 224 mm SL (= PARATYPE); 1*, ZMA 119.467, near Wyndham, 12 April 1981, coll. L. Turner, 244 mm SL (= PARATYPE); 1*, WAM P.28776-001, Lake Argyle, mid-1980, coll. N. Morrissy, 166.5 mm SL (= PARATYPE); 13, unreg., Lake

Argyle, mid-1980, 170-385 mm SL; 12, WAM P.21338-001, Ord River, 4 Oct. 1971, coll. J. Dell & R.J. McKay, 128-185 mm SL; 2, AMS I.16838-006, same data, 137 & 151 mm SL; 4*, WAM P.21338-002 (ex WAM P.21338-001), same data, 133-161 mm SL (= PARATYPES); 1*, AMNH 57082, Ord River below Duncan Highway crossing, 7 May 1969, coll. G. Nelson, D. Rosen & H. Butler, 152 mm SL (= PARATYPE); numerous specimens captured during commercial fishing operation, Oct. 1987, max. size 13.5 kg whole weight.

6.6.15

"*Arius*" species 2

(Figures 230, 231, 232, 233; Tables 37, 38)

Hemipimelodus velutinus: Weber, 1908: 225 (in part)
Arius leptaspis: Weber, 1908: 227 (in part)
Tachysurus leptaspis: Fowler, 1928: 62 (in part)
Hexanematichthys leptaspis: Munro, 1958: 123 (in part)
Arius sp."C": Allen and Boeseman, 1982: 74,99

DEFINITION

Fine teeth in four isolated, oval patches across front of palate; usually no rakers on posterior aspect of first two gill arches. A 18-22; P 9-10; total gill rakers (first arch) 13-22; vertebrae 17-20+6-7+28-31. Maxillary barbel 28-50 %SL; mouth broad, gape 46-56 %HL; jaws strong; head shield rough, granules extending forward along midline; supraoccipital process oblong or broadly triangular. Body compressed and tapered distally, caudal peduncle shallow, its depth 6-8 %SL. Fresh colouration dark blue to olive, vertical series of golden spots arranged along upper sides.

DESCRIPTION

D I,7. P I,9-10. A 18-22. GR (first arch) 13-22, of which 4-7 on upper limb. GR (last arch) 16-21. Number of vertebrae 53-55 (45-48 free).

Body slender and robust; depressed anteriorly, compressed posteriorly. Predorsal profile almost straight, slightly convex at nape. Snout rounded or slightly pointed (in small juveniles); lips moderately fleshy (juveniles) and forming muscular lobe at corners of mouth, scalloped along inner margin. Many fine papilla-like structures scattered over anterior half of head in mature males and some small specimens; short, crescentic groove at midline on dorsum of snout in juveniles. Jaws strong, slightly upturned at symphysis; mouth broad and curved, subterminal; none or 1/4 of premaxillary tooth band exposed when mouth closed. Nostrils ovate, anterior one usually directly in front of posterior one. Eye rounded or ovate, free of head skin; eye situated dorsolaterally (visible from above) slightly before mid-head length. Gill opening wide; membranes meeting at approximately a right angle, leaving broad, free margin.

Teeth in jaws and palate small, slender and curved; tips sharp; teeth depressible and embedded in soft tissue. Premaxillary band with 4-8 irregular series of teeth; mandibulary band with 4-6 series, band divided at symphysis by narrow edentulous space. Four ovate groups of many teeth arranged across front of palate; space between tooth patches narrow yet always distinct. Palate mostly smooth; two low, oblique ridges of epithelial tissue usually lie posteriorly on palate.

Head shield heavy and extensive, of many coarse granules arranged into series or scattered in patches, from above anterior of eye to origin of gill opening and over supraoccipital process. Dorsomedian head groove short, lanceolate, extending from between nostrils to distance of one eye diameter behind eye (narrow posteriorly and more extensive in juveniles). Supraoccipital process broad, oblong or triangular; median keel present in juveniles. Humeral process smooth or striate, coarsely granular with age; heavily ossified anteroventrally. Process triangular; shaft acute, reaching 1/3 distance along pectoral spine. Axillary pore tiny and rounded.

Barbels moderately flat. Maxillary barbel reaches to or beyond last dorsal ray in juveniles, to tip of humeral process or less, in adults. Mandibulary barbel reaches to below pectoral base or as far as mid dorsal base (juveniles). Mental barbel attains ventral head margin or pectoral spine base (adults). Chin barbels moderately staggered.

Gill rakers stiff and rather acute, half as long as opposing filaments. Usually no rakers along posterior aspect of first and second arches (rarely, one to 3), 14 to 22 (mean 18.6) along posterior aspect of third arch. Smaller fish have low, crenulate-edged flap of tissue posterodorsally on second arch and often have 3-5 series of low papillae along posterior of first two arches.

Fin spines strong, slightly compressed; fine or rugose striae along lateral aspect. Short filament usually present at spine tips. Front margin of all spines with transverse, granular ridges, replaced towards tip by 3-4 low serrae (dorsal spine), or 5-8 serrae (pectoral spine). Posterior edge of spines with serrae: 5-8 on dorsal, 11-16 (triangular, larger) on pectoral. Dorsal fin first ray 2.6-3.3 times length of last ray. Pectoral extends to or beyond vertical line from end of dorsal base. Ventral oblong, usually reaching anal origin (males) or about 4th anal ray (females). Sexually mature females with thick, cushy pad of epithelial tissue along upper aspect of 6th ventral ray. Adipose fin short-based, situated above posterior 2/3 of anal. Anal margin concave, longest ray 2.4-3.2 longer than last ray. Caudal lobes broad and tapered, lower lobe subequal to upper one.

Caudal peduncle long and compressed. Lateral line elevated below dorsal fin, turned dorsad at caudal base. Numerous branching, oblique short lines diverge from line, extending short distance over upper and lower sides.

Fresh colouration: Dark blue or olive above, white or cream below; iridescent bronze sheen over body, vertical series of pores from lateral line often highlighted golden. Dorsal, adipose and caudal fins brown or dark grey, other fins dusky. Maxillary barbels dark brown.

Preserved colouration: Very dark brown (adults), "smokey" brown or charcoal (juveniles) over upper 2/3 of body, cream or pinkish below. Maxillary barbel dark brown, other barbels cream or white. Dorsal, adipose and caudal fins mostly brown; anal and ventral brown; dorsal aspect of pectoral fins dark brown, underside of this and ventral fins cream. Peritoneum pale pink or cream.

DISTRIBUTION

NEW GUINEA: north-draining rivers. Mamberamo and Idenburg Rivers, Moaif River, Tami River entrance, Murik Lakes, Sepik River from Angoram region to Pagwi, Tsenap (or Zenap) and other regional villages inland, the Kerame and Kwatit Rivers to the lower Ramu River.

BIOLOGY

Habitat: Brackish water, tidal reaches of rivers and freshwater. Coates (1983) obtained "Arius" species 2 from the main river channel, and less frequently or rarely from oxbow lakes and over the floodplain (wet season). It is usually well represented at the Angoram fish market, with peaks in abundance during March, April, June, August and October. As noted by Weber (1913:544), the species "does not shun brackish water" (transl.).

Maximum size: 450 mm SL (Coates, 1983).

Diet: This species ingests a variety of food, although there is a preference for larger items. Coarse detritus, large crustacea (prawns) (Caridina spp., Macrobrachium spp.), larger insect larvae and nymphs, and fish scales (no whole fish) were in stomach contents reported by Coates (pers. comm., 1983), who observed that fish scales were a very important food item. "Arius" species 2 increases feeding activity during the dry season. Coates found that the amount of body fat laid down increased significantly from May/June to peak in November/December. Stomachs of my material contained higher plant material, a large, whole prawn and insect larvae.

Breeding: This species appears to spawn from the end of the dry season and the middle of the wet season. Two of my specimens are spent females, captured in April; and a male captured in May has moderately swollen buccal cavity, indicating that it was brooding. Other adult specimens have gonads in early stages of maturity in January and May; and juveniles were collected in freshwater during October. I have no information on fecundity.

DISCUSSION

All literature references to "Arius" leptaspis (Bleeker) in northern New Guinea are based on misidentified specimens of "Arius" species 2. Weber (1908) provided details of a 370 mm long specimen from the Moaif River, comparing it with "A." leptaspis from southern rivers and with Bleeker's (1862) description; Weber and de Beaufort (1913) recorded the species (as *A. leptaspis*) from the Sepik and Moaif Rivers; Hase (1914) reported it from Reganbiwak (= Sepik) River and the Tami River; Hardenberg (1941) described one of two specimens from the Mamberamo River; Herre (1936) collected specimens from Ambot (on the Kerame River), Marienberg, Malu, Tsenap, Koragu and Kabarao (all on the Sepik River); and Munro (1958) recorded it from Murui (Sepik River). Apparently Herre was uneasy about the determination of his material, as on cloth labels attached to two of his specimens (CAS(SU) 68882 from Ambot; CAS(SU) 68631 from Kanganaman) he wrote "co-type. *A. tsenapensis* Herre". However, no formal description was ever published (his material from Tsenap must also have referred) and indeed, in 1936 he made no mention of the differences between the northern and southern "forms" of *leptaspis* Bleeker.

The 12 type specimens of "*A.*" *velutinus* (Weber) from the Tami River mouth almost certainly represent "*Arius*" species 2 (refer "*A.*" *velutinus*: Types). Desoutter (1977) noted that five of the six in ZMA 112.655 have tooth patches across the palate, as has a sixth (RMNH 8001 - my material). She identified them as *Tachysurus leptaspis* (Bleeker). Desoutter did not comment on the condition of the 293 mm syntype in ZMA 112.655. Furthermore, there are no reliable records of "*A.*" *velutinus* from marine or brackish water, whilst the Tami River (the source of Weber's series of included syntypes) is salty (*fide* Desoutter, 1977).

The realisation that the nortnern populations of "*A. leptaspis*" are not conspecific with "*A.*" *leptaspis* Bleeker has effectively resolved the zoogeographic "problem" of "*A.*" *leptaspis* being the only New Guinea ariid occurring in both northern and southern rivers. This topic was discussed by Weber (1913), Munro (1964) and referred to by other authors such as Herre (1936), Hardenberg (1941) and Allen and Boeseman (1982).

"*Arius*" species 2 is most similar to "*A.*" *leptaspis* (Bleeker) from which it can be distinguished by: the number of trunk vertebrae (13-15 in *leptaspis*), eye position (more dorsad in "*Arius*" species 2 than similar-sized *leptaspis*), HL (shorter in species 2; fig. 234), thickness of head skin (thicker in *leptaspis*) and anal ray count (fig. 235). Stepwise discriminant function analysis revealed functions which together separated these species 98 % of the time. They are: interdorsal distance + pectoral fin count + tooth form + eye/snout ratio + head height/head width ratio + anal base as %SL (*cf.* fig. 236) + caudal peduncle depth as %SL (*cf.* fig. 237) + dorsal spine length as %SL (refer also Tables 37 to 40; Z function in Appendix C).

Comparison with other, similar Australo-Papuan ariids "*A.*" *latirostris* and "*A.*" *velutinus* is made under the Discussion on those taxa.

TYPES

Types have not been nominated for this species.

ETYMOLOGY

This species has not been named.

MATERIAL EXAMINED

NORTHERN IRIAN JAYA - 1*, RMNH 28814, Tami River entrance, 1954, coll. M. Boeseman, 88 mm SL; 1*, ZMA 116.459, Pioniersbivak, Mamberamo River, 5 Jan. 1921, coll. W.C. van Heurn, 250 mm SL; 1*, ZMA 116.460, Prauwenbivak, Idenburg River, 18 Sept. 1920, coll. W.C. van Heurn, 267 mm SL; 1*, RMNH 8001, outlet of Tami River, 12 May 1903, coll. Weber(?), 149 mm SL (= SYNTYPE of Hemipimelodus velutinus Weber). NORTHERN P.N.G. - 1*, AMS I.25406-001, Murik Lakes, May 1980, coll. J. Campbell, 270 mm SL; 1*, QM I.21674, Murik Lakes, May 1980, coll. J. Campbell, 294 mm SL; 2*, AMS I.25406-002, same data, 242 & 284.5 mm SL; 1*, SAMA F.6254, Keram, May 1980, coll. A. Richards, 175.5 mm SL; 1*, WAM P.28224-001, Angoram, July 1982, coll. D. Coates, 252.5 mm SL; 1*, CSIRO C.3532, Murui, 2 May 1954, 122 mm SL; 1*, CAS (SU) 68631, Kanganaman, 15 May 1927 (? = 1929), coll. A.W. Herre, 198 mm SL; 1*, CAS (SU)28204, Malu, 16 May 1929, coll. A.W. Herre, 218 mm SL; 1*, CAS (SU)68882, Kerame River at Ambot, 25 May 1929, coll. A.W. Herre, 198 mm SL; 2*, CAS 13482, Sepik River, 1929, 215 & 280 mm SL; 1*, CAS 13481, Sepik River, 1929, 380 mm SL; 4*, WAM P.27846-001, 8 km downstream from Pagwi, Sepik River, 27 Oct. 1982, coll. G.R. Allen & D. Coates, 97-133 mm SL; 11*, WAM P.27847-009, Kwatit River at junction with Sepik River, 28 Oct. 1982, coll. G.R. Allen & D. Coates, 48-51, 84-118 mm SL; 2*, KFRS F.5517-01, Keram, 17 April 1980, coll. A. Richards, 297 & 325 mm SL; 2*, NTM S.11904-001, Angoram, Sepik River, 1981, coll. D. Coates, 252 & 258 mm SL; 1, KFRS F04107, Murik Lakes, May 1972, 200 mm SL; 1, WAM P.28218-001, Sepik River, no date, 400 mm SL; 1, CAS (SU)28204, Malu, Sepik River, May 1929, 216 mm SL; 2, KFRS F0091, lower Ramu River, Nov. 1960, 52 & 55 mm SL; 2, KFRS F0090, same data, 49 & 59 mm SL; 25, KFRS F.5470-01, Ramu River at Bunapas Mission, Oct. 1987, SL's not noted; 3, CAS 63457, Bosngun River, trib. of Ramu River, Oct. 1987, 65-132 mm SL; 4, CAS 63428, Ramu River at 04°15'S, 144°40'E, Oct. 1987, 45-50 mm SL; 23, CAS 63465, Ramu River at 04°13'S, 144°40'E, Oct. 1987, 48-108 mm SL; 6, CAS 63421, Ramu River at 04°14'S, 144°41'E, Oct. 1987, 115-163 mm SL.

6.6.16

"*Arius*" species 6

(Figures 165, 238, 239, 240; Tables 39, 40)

DEFINITION

Four patches of conical teeth across front of palate: rounded vomerine patches well-separated; outer patches oval or crescentic, 2-3 times larger than inner patches. Snout fleshy, overhanging mouth. Low papillae on palate and posterior of gill arches; rakers rarely on posterior of first two gill arches. Barbels thick proximally, thin distally. Head shield very granular and extensive posteriorly; triangular supraoccipital process short and very broad. Eye small, dorsolateral, 8-11 %HL. A 16-18; total gill rakers (first arch) 10-14; vertebrae 19+5+26. Adipose fin large, base longer than anal base. Fresh colouration dark grey; inner, dorsal aspect of paired fins charcoal blue.

DESCRIPTION

D I,7. P I,9-10. A 16-18. GR (first arch) 10-14, of which 3-4 on upper limb. GR (last arch) 9-13. Number of vertebrae 50-52 (43-46 free).

Body robust, moderately slender. Head broad and depressed; predorsal profile almost straight, slightly convex at nape. Snout rounded to slightly acute and prominent; lips moderately thick and fleshy, inner margin crenulate. Tiny, fine papilla-like structures on snout and around mouth in all specimens. Mouth very broad and curved, more inferior than subterminal; 1/4-1/2 upper jaw tooth band exposed when mouth closed. Nostrils rounded, anterior one slightly lateral to posterior one. Eye small, not completely free of head skin; situated dorsolaterally and well to slightly before mid-head length. Gill opening moderately wide, united membrane concave over isthmus, margin broad and free.

Teeth conical, tips sharp or compressed; very slightly depressible; embedded in thick tissue. Five-8 irregular series of teeth in premaxillary band, 4-6 in lower band which is divided by narrow edentulous space at symphysis. Four tooth patches across front of palate, separated by narrow spaces. Vomerine patches rounded; outer patches large, oval, at least twice larger than vomerine patches. Palate smooth or with few scattered low papillae, and two oblique low ridges of epithelial tissue posteriorly before branchial chamber.

Head shield extensive, very granular, granules low and coarse in large individuals. Ridges of striae flank dorsomedian head groove posteriorly and broader striae extend over supraoccipital process. Groove lanceolate, beginning on snout, extending to base of supraoccipital process; flat anteriorly, narrow and deeply excavated posteriorly. Supraoccipital process very broad and triangular; sides almost concave; longitudinal median keel. Sides of head slightly venulose; small, oval, naked space in head shield above operculum. Humeral process broad-based, heavily ossified anteroventrally; its triangular shaft extending 1/3 distance along pectoral spine. Axillary pore moderately large.

Barbels flat, thick proximally, thin and wisp-like distally. Maxillary barbel extends to base of pectoral fin or to below dorsal base (juveniles). Mandibulary barbel reaches pectoral base. Mental barbel ends midway between eye and pectoral base. Bases of chin barbels moderately staggered.

Gill rakers well-spaced, half as long as opposing filaments. Numerous, low papillae along back of first two gill arches (few in larger fish); no rakers on posterior of first arch; rarely 1-3 rakers posterodorsally on second arch; 9-10 rakers on posterior face of third arch. Narrow pads of epithelial tissue on gill arches posterodorsally, best developed on second.

Fin spines robust, tips very sharp. Outer spine margin with low granules and 1-3 serrae distally; posterior margin with 3-5 serrae (dorsal) or 5-10 large antrorse serrae (pectoral). Longest dorsal ray 1.9-2.2 times last ray. Pectoral extends to below mid-dorsal fin. Ventral short of or to, anal fin origin [no mature females in my material]. Adipose fin oblong and long-based, beginning noticeably before anal origin and opposite all of anal. Anal margin concave, longest ray 2.4-3.2 times last ray. Caudal fin moderately short, lobes broad and tapered.

Caudal peduncle moderately deep. Lateral line turned dorsad at tail base and elevated below dorsal. Low, short lines diverge from length of lateral line, more abundant anteriorly.

Fresh colouration: Brown to dusky mauve above, pale yellow or fawn below; iridescent gold on sides. Fins dusky mauve or brown. Barbels pale yellow.

Colour in preservative: Light brown or tan, paler below; fins brown; barbels fawn. Peritoneum pale.

DISTRIBUTION

NEW GUINEA: south coast. Vogelkopf Peninsula~~r~~ to the Fly River mouth.

BIOLOGY

Habitat: Muddy, shallow coastal waters and tidal rivers.

Maximum size: 254 mm SL.

Diet: Uncertain. The combined gut contents of four ariid taxa (including "*Arius*" species 6) misidentified by Maunsell and partners (1982) were crustacean fragments, insects, detritus and a small fish. I was unable to examine the stomach of the two largest specimens, and the alimentary canal of the remaining three had been removed.

Breeding: This species is reported to spawn in coastal waters during the late dry season and early wet season (U. Kolkolo, pers. comm., 1988). However, the smaller fish, collected in late July, appear to be only newly-liberated juveniles.

DISCUSSION

On a label attached to the largest specimen from Merauke, was written "*Arius uniformis* Hardenberg". Hardenberg did not publish a description, and there are no manuscripts at the ZMA.

This species probably attains a reasonable size. It could have been mistaken in collections for several other species such as "*A.*" *proximus* and *Cinetodus* species. From "*A.*" *proximus*, species 6 can be distinguished by its larger adipose fin (12-19 %SL *cf.* 6-12% in *proximus*), mouth shape, eye diameter (fig. 158), head shield size and supraoccipital process shape, and swimbladder form (margins smooth *vs.* scalloped in *proximus*). The supraoccipital and mouth shapes, paired fin colouration and adipose fin size of species 6 are similar to those of *Cinetodus* species. However, these taxa have rakers along the posterior of the first two gill arches, different palatal dentition and more restricted gill opening.

TYPES

No types have been nominated.

ETYMOLOGY

This species has not been named.

MATERIAL EXAMINED

SOUTHERN IRIAN JAYA - 1*, NCIP 436, Merauke, 4 Aug. 1931, coll. J.D.F. Hardenberg, 254 mm SL; 1, WAM P.29966-001, Manimeri River, Bintuni Bay, 28 March 1989, coll. G.R. Allen, 250 mm SL.

SOUTHERN P.N.G. - 2*, AMS I.29291-001, Fly River delta, 16-22 July 1981, coll. J. Watson, 59.5 & 74.5 mm SL; 1*, QM I.26088, same data, 56 mm SL.

6.6.17 *Incertae sedis*

The definition and position of two taxa within the Australo-Papuan Ariidae is uncertain. They are species 4 and *macrorhynchus* Weber.

6.6.17.1

"*Arius*" species 4

(Figures 241, 242, 243, 244; Tables 18, 19)

Nedystoma dayi: Tortonese, 1964: 24

Nedystoma dayi (in part): Kailola, 1975: 42

Nedystoma sp. Liem & Haines, 1977: 25

DEFINITION

Palate without teeth (but autogenous tooth plate present); jaw teeth slender, in short, oblong band. Lips fleshy and thin; mouth small. Barbels thin and short, maxillary barbel reaching only just beyond eye; bases of chin barbels close together. Eye large, 14-24 %HL, lateral. Dorsomedian head groove elongate, deep posteriorly. Gill rakers along posterior of all arches; gill opening slightly restricted; two large epithelial flaps on palate posteriorly and double folds on upper limb of first two gill arches. A 20-23; total gill rakers (first arch) 28-37. Longitudinal furrows over "shoulder". Fin spines thin, long and slender; adipose fin short-based, over posterior 2/3 of anal; sexually mature female's ventral fin pad scalloped and tapered. Fresh colouration dark grey above and iridescent purple; branchial chamber sometimes purplish or dark grey.

[Additional character states: posterior dorsomedian fontanel always open; metapterygoid enlarged, ending well past quadrate hind border; frontals broad posteriorly, their arms narrow; frontal-lateral ethmoid space large; short posterior cleithral process.]

DESCRIPTION

D I,7. P I,8-10. A 20-23. GR (first arch) 32-37, of which 10-12 on upper limb. GR (last arch) 30-37. Number of vertebrae 49-50 (43-44 free).

Body moderately elongate and cylindrical; head slightly depressed. Predorsal profile straight from behind snout, abruptly convex at nape. Snout slightly rounded or truncate, curved ventrad and overhanging subinferior mouth. Lips thin and fleshy or "rubbery", inner aspect spongy and papillose. Mouth gape moderately wide, lower jaw truncate or horizontal; all of premaxillary tooth band visible when mouth closed. Nostrils large and rounded, anterior nostril slightly median to posterior one. Shallow groove usually present on snout between posterior nostrils. Eye large, rounded and prominent, situated laterally at or slightly before mid-head length, its margin free of head skin. Lateral ethmoid prominent. Gill openings somewhat restricted ventrally, membranes attached broadly to isthmus, margin concave.

Teeth in jaws slender, long and depressible; very fine and embedded in tissue; in 5-6 series. Tooth band interrupted at symphyses by edentulous space. Premaxillary bands elongate-oval. No teeth on palate, which is almost smooth or has low, scattered papillae. One very large pair of epithelial tissue folds hang from palate into anterior of branchial chamber.

Head shield rugose or finely granular. Granules conspicuous and usually sharp, arranged in series along dorsomedian head groove and along edge of shield in larger specimens. Dorsomedian groove begins at level of nostrils and continues to supraoccipital process base. Groove flat anteriorly to about level of eye, thence deeply excavated and conspicuous. Rugose supraoccipital process triangular with straight sides and prominent, usually sharp median keel. Naked space in head shield above gill opening. Large venules on sides of head. Lateral head skin and "shoulder" skin develop 7-10 longitudinal furrows or ridges with age: most apparent in individuals longer than about 150 mm SL. Humeral process triangular, indented above and heavily ossified anteroventrally, its shaft oblique and acute. Granules arranged in series along process. Moderate sized, slit-like axillary pore present.

Barbels thin, rounded proximally, flattened and wisp-like distally; bases of lower jaw barbels almost transversely aligned. Maxillary barbel reaches to eye or halfway between eye and gill opening (juveniles); mandibulary barbel extends to below middle of eye; mental barbel not or just reaches front eye margin. Chin barbel bases close together, transversely aligned.

Gill rakers long, equal to gill filament length. Shorter rakers along posterior face of all arches: 32-36 along first arch, 33-40 on second, 30-34 on third. Curious large double fold (or pouch) of epithelial tissue links upper limb of first two arches.

Fin spines long, slender and rather compressed: sides smooth to finely striate; anterior border with sharp granules or ridges. Low serrae along distal part of dorsal spine hind border and 25-35 sharp, large retrorse serrae along pectoral spine hind border. Last dorsal ray 3-3.7 in longest ray. Pectoral fin reaches just beyond dorsal. Ventral narrow in males, reaching 2nd-3rd anal ray; broad in females, extending to about 5th anal ray; sexually mature females with curiously-shaped thickening along dorsal aspect of 6th ray consisting of series of lobes and proximally a short, lateral horizontal process (fig. 243, F,G). Adipose fin short-based, oblong; above middle of anal fin. Anal fin outer margin truncate (adult) to deeply concave (juveniles), last ray 2.8-3.2 in longest ray. Caudal lobes narrow and tapered, upper lobe slightly the longer.

Lateral line elevated below dorsal fin and curved dorsad at tail base. Thin, dorsally-directed branchlets of lateral line conspicuous; vertical series of fine pores diverging from lateral line extend over upper body surface. Caudal peduncle moderately deep.

Fresh colouration: Dark grey above, white below; iridescent purple on back. Sharp division between dorsal and ventral colours. Fins pale. Lining of branchial chamber sometimes purplish or dark grey.

Colour in preservative: Dark brown or charcoal grey over upper 2/3 of head and body, pale orange-fawn or dusky grey below. Both lips pale. Dorsal, adipose and caudal fins dusky tan with broad, brown margins. Upper aspect of pectoral fin dark grey or brown; upper ventral fin, anterior anal rays and anal margin dusky. Peritoneum pale or light fawn. Barbels brown.

DISTRIBUTION

NEW GUINEA: southern coast from Katau (west of Fly River delta) to Aird Hills and Oreke River.

AUSTRALIA: vicinity of Darwin to the southern Gulf of Carpentaria.

BIOLOGY

Habitat: Predominantly in marine waters of the lower estuaries, along the coast and off river mouths. The species is common in the lower Era River-Morowan area, and small populations are present in the mangrove areas (Haines, 1979).

Maximum size: to 302 mm SL.

Diet: "Arius" species 4 consumes fruit and detrital matter. Eight of 12 stomachs from fish captured in the mangrove zones by Haines (1979) contained food: molluscs in one, fruit in 6, mud and detritus in one, copepods in one. Gut contents of fishes I examined were: detritus, mud and tiny insect larvae.

Breeding: Breeding probably occurs at the beginning of and continues through the wet season. The largest specimen, captured in

December, is a mature female with gonads at stage V or VI: the ova are 11-11.5 mm in diameter. About 16 large ova can be seen through the RHS ovary wall (without disturbing the gonad). A 200 mm SL male specimen captured in September has maturing gonads. Specimens of 228 and 174 mm SL examined are either spent or in early maturation stages. The smaller specimens I examined (e.g. 88-135 mm SL) were caught between May and early September. Haines (1979) recorded size at first maturity as 20 cm FL.

DISCUSSION

Species 4 superficially resembles _Nedystoma dayi_ in having a toothless palate, epithelial folds around and before the anterior gill arches, and many gill rakers. However, the posterior head groove and mature female ventral fin shape, short barbels (maxillary barbel 29-56 %HL, _cf._ 46-76 %HL in _dayi_), longer snout (37-43 %HL, _cf._ 30-36 %HL in _dayi_) are among distinguishing characters. The species also occupy different habitats.

Tortonese's (1964) _dayi_ from Katau must be referable to this species.

TYPES

No types have been nominated.

ETYMOLOGY

The species is unnamed.

MATERIAL EXAMINED

SOUTHERN IRIAN JAYA - 1, WAM P.29965-002, Manimeri River, March 1989, coll. G.R. Allen, 94 mm SL.

SOUTHERN P.N.G. - 1*, AMS I.25995-001, Baimuru, 12-14 Sept. 1974, coll. A.K. Haines, 204 mm SL; 1*, QM I.22657, Morowan, Ini Island, 15 May 1975, coll. A.K. Haines, 228 mm SL; 1*, AMS I.27414-001, same data, 237 mm SL; 1, unreg., Aird Hills, Dec. 1974, 174 mm SL; 1, KFRS F03990, Murua, Matupi River, Oct. 1971, 181.5 mm SL; 2, AMS I.27413-001, Arehava, tidal creek, Sept. 1974, 108 & 151 mm SL; 1*, USNM 288553, Gulf of Papua, 13 July 1981, coll. S. Frusher, 135 mm SL; 3*, KFRS F04093, off Oreke River mouth, 3-4 May 1973, coll. P. Kailola & J. Koaia, 115-193 mm SL; 1*, AMS I.25996-001, Gulf of Papua, May 1975, coll. A.K. Haines, 136 mm SL; 3, unreg., Sagero, N bank of Daru Island, Sept. 1988, 185-200 mm SL.

QUEENSLAND - 1*, CSIRO C.3799, Norman River at Karumba, 1969, coll. D.J. Turner, 187 mm SL.

NORTHERN TERRITORY - 1*, NTM S.11507-001, Ludmilla Creek, Darwin, 19 Dec. 1984, G. Cole & A. Howard, 304 mm SL; 2*, NTM S.10190-002, Mickett Creek, Melville Island, 26 June 1975, coll. D. Grey, 88 & 88.2 mm SL.

6.6.17.2

"*Arius*" *macrorhynchus* (Weber)

New combination

(Figures 245, 246, 247, 248; Tables 25, 26)

Hemipimelodus macrorhynchus Weber, 1913: 549, 608, fig. 27 (Lorentz River)

Hemipimelodus aaldereni Hardenberg, 1936: 367 (Middle Digoel River)

Nedystoma dayi (in part): Kailola, 1975: 42

DEFINITION

Snout prominent, moderately acute, indented at nostrils; nostrils lateral; mouth small and inferior, 30-40 %HL; lips absent except at mouth corner. Eye dorsolateral, 13-19 %HL. Palate without teeth. First two gill arches with 1-4 rakers posterodorsally, otherwise lacking posterior rakers. Barbels rounded in cross-section anteriorly, very long, maxillary barbel 33-44 %SL; barbel bases on chin well staggered. Gill opening slightly restricted. Fin spines slender; adipose fin short-based, base 5-8 %SL, over posterior of anal. A 20-22; total gill rakers (first arch) 12-15; vertebrae 17+5-6+28-29. Fresh colouration brown and bronze, top of head and snout iridescent green or golden.

[Additional character states: nasals expanded; mesethmoid transversely creased, anteriorly forming blunt apex; short suture between metapterygoid and hyomandibular; laminar bone moderately extensive over anterior vertebrae.]

DESCRIPTION

D I,7. P I,10-11. A 20-22. GR (first arch) 12-15, of which 4-5 on upper limb. GR (last arch) 15-19. Number of vertebrae 51-52 (44-45 free).

Body elongate and cylindrical, torpedo-shaped; head pointed, flattened anteriorly. Predorsal profile straight. Snout fleshy, prominent and acute, projecting beyond inferior mouth and somewhat indented at level of nostrils. Nostrils ovate, situated more laterally than dorsally on snout; anterior nostril slightly median to posterior one. Mouth well-curved, moderately wide; lips thin, tightly applied, forming short, fleshy lobe at corners; half or all of premaxillary tooth band exposed when mouth closed. Eye almost rounded, free of head skin, dorsolateral, just before mid-head length. Gill openings moderately wide, membranes broadly united and attached across isthmus, leaving wide, free margin.

Jaw teeth fine, curved and sharp, depressible; in 8-9 obliquely arranged series in upper jaw, 6-7 series in lower jaw. Short edentulous space in band at symphysis of lower jaw. No teeth on palate. Palate epithelium soft and fairly smooth; with two slightly developed ridges of epithelial tissue posteriorly.

Head shield rugose posteriorly, remainder smooth or venulose. Straight borders to slightly granular triangular supraoccipital process, which bears a low, rounded median keel; shield often concealed by thick skin. Dorsomedian head groove lanceolate, flattened anteriorly; reaches to process base posteriorly. Humeral process rugose or smooth, moderately thickened anteroventrally; triangular shaft of process horizontal, blunt-tipped, extending 1/3 length of pectoral spine. Axillary pore tiny.

Barbels long, rounded anteriorly and flattened posteriorly. Maxillary barbel reaches below dorsal base to noticeably beyond base; mandibulary barbel extends to or beyond pectoral base; mental barbel reaches to or beyond ventral head margin. Bases of chin barbels moderately well staggered.

Gill rakers short, half length of gill filaments. Gill arches smooth. Usually 1-4 short rakers present on upper posterior aspect of first two arches; 14-15 on third arch. Low pad of thickened epithelial tissue on second arch posterodorsally.

Fin spines moderately long, robust, slightly compressed; finely striated laterally. Short filament at spine tips. Pectoral spine subequal to or slightly shorter than dorsal. Anterior border of spines rough and low serrae towards tip. Dorsal spine with 5-10 low, retrorse serrae on posterior border near tip; pectoral with 20-25 moderately large serrae along posterior border. Last dorsal ray 2.9-3.2 shorter than longest ray. Pectoral fin noticeably low on sides, extending to below 5th-7th dorsal ray. Ventral base equally broad in both sexes: fin reaches to about 3rd anal ray in females; fails to reach anal origin by 1/2 eye diameter's distance in males. Condition of inner ventral rays in sexually mature females unknown. Anal moderately long-based, outer margin concave; last ray 2.4-2.9 shorter than longest ray. Adipose fin moderately small, situated above posterior 2/3 of anal. Caudal lobes broad and long.

Caudal peduncle long but stout. Lateral line sloped dorsad anteriorly, sharply dorsad at tail base. Long, branching venules extend from line anteriorly. Conspicuous series of pores diverge at right angles both above and below whole length of lateral line, forming clusters distally.

Fresh colouration: Upper half of body brown with bronze sheen, lower half fawn, cream or dusky white. Top of head anteriorly iridescent green and bronze. In life, snout bright golden or bronze (Roberts, 1978; Haines, 1979). Barbels dark brown. Fins dark reddish grey or brown, ventral and pectoral fins darker above. Pores in vertical series across back conspicuously brown.

Colour in preservative: Charcoal grey or dark brown over upper half of head and back; underside of snout, head and lower half of body grey, fawn or dusky cream. Barbels dark brown. Fins brown, darker along margins or on dorsal aspect. Branchial chamber pale; peritoneum grey.

DISTRIBUTION

NEW GUINEA: south-draining rivers. The upper and middle section of the Lorentz, Digoel, Fly and Purari Rivers. Maunsell and partners (1982) found "_A._" _macrorhynchus_ in the middle and upper Fly at an elevation of 20-40 metres, never closer than 460 km to the river mouth. Haines (1979) did not collect this species from the Kikori and Era Rivers.

BIOLOGY

Habitat: Always fresh water: major tributaries, mainstream of rivers, side channels and backwaters. Water turbid or clear, reddish, moderately fast-flowing, slow-moving or still (Roberts, 1978; Haines, 1979).

Maximum size: 463 mm SL (USNM 217075).

Diet: "_A._" _macrorhynchus_ consumes mainly higher plants, autochthonous fruits, and terrestrial insects. Roberts (1978) found in 6 stomachs: several fruits, parts of plants, ants, grasshoppers, beetles, bugs, few crabs and prawns; no aquatic insects. Maunsell and partners (1982) recorded terrestrial insects, fruit and plant detritus from 8 specimens (170-380 mm TL). Additional items noted by Haines (1979) in the 13 stomachs he examined were: a fish, mud, algae and detritus (although he had confused this species with _A._ _taylori_). Gut contents of specimens I examined were: pulpy fruits, mud, plant detritus, larval insect remains, beetles and grasshopper remains.

Breeding: Specimens from Kone collected at the end of November are maturing, the females at about gonad stage III. Haines (1979) observed that spawning occurred in January, in both the lower river and inundation zone. Weber's four juvenile specimens (125-175 mm SL) were collected between May and September - supporting a January to March spawning. However, Maunsell and partners (1982) recorded a 340 mm SL female with ripe ovaries from Bosset Lake entrance in early July. This apparent contradiction in spawning times (associated with the early wet season) could be explained by the different wet season periods in the Gulf of Papua (?and parts of southern Irian Jaya) and the remainder of southern New Guinea-northern Australia.

DISCUSSION

Desoutter (1977) accurately described "*A.*" *macrorhynchus*, and she located the tiny axillary pore overlooked by Weber (1913). I and Roberts (1978) support her conclusion that *H. aaldereni* Hardenberg is a synonym of "*A.*" *macrorhynchus*.

My specimens agree with Roberts' (1978) description of Fly River material except that the epithelial folds above the branchial chamber are thin ("moderately thick" according to Roberts) and the snout is slightly indented (*cf.* "sharply indented").

Haines' (1979) data on the species is clouded because he occasionally confused "*A.*" *taylori* Roberts with "*A.*" *macrorhynchus*. The two species are very similar, yet can be distinguished by such (external) characters as barbel form and length, snout shape, lip development, head width and colouration (and see Tables 25-26, 33-34). From other Australo-Papuan ariid taxa, "*A.*" *macrorhynchus* is easily distinguished by its mouth and snout shape, and barbel length and position.

TYPES

Hemipimelodus macrorhynchus: Weber (1913) nominated four syntypes. Three specimens are in the ZMA, numbers ZMA 111.085

(2: Van Weelskamp, 29 May 1907, 137 & 140 mm SL; 170 and 175 mm TL) and ZMA 111.086 (1: Biwak Island, 4 July 1907, 170 mm TL) (Nijssen *et al.*, 1982). The whereabouts of the figured specimen (from Alkmaar Bay, 20 September 1909, 125 mm TL) is unknown.

Hemipimelodus aaldereni: Based on a single specimen. The 460 mm TL holotype is in the ZMA, number 110.782.

I have not seen type material. Roberts (1978) examined two syntypes and concluded that the species is distinct. I am confident that my material is conspecific with *macrorhynchus* Weber as defined.

Condition of types: None examined.

ETYMOLOGY

Greek, *makros* = long; *rhynchos* = nose, snout. Refers to the species' prominent snout.

MATERIAL EXAMINED

SOUTHERN IRIAN JAYA - 6*, RMNH 28818, Digoel River near Tanah Merah, 14-17 April 1955, coll. M. Boeseman, 167.5-280 mm SL.

SOUTHERN P.N.G. - 1, KFRS F.4685-01 (ex USNM 217075), upper Fly River near Kiunga, Oct. 1975, 348 mm SL; 1*, AMS I. 25998-002, Kone, Wabo damsite, Purari River, 23 Nov. 1974, coll. A.K. Haines, 300 mm SL; 3, AMS I.25998-001, same data, 280-313 mm SL; 1*, NTM S.12351-001, same data, 211 mm SL; 1*, AMNH 58708, same data, 277 mm SL.

7. ZOOGEOGRAPHY OF AUSTRALO-PAPUAN ARIIDS

7.1 "ORIGIN" OF THE ARIIDAE AND IDEAS ABOUT OSTARIOPHYSAN BEGINNINGS

The Siluriformes are believed to have diverged early from the ancestral ostariophysan line (Gosline, 1973, 1975; Roberts, 1973; Briggs, 1979). Of them, the Ariidae is the earliest catfish family found in the fossil record, and it is highly improbable that any catfish group has been derived from them (Regan, 1922; Gosline, 1975; Chapters 1 and 5, this thesis). Ariid fossil material, such as the euryhaline +Vorhisia from South Dakota, has been recorded from the Upper Cretaceous (approximately 85 million years ago [mya]) through the Palaeocene and Lower Eocene (65-50 mya) (Berg, 1940; Novacek and Marshall, 1976; Fitch, 1975 - cited in Fink and Fink, 1981). ~~(refer also: de Muizon et al., 1983).~~

+Rhineastes, a freshwater genus referred to the Ariidae by Lundberg in 1975 is well-documented from the Upper Cretaceous (Berg, 1940; Chardon, 1967) to the Eocene (e.g. Woodward, 1901; Lundberg, 1975). It may have become extinct along with +Hypsidoris in North America during the later Tertiary (Grande, 1987). Catfish fossils have been obtained from many global localities including Europe, England, Brazil, Belgium, Bolivia, Egypt, West and central Africa, north America (Regan, 1922; Gosline, 1975a). Grande and Eastman (1986) have reported morphologically primitive siluroids (not ariids) from the Antarctic Peninsula, laid down at the Late Eocene-Early Oligocene (approximately 38 mya). Because Eocene fossil siluroids are osteologically comparable to recent catfishes and (some) were salt-tolerant, scientists consider that the group is probably much older than the Upper Cretaceous.

Several assessments have been presented on the age of the superorder Ostariophysi (of which siluroids comprise a part). These include:

- Patterson (1975a), noting that the fossil record extends as far as the Upper Cretaceous, surmised that ostariophysans originated at about the Cretaceous-Jurassic boundary (145 mya); i.e. the Upper Cretaceous is the minimum age. Regan (1922) also believed that this group originated in the Early Cretaceous.
- A fossil chanoid species (Order Gonorhynchiformes, sister group to the remaining Ostariophysi: refer 1.6.1) has been obtained from three Lower Cretaceous localities (West Africa, Brazil, Italy [=Tethys]) approx. 130 mya (Rosen and Greenwood, 1970; Patterson, 1975a). This fossil is little different from modern chanoids, suggesting that the common ancestor is much older (ibid.). Novacek and Marshall (1976) noted that pre-Ostariophysi occurred in Africa-South America to the Late Jurassic. They concluded that the Ostariophysi evolved from a gonorhynchiform-like ancestor during the very Early Cretaceous.
- Myers (1967) placed the origin of the ostariophysans in the Late Triassic period, approx. 220 mya, although Briggs (1979) believed that the early ostariophysans developed later, in the Lower Cretaceous, perhaps even earlier (= Late Jurassic).

The fossil record is mainly Tertiary, with unmistakable ostariophysan fossils having been laid down in the Lower Palaeocene and Eocene to Recent times.

There are several pre- and post-continental drift theories of the "centre of origin" of the ostariophysans, such as:

1) Ostariophysi originated and evolved in the one continent formed by South America, Africa and Greater India (Regan, 1922);

2) South America is the continent of origin for characins and catfishes (Chardon, 1967);

3) After analysis of earlier views of ostariophysan biogeogeography, Novacek and Marshall (1976) concluded that there are three likely areas of origin: Gondwanaland, Africa or South America. They finally favoured South America;

4) The "Oriental Region" is the "modern center of evolutionary radiation" of the ostariophysans (Briggs, 1979: 116). He rejected Novacek and Marshall's views;

5) Southeast Asia and South America were primary centres for diversification (Gosline, 1973; 1975), with the "zoogeographic difficulty" (p. 25) of Africa in-between. Roberts' (1975: 279) observation that "One of the most intriguing gaps in the African fossil record is the absence of any ostariophysans prior to the Eocene" echoes this dilemma;

6) Working from the past and present distribution of the gonorhynchiform fishes, Gery (1969), Patterson (1975a) and Roberts (1975) concluded that Africa was the site of ostariophysan origin.

From analysis of these and other authors' views (e.g. Greenwood _et al._, 1966), there emerges compelling evidence that the Ostariophysi originated in West Gondwana, at least before the separation of Africa - South America, which commenced (for Africa) in the Jurassic period. Further evidence of this comes from my study, that is: a) the freshwater Madagascan siluroid _Ancharius_ is almost certainly referable to the primary freshwater family Mochokidae (and _not_ to the Ariidae) (so dispelling Patterson's [1975a] hesitation); and b) _Galeichthys_, probably the most plesiomorphic ariid taxon, is confined to southern Africa and SW South America.

7.1.1 Salt-water or fresh?

Many fish biogeographers believe that ostariophysans originated and evolved in freshwater (e.g. Regan, 1922; Gosline, 1973, 1975, 1975a; Briggs, 1979; McDowall, 1981; Springer, 1982). Gosline (1973; 1975a) surmised that catfishes may have become the first of the ostariophysans to have developed large-river, thence estuarine types; and that they dispersed widely over waters at that time impassable to other ostariophysans.

In contrast, Patterson (1975a) cogently expounded the thesis that the original ostariophysans were more salinity-tolerant than the present-day taxa, and he disputed Myers' (1967) and Greenwood *et al.*'s (1966) view that Mesozoic teleostean groups mostly occurred in freshwater. Patterson deduced that the life history of *Chanos* (Gonorhynchiformes, ostariophysan sister group, Lower Cretaceous fossils), which breed in highly variable, saline inshore and brackish waters, is plesiomorphic: i.e., if the primitive *Chanos* is euryhaline, fully freshwater life is a *derived* habitat preference.

If Patterson is correct, it is reasonable to expect phylogenetic studies to show that the euryhaline ariids and plotosids are the most primitive catfishes; and that from them, all other catfish evolved. This is not so (refer for example, to character analyses, Chapters 3 and 4, this thesis). On the other hand, if freshwater is the primitive water habitat, is there any life cycle stage of the coastal ariids when salinity is least tolerated? Harvey (1972), Rimmer and Merrick (1983) and I (biological notes, Chapter 6) have recorded that salt-water inhabiting ariids are least salt-tolerant as larvae and young, only becoming able to osmoregulate successfully in higher salinities with increasing age. Accordingly, as larval growth proceeds, the brooding parent moves from lower to higher salinity water. Generally, euryhaline ariids also inhabit lower salinity water for spawning (Lowe-McConnell's statement [1987: 173] is essentially incorrect for the ariids).

Comparative studies of catfishes and all ostariophysans with respect to salinity tolerance, is long overdue. In conjunction with continuing phylogenetic studies, it should do much to elucidate the zoogeography of fishes.

7.2 ARIIDS IN AUSTRALIA AND NEW GUINEA

Australia remains the only large landmass once part of Gondwana, where primary freshwater ostariophysans (refer Myers, 1951; Roberts, 1975) do not (and did not) occur. The reasons why such fishes are not in Australia and New Guinea are: 1) temperature (Patterson, 1975a); 2) an early loss of connection between Australia and other continental (Gondwanan) landmasses (Gosline, 1975a); and 3) the great distance across Gondwana between South America and Australia (Tyler, 1979).

The almost total absence of primary and secondary (*sensu* Myers, 1951) division fishes in this region has enabled the adaptive radiation of ariid and plotosid catfishes (Roberts, 1978) in estuaries and rivers (the primary freshwater osteoglossid *Scleropages* and the secondary freshwater *Lepidogalaxias* and lungfish *Neoceratodus* appear to be remnants of ancient ichthyofaunas [Patterson, 1975a; McDowall, 1981]). The Ariidae as a unit are peripheral division freshwater fishes. They live readily in both fresh and salt-water, "so that the sea serves as a highway to their dispersal" (Roberts, 1975: 253). Some peripheral division fish may evolve endemic freshwater forms, or exist for generations solely in fresh water (*ibid.*).

Primary and secondary division fishes exhibit a tendency to exclude more euryhaline (e.g. peripheral) fish from the freshwater habitat they occupy (Roberts, 1975). The global distribution of Ariidae epitomises this phenomenon: although there are endemic suites of ariid taxa along the Atlantic and Pacific coasts of central America and NE South America, West Africa, the Indian subcontinent and many areas of S.E. Asia, ariids are largely absent from the freshwater rivers of these regions - where primary and secondary division fishes are dominant. On the other hand, endemic riverine or lacustrine ariids have evolved in Australia and New Guinea, parts of S.E. Asia (e.g. burmanicus, acutirostris, borneensis, magatensis - refer Appendix A), and central American lakes (e.g. Potamarius species, "Cathorops" aquadulce [Meek]). Roberts (1978) compared the Fly River ichthyofauna with that of the Kapuas River in Borneo and speculated on the effect domination by primary division fishes may have had on early ichthyofaunas.

Trophic specialisations and large size have been the main adaptations exhibited by Australo-Papuan ariids - moreso than other fishes in the Fly (Roberts, 1978) and Purari (Haines, 1983) river systems. Despite the high number of endemic ariids in this region and the absence of competition, the adaptations to riverine conditions they possess are "modest" (Roberts, 1978: 19) when compared to those of other tropical, continental ichthyofaunas. Nevertheless, because (1) ariids are a "second order" member of the "taxon cycle" (Roberts, 1975), this minimum adaptive level may not be unusual at that category; and (2) the duration of these ~~water~~ habitats has been very short in geological time, one could expect that adaptive radiation is still taking place - for example, regionally different morphology and colouration in "A". leptaspis (refer 6.6.13) and "A". berneyi (refer 6.6.9.2).

Biogeographic rationalisations of Australo-Papuan ariid speciation depend on several factors: a) determination of phylogenetic relationships between taxa (Brundin, 1975; Patterson, 1975a; Nelson and Platnick, 1981; McDowall, 1981, among others); thence b) the effectiveness of vicariant events as barriers to dispersal and promoters of speciation (Rosen, 1978; Nelson and Platnick, 1981; Wiley, 1981); and c) dispersal and vicariant events (Nelson, 1984; Humphries and Parenti, 1986). General evolutionary patterns and consideration of ariid "properties" are also relevant. I have addressed the first factor in Chapter 5, and discuss the remainder below. An appropriate introduction to that discussion, is a description of species distribution in this region.

7.2.1 Distribution of Australo-Papuan ariids

Early observations on the distribution and speciation of freshwater fishes in New Guinea and Australia generated the concept of fluvifaunal provinces. These "fluvifaunulae", zoogeographic regions and areas which "coincide with the divisions indicated by geological and botanical research" were first defined by Iredale and Whitley (1938), and contain distinct, faunal assemblages. Subsequent workers, including Whitley (1947), Munro (1964) and Lake (1971), redefined and discussed the freshwater fish fauna of these provinces or drainage basins. McDowall (1981: 1267) correctly pointed out however, that these biogeographically convenient provinces cannot represent the "dynamics of fish distribution and dispersal". The distribution of freshwater and, to a large extent, coastal Australo-Papuan ariids generally concurs with these defined "fluvifaunulae" (at least in northern Australia and New Guinea). Whilst I agree with McDowall, it is "convenient" to describe ariid distribution in this region by relating it to these faunal provinces.

Iredale and Whitley's Leichhardtian province (fig. 249), from Port Essington eastwards to the west of Torres Strait, incorporates the southern half of New Guinea - a province later termed the Riechian (refer Munro, 1964). Lake (1971) split the northern Australian Leichhardtian into two drainage basins: his area 4 encompassing the Gulf-draining rivers, from Cape York to Arnhem Land; his adjoining area 5 spanning the Kimberley region to SW of the Fitzroy River. Finally, the rivers in New Guinea north of the central cordillera which runs lengthwise through the major axis of the land, form the Gaimardian province.

Weber (1913) and Munro (1964) presented comprehensive ichthyofaunal lists of New Guinea and drew comparisons between the southern and northern components. Munro (1964) also compared them with the Leichhardtian province fishes. Approximately one quarter of the southern New Guinea freshwater fish taxa occur in northern Australia (Munro, 1964; Allen and Boeseman, 1982), and the link between these areas is well-recognised (e.g. Berra, Moore and Reynolds, 1975; Roberts, 1978; Allen and Hoese, 1980; McDowall, 1981). However, the northern (Gaimardian) and southern (Riechian) New Guinea freshwater fish fauna are not closely linked, sharing only approximately 7% of fishes (Allen and Boeseman, 1982: Munro's (1964) estimate of 40% refined downwards as a result of taxonomic revisions and further collecting).

The Australo-Papuan ariids are divided among these regions as follows (and refer species distribution maps in Chapter 6):

a) *Leichhardtian*. This province contains two freshwater taxa ("*A*". *midgleyi*, "*A*". *berneyi*); four freshwater-estuarine taxa ("*A*". *leptaspis*, "*A*". *graeffei*, "*A*". (*Hemiarius*) species 1, *Cinetodus froggatti*); and six largely shallow coastal-estuarine taxa ("*A*". (*Hemiarius*) species 5, "*A*". (*Hexanematichthys*) *mastersi*, "*A*". *proximus*, "*A*". species 3, "*A*". *armiger*, "*A*". species 4). The two subspecies of "*A*". *midgleyi* have allopatric distribution, one in each of Lake's (1971) drainage basins 4 and 5 (fig. 229); and "*A*". *berneyi* largely inhabits Lake's area 4 (fig. 188). The remaining taxa exhibit a narrow (e.g. species 4, species 5, *froggatti*) to wide (e.g. *graeffei*) distribution in northern Australia. "*A*". *graeffei* and "*A*". *proximus* also occur along the east coast of Australia - inside (i.e. west of) the coral barrier reefs (Jardinean to Lessonian provinces of Iredale and Whitley [1938]; area 3 and 2 of Lake [1971]).

b) *Riechian*. All taxa present in fresh, estuarine and coastal waters of Australia, except for "*A*". *midgleyi*, are also found here (i.e. they are "bidomicilic" [Tyler, 1972]). There are also: eight freshwater taxa (*Nedystoma dayi*, *Cinetodus carinatus*, *Cinetodus* (*Pachyula*) *crassilabris*, *C*. (*P*.) *conorhynchus*, "*A*". *taylori*, "*A*". *augustus*, "*A*". *latirostris*, "*A*". *macrorhynchus*) and four freshwater-estuarine taxa (*N*. *novaeguineae*, "*A*". (*Cochlefelis*) *danielsi*, "*A*". (*C*.) *spatula*, "*A*". species 6). Based on known distribution (reflecting collecting effort) therefore, most ariid taxa occur largely in central southern New Guinea rivers and coastal waters, the region in New Guinea most richly bestowed with freshwater fishes. Ariids are not found east of the Laloki River system (the eastern limit of *latirostris* and *graeffei*).

c) *Gaimardian*. In this province are four freshwater ariid taxa ("*A*". (*Brustiarius*) *nox*, "*A*". (*B*.) *solidus*, "*A*". *velutinus*, "*A*". species 7) and one freshwater-estuarine taxon ("*A*". species 2). Weber (1913) and Allen and Boeseman (1982), have compared the northern and southern New Guinea freshwater fish faunas. The northern rivers have a much less diverse fauna; and ariids do not inhabit rivers (e.g. the Gogol) east of the Ramu River (G.R. Allen, pers. comm.). No endemic freshwater-coastal ariids are common to the Gaimardian and Riechian provinces.

Of the marine taxa finally, "*A*". *thalassinus* and "*A*". *bilineatus* range throughout tropical and subtropical New Guinea and Australia. However, Genus 1 *argyropleuron* and *nella* are only found off northern Australia (as far south as Moreton Bay and Townsville, respectively) and southern New Guinea, whilst Genus 1 *polystaphylodon* occurs only along the central northern New Guinea coast.

The recognised endemic ariid fauna extends to the limit of the Sahul Shelf, biogeographically defined as Lydekker's Line (Woodland, 1986). For example, "*A*". *proximus* and "*A*". *leptaspis* occur around the Aru Islands, *leptaspis*, *latirostris*, *graeffei*, *armiger*, species 4 and species 6 have been collected from the (southern) Vogelkopf Peninsula, and ariids are not present in the Coral Sea. Genus 1 *polystaphylodon* and other northern New Guinea taxa encroach onto the Pacific Plate western margin, within the region biogeographically and geologically distinguished as the Andesite Line (Springer, 1982).

Several allopatric and disjunct distribution patterns of Australo-Papuan ariids and related S.E. Asian taxa indicate the effectiveness of vicariant and/or ecological events as barriers and their influence on speciation:

- one in 12 Australian (freshwater) and 12 of the southern New Guinea ariids (8 freshwater and four freshwater-estuarine taxa) are not bidomicilic, i.e. *midgleyi* has not "moved" into the Riechian province, nor have eleven southern New Guinea taxa "moved" into the Leichhardtian.
- "*A*". *leptaspis* and "*A*". species 2 have allopatric distribution in New Guinea (figs 216, 233). Although phylogenetic analysis failed to show a clear sister-species relationship (Chapter 5), these taxa are morphologically and ecologically very similar.
- the closely related "*A*". *velutinus* and "*A*". *taylori* also have allopatric distribution (figs 162, 165).
- the ancestral taxon *midgleyi* formed two allopatric subspecies in northern Australia.
- members of the subgenus *Hexanematichthys* have disjunct distributions: *sagor* occurs west of (the biogeographer's) Wallace's Line (Woodland, 1986) (i.e. on the Sunda Shelf) whilst *mastersi* occurs to the east of Lydekker's Line (i.e. on the Sahul Shelf).
- members of the subgenus *Hemiarius* are similarly distributed: *stormii* in the west, species 1 and species 5 in the east.
- *Cinetodus* subgenus: *froggatti* generally lives in fresh and estuarine waters between the Digoel River and Gulf of Papua, and in freshwater of the Roper River (Australia); yet whereas it is found only in the freshwater Lake Murray of the Fly River system, in the Purari River system it inhabits only estuaries (Haines, 1983). *C*. *carinatus*, having only a wide, freshwater distribution in Papua (Lorentz to Lakekamu River) however, is completely absent from the northern Gulf rivers Kikori, Era and Vailala.
- similar, disjunct distribution patterns have been noted in other ariids, for example "*Arius*" *macrorhynchus* is absent from several Gulf

rivers, and "*Arius*" *latirostris* is locally abundant or rare throughout its range.

The converse of this, is the wide distribution of two representative of the species group *Netuma*: *thalassinus* and *bilineatus*. The vicariant events to the western margin of the Australia Plate, which affected the distribution of other ancestral ariid taxa, do not appear to have influenced this species pair. Possibly comparable to that, are the representatives of Genus 1 in Australia and New Guinea. They have a disjunct distribution in this region, yet range throughout S.E. Asia to Sumatra (*polystaphylodon*) and the east coast of India (*nella* and *argyropleuron*).

7.2.2 Ariid success and evolution

The success of the Ariidae in the Siluroidei, as demonstrated by their historical longevity and extensive global distribution is, in my view, largely due to three factors:

1) their tolerance of a variety of ~~water~~ salinities. Use of a range of ~~water~~ salinity from sea water (35 ppt) to fully fresh water enables access to much greater habitat diversity. Movement from a salt to a fresh water environment or vice versa, poses significant osmoregulatory problems for fish (i.e. to retain salt in fresh water, retain water in sea water). It is worth noting that even intraspecific races can vary physiologically with respect to salt tolerance, depending on the characteristics of the water in which they occur (Lagler *et al.*, 1962; Marshall, 1966); and many stenohaline fishes can gradually adjust to living in considerably less saline waters. According to Lowe-McConnell

(1987), they cannot withstand "significant" salinity changes, *cf.* euryhaline coastal and estuarine fishes able to withstand such changes.

In considering fishes, relative salinity should form a barrier to some extent. Authors differ on this issue. Lowe-McConnell (1987) believed that most primary freshwater fishes cannot tolerate sea crossings and that faunal exchanges of primary fishes between land masses took place in the Pleistocene when sea levels were lowered. Yet Gosline (1975a) stated that few, if any, freshwater groups cannot tolerate brackish or salt water, and he cited disparate examples of salt-tolerant primary freshwater fishes. Roberts (1973) and Briggs (1979) believed that siluroids crossed salt water to access different landmasses. Much of the low salinity Aral Sea's fish fauna are cyprinoids (Marshall, 1966), and Lagler *et al.* (1962) cited two cyprinid taxa which tolerate salinities up to 17 ppt.

2) oral incubation of the young. Parental care in fishes most likely evolved in freshwater (1.~~1~~.2; refer 7.2) in the face of competition which reduced suitable juvenile habitats (Baylis, 1981) and predator pressure (Lowe-McConnell, 1987). From nest-building, territorial guarding and egg fanning, parental care evolved to the pinnacle of oral brooding. It is usually performed by the male parent, as this is more reproductively cost-effective: the "parental investment strategy" of Trivers (1972; cited in Lowe-McConnell, 1987).

This mode of parental care enables ariids to disperse very effectively and colonise a wide~~r~~ habitat range. They have no "fixed" territory to defend (as, for example, for reproductive purposes), and they take their young with them. Brooding males inhabit a series of suitable water environments as the young grow.

3) their ability to morphologically diversify to take advantage of "vacant" habitats. In Chapters 3 and 4, I pointed out features of ariid

morphology which are either "general" (plesiomorphic) or apomorphic (and/or adaptive). This combination has enabled the ariids to take advantage of (new) habitats which became available over time. In so doing, they have frequently undergone adaptive change, culminating in speciation.

The speed and manner in which evolution and hence speciation occurs have been the subject of several works. Stanley (1979; 1982), Mayr (e.g. 1963) and Eldredge and Gould (1972) advocated the "punctuational model" in which speciation occurs in localised populations - often rapidly after long periods of stasis (i.e. in fits and starts). Conversely, the traditional, "gradualistic" model of Dhobzhansky (1972~~)~~, cited in Stanley, 1982 assumes that evolution occurs as a continuum within established species (i.e. by gradual change). Stanley (1982) also recognised *adaptive* radiation (a function of punctuated evolution) as an alternative to *divergent* speciation.

Lundberg *et al*. (1986) recognised evolutionary stasis of at least 15 million years in the serrasalmine *Colossoma*, albeit noting dental diversity in this group indicative of past evolutionary lability. Several other fossil South American fishes are also known to have long, conservative histories, and Lundberg *et al*. (1988) discussed extant pimelodid catfish taxa which are unchanged since the Miocene. These are also the legacy of persistent and continuous habitats - such as large, lowland rivers. The sea, inhabited by most "*Arius*", constitutes another persistent habitat. However, changed salinity regimes, bottom types, water temperature and clarity, as well as input of enormous quantities of mud, silt and organic material from relatively recently formed tropical rivers, create new and unstable habitats in which adaptive speciation can take place [and refer McDowall's (1981) point on fragmentation of gene pools].

The punctuational model, as expounded by Stanley (1982) is appropriate to the Ariidae. Although the majority of ariid taxa appear to be largely phyletically unchanged over millions of years (Newton, 1889; Regan, 1922) rapid ariid speciation has occurred in particular areas - in this instance, New Guinea and Australia. "Parent" taxa (e.g. "*Arius*") may continue to evolve in a very slow manner in response to the continually changing environment, even when major geological changes have occurred; yet localised populations are able to "suddenly" transform into distinct, new taxa (e.g. Australo-Papuan endemics).

Vari (1988) and Miller (1986) considered the influence of speciation rates, phylogenetic patterns, historical vicariant events and other factors on areas of endemism in central and South American fishes. Again, relevant to the Ariidae, Vari (1988: 363) stated: "the common distribution of a species in two areas of endemism may reflect its ability to overcome barriers between the areas of endemism: it is an index of the vagility of the species relative to such barriers rather than necessarily of the historical relationships between particular areas". This statement supports Woodland's (1983) observation that, as isolation is a function of a species' potential for colonisation, a species' "life-style" can be correlated with its distribution and potential for speciation. Hence, the more vagarious [stet] a species, the broader will be its distribution and the less likely it is to speciate. The wide-ranging "*Arius*" species *thalassinus*, *bilineatus* (*Netuma* species group) and possibly Genus 1 taxa (*dussumieri*, *nella*, *polystaphylodon* and *argyropleuron*) are examples (yet see below, 7.4.5).

7.3 PALAEOHISTORY OF NORTHERN AUSTRALIA AND NEW GUINEA

7.3.1 Palaeogeography

Although the Australian Plate began to separate from Antarctica about 90 mya, it remained attached to that continent through the southeastern section until approximately 55 mya (Coleman, 1980; Whitmore, 1987). After marine incursions from the west and significant seafloor spreading during the Early Tertiary, Tasmania finally disengaged. The northward drift of the Australian Plate which then commenced, continues to this day. By 35 mya, the juvenile Southern Ocean had become an extensive seaway.

India, Africa and more recently, South America, had separated from Antarctica well before Australia-New Guinea began its northward drift. Several continental fragments, now forming present-day Tibet, Burma, Malaya and Sumatra, and some other S.E. Asian islands, were once part of northern and northwestern Australia-New Guinea (i.e. the north margin of eastern Gondwanaland). These fragments were rifted from the Australian Plate in the Mesozoic at about 160 mya (Late Jurassic) (Whitmore, 1987; Audley-Charles, 1987) and collectively are recognised as Sundaland. The Sundaland block lay well east of Greater India until the Late Cenozoic (Powell et al., 1981). Brundin had in 1975, suggested an ancient association of these Asian regions with Australia.

After Greater India had moved further north, outliers of Laurasia (including Sundaland) and Gondwana converged during the mid- to Late Tertiary, bringing the margins of the Indian + Australian and Pacific Plates into collision (yet Audley-Charles [1987] cited suggestions that Australia and Asia were connected as far back as the Early Tertiary and mid-Cretaceous). The collision occurred at about the position of Sulawesi in the mid-Miocene, a tectonic suture forming between Western and Eastern Sulawesi. These events, and a generally tectonically active region, resulted in the present configuration of new islands (such as Java, Timor, the Moluccas) and sea basins between Australia and mainland Asia. S.E. Asia has remained in its present latitude since the mid-Cretaceous (Powell et al., 1981). A great subduction system is continuous from Burma around the Banda Arcs, where collision with the Australia-Arafura-New Guinea continental shelf is current (Hamilton, 1988). Formerly southward-facing, these arcs have rotated and folded significantly anticlockwise and clockwise with the rapid northward movement of the Australia Plate and the westward movement of the Pacific Plate and Sundaland (Powell et al., 1981; Hamilton, 1988); events which caused S.E. Asian landmasses to rotate approximately 45° since the mid-Cretaceous.

There have been highly complex geological phenomena in the Malesian Region (i.e. approximately Sumatra to eastern New Guinea) over the past 30 million years. Largely according to Audley-Charles (1987), the island relationships and vicariant events which may have been significant in ariid dispersal and subsequent speciation in Australia and New Guinea are:

- most of the islands between New Guinea and Sulawesi (including Ceram, Kai, Tanimbar, Timor and Roti) belong to Australian Gondwanaland (Hamilton, 1988). These non-volcanic islands have either: risen as a result of sediments from the Australian Plate being piled up on the Asian side of the Banda Arc trench; or formed by plate rupturing as a result of overthrusting of the trench and the Plate's collision with the inner Banda Arc. Either event occurred in the Pliocene, approximately 5 mya;

- shallow seas probably existed in front of the Banda Arc, before its collision with the Australian continental margin;
- the northwestern Molucca Islands near Sulawesi (Banggai and Sula) are a rifted Gondwanan continental fragment from New Guinea;
- the north Moluccas (Halmahera, Bacan) have affinity with New Guinea and are connected by shallow seas with the Vogelkopf Peninsula. The Moluccas are tectonically detached from New Guinea;
- Eastern Sulawesi probably separated from New Guinea in the Palaeogene (approximately 30 mya) and began to emerge as an island in the mid-Miocene;
- Western Sulawesi separated from Borneo by a flooded Makassar Strait at about the Early Miocene;
- the Banda Sea floor, which in places is extremely deep, is most likely a piece of Late Jurassic Tethys Ocean floor.

New Guinea underwent considerable geological activity during the Cenozoic. Central and northern New Guinea were cut into large fault block slivers with strong vertical and sinistral movement as a result of the Plate convergences (Coleman, 1980). Eastern New Guinea experienced four subduction zones at various times, at least three episodes of sea floor spreading, and three different continental/island-arc collisions and consequent elevations (along the Aure-Moresby Trench - Late Eocene; the Wewak-Trobriand Trench - Late Miocene; New Britain Trench - Quaternary) (Kroenke, 1984). New Guinea's outer rim and "tail" shifted to the northwest early in the Cenozoic (Coleman, 1980); and between 22 and 15 mya (mid-Late Miocene), the rifted leading edge of New Guinea collided with and accreted ancient rock fragments on the margin of the Pacific Plate, generally accepted as being part of the Outer Melanesian Arc (Coleman, 1980). By the end of the Pliocene (2 mya), most of the present island of New Guinea had been created, and the Sepik-Ramu basins formed, probably from the collapse of upper crustal rocks and rifting. Also in the Quaternary, the NE (Finisterre-Huon Peninsula) coast of New Guinea was uplifted (Kroenke, 1984). The sedimentation of the northern New Guinea basins has been detailed by Harrison (1969) and Loffler (1977). These areas have been sequentially inundated by the sea right up to Recent times.

During the world-wide sea-level rise through the Jurassic and into the Cretaceous, much of Australia and New Guinea was flooded by marine transgressions; but by the Late Cretaceous, almost all of the continent was above sea level. According to Audley-Charles (1987), this situation existed during the Early Tertiary, although Harrison (1969) and Coleman (1980) detailed extensive sea and lake systems to more recently than 10 mya. Because of continuing convergence, tectonic uplift and collisions in eastern Indonesia since the mid-Miocene, it is however, very difficult to determine how much of Malesia was covered by sea during the Cretaceous and Early Tertiary.

The area between New Guinea and Australia known as the Carpentaria Basin, was isolated from the Arafura and Timor Seas between approximately 75,000 and 10,000 years ago (Torgersen et al., 1985). In pre-Pleistocene times, the Fly River (and probably the Digoel) maintained a ~~competent~~ consistent, moderately large inflow to the Carpentaria Basin from the northeast, and more seasonal inflow came from Australian rivers. To the west, a broad outflow channel extended to the edge of the continental shelf (Nix and Kalma, 1972; Torgersen et al., 1983), incised through the Arafura Sill to a depth of approximately -105 m below present sea level. Torgersen et al. (1983; 1985) confirmed Nix and Kalma's (1972) prediction that a large lake (Lake Carpentaria) existed there during the low sea levels of the last Pleistocene glacial maximum, but from around 26,000 to 10,000 years ago. The "Arafura Sill", at -53 m below present sea level, formed the broad western shoreline of Lake Carpentaria. The catchment area of the lake (fig. 250), which at its maximum would have covered more than 165,000 km^2, and have a maximum depth of only 16 m, also included the extent of all the present-day Gulf-draining rivers, i.e. the Leichhardtian fluvifaunulae (7.2.1).

Before 36,000 years ago, the Carpentaria Basin contained marine or brackish water, despite the high inflow of fresh water (Torgersen et al., 1985). However, the East-West Quaternary uplift along the Oriomo and Morehead axes diverted the flow direction of the New Guinea rivers: the Digoel to the Arafura Sea, the Fly-Strickland to the Coral Sea (Torgersen et al., 1983). The Basin subsequently, would have experienced increasingly dry conditions, high evaporation, and aeolian infilling and deposition along its margins. The fresh to brackish water it contained could still have flowed seaward through the deep western channel. Lake Carpentaria became identified approximately 26,000 years ago. Up to 10,000 years ago, when rising sea levels restored fully marine conditions, it contained brackish to saline water of variable levels.

Despite extensive areas of land in the Pleistocene, the seaway between Timor and northwestern Australia persisted, although it was reduced both in depth and width (the Sahul Shelf margin was less than 100 km from Timor: Van Andel et al., 1967). The Bonaparte Depression on the Sahul Shelf between NW Australia and Timor, now only 145 m deep and connected to the deep Timor Trough by the 240 m deep Malita Shelf Valley (Van Andel et al., 1967), would have been an enclosed, large lagoon or inland sea in the Pleistocene. All large and many smaller rivers drained into the (then) Bonaparte Lagoon from the adjacent Australian-New Guinea continent eastwards, and some shorter streams entered it from the west. The lagoon was a normal, shallow marine environment, with little open sea communication (Van Andel *et al.*, 1967).

7.3.2 Palaeoclimatology

In the Late Cenozoic, there was repeated alternation of glacial and interglacial periods globally which initiated complex environmental changes. During the glacials, the world experienced reduced sea level, a cooler climate, and increased aridity, which in turn had profound effects on floral and faunal distributions.

1) Sea levels. S.E. Asia experienced a variety of sea levels over the Late Tertiary. The global maximum lowering in the Quaternary (to 2 mya), was approximately 200 m (but estimates vary), most likely during the mid-Pleistocene (Morley and Flenley, 1987). During this event, the Sunda and Sahul Shelves would have been exposed, and submarine channels show the probable courses of rivers across them.

Widely fluctuating sea levels occurred in the Arafura and Timor Seas and Torres Strait over the past 140,000 years (Torgersen *et al.*, 1985) and over approximately the past half million years, three to six periods of lower sea levels have been sufficient to close the Torres Strait (Woodland, 1983; Torgersen *et al.*, 1985). Jongsma's (1970) estimates of sea level heights and presence in this region differ somewhat from those of Torgersen *et al.* (1985), who estimated the lowest sea level was -140 m below present at approximately 20,000 years ago. Galloway and Loffler (1972) claimed that the land connection with Torres Strait was most recently broken between 6,500 and 8,000 years ago.

Curray (1965 - cited in Van Andel et al., 1967) estimated lowest sea level in the Timor area occurred 18,000 years ago, and there have been no subsequent fluctuations. Sea level rise was at first rapid (shelf edge regressing landward by 25-45 m per year), but slowed down considerably about 8,000 years ago.

2) Seasonality and rainfall. The Early to mid-Tertiary climate in Australia-New Guinea was warm and moist tropical (Kemp, 1978; Coleman, 1980) and interglacials saw rainforest predominating. Van Andel et al. (1967), Nix and Kalma (1972) and Morley and Flenley (1987) cited evidence of strongly seasonal climates in S.E. Asia and Australia over the Late Tertiary and Quaternary at times of lowered sea levels - lower winter and higher summer temperatures than at present. Parts of the Sahul Shelf were arid or semiarid. Rainfall was greatly reduced along the present Australian coastline (and hence, inland) because of reduced tropical cyclonic activity caused by lower sea surface temperatures (Webster and Streten, 1972; Torgersen et al., 1983); and less moisture in the NW monsoon winds because of the large, exposed land areas (Nix and Kalma, 1972). Approximately half of the present rainfall totals would have been received, both winter and summer. A similar situation would have existed in south-central New Guinea. Rainfall in the Torres Strait area was so low during the glacial maxima, that insufficient fresh water flowed into the Bonaparte Lagoon to significantly reduce its salinity (Van Andel et al., 1967). Essentially, all winter precipitation was eliminated, and the Sahul Shelf experienced a steppe climate. After sea level rose but before Torres Strait finally flooded, the "ponded" Gulf of Carpentaria water warmed, producing high evaporation and a warmer and wetter climate than at present (Nix and Kalma, 1972). Widespread lakes and swamps, and rivers with sustained

flow, would have contributed to surplus water from runoff and drainage levels 30-40% higher than at present.

3) Temperature changes. The northern Australia-southern New Guinea sea surface temperature in the late Quaternary maximal glacial conditions, was 2-3°C lower than it is today - especially in the western regions (Webster and Streten, 1972). Compared to today's mean air temperature, it would have averaged from 3.5°C less at 20,000 years ago to 1°C more at 8,000 years ago (Nix and Kalma, 1972). Changes in planktonic Foraminifera in the Torres Strait at the end of the last glaciation, also suggest slightly cooler water (Van Andel et al., 1967) at the height of the glacial period. These lower temperatures were caused by varied ocean current regimes: the warm Pacific tropical water not reaching the area because of the closed Torres Strait, and cooler, NE currents off the western Australian coast entering the Timor Sea.

4) Vegetation. Vegetation zonation in Australia was in effect virtually by the mid-Miocene (Kemp, 1978), and would have been encouraged by the fluctuating Quaternary climate. Nix and Kalma (1972) outlined the main vegetational types in New Guinea and northern Australia from the most recent glacial maxima to the present. The open forest and woodland areas were more extensive between 17,000 and 14,000 years ago, during the driest period, and broadleaf, open forest covered the northern and southern New Guinea drainage basins. At approximately 8,000 years ago, when a wetter and warmer climate existed in the Gulf of Carpentaria, closed forest covered New Guinea except for the central-southern region, and open woodland and forest extended to approximately 16°S latitude. Tropical, closed and broadleaf forests have not existed on northern Australia over the past 20,000 (except narrowly on the NE coast).

7.3.3 Present-day geography

The Torres Strait area ranges from 13-80 m deep. Most of the Arafura Sea is 40-80 m deep, the Gulf of Carpentaria has a maximum depth of 69 m (Torgersen et al., 1985), and the westward continental shelf margin ranges from 120-200 m below sea level (Galloway and Loffler, 1972). Papua and northern Australia are separated by a 150-500 km wide sea (excluding islands). Sea surface temperatures (Timor Sea) range from 26-28°C in winter to more than 29°C in summer (Van Andel et al., 1967).

The modern coastal fringes of these landmasses have similar depositional landscapes. New Guinea is largely covered by closed forest, although central-southern New Guinea shares with northern Australia an open, deciduous forest, or monsoonal woodland. Coastal New Guinea and northern Australia experience a marked, monsoonal climate (or "wet-dry tropics"): the highest rainfall occurs between December and May over most of the region, and between May and August in the northern Gulf of Papua.

Northern New Guinea has four large rivers generally flowing northwards. The origin of the largest river, the Sepik, is separated at its source by only a few kilometres from the Fly-Strickland River system. The northern rivers generally meander across broad, alluvial plains of billabongs, swamps covered with forest, to shrubs and extensive grasslands. There are few estuarine and mangrove areas associated with the river mouths; and the continental shelf is narrow, with deep water close inshore.

The Gulf of Carpentaria and Timor Sea drainage systems (Lake, 1971) have high annual discharges, almost all of it during the summer monsoon; and many rivers are reduced to chains of waterholes during the dry season. Most Gulf rivers have low gradients and flow through a flat coastal belt for approximately 150 km from the sea. Timor Sea draining rivers often flow through very deep gorges. Within each drainage system, the rivers are linked by numerous anabranchs and tributaries in the wet season.

The riverine habitats of southern New Guinea were described by Roberts (1978) and Haines (1979; 1983); and those of northern New Guinea by Coates et al. (1983) and G.R. Allen (pers. comm.). Most rivers flow through dense, tropical rainforest and are considered relatively stable "reservoir" rivers. Very rare dry years do not impede the rivers' flow. Generally, upper river sections have torrential, turbid flow; middle river sections are clear or moderately turbid and fast-flowing, often with associated swamps, backwaters and lagoons, the banks densely vegetated; and the lower sections are increasingly turbid, with more sluggish flow. Tidal influence may extend far upstream and, as in other tropical rivers, the estuaries are rich in organic sediments and biota. The extensive estuaries and wide deltas present on Papuan rivers (e.g. the Fly) are largely absent form the younger Sepik and Ramu Rivers. The large rivers exert a considerable influence on adjacent coastal waters, sediment plumes extending 6-8 km out to sea, with accompanying lowered salinity, during periods of high outflow (Haines, 1983).

7.4 FACT OR FICTION: THE HOW AND WHEN OF AUSTRALO-PAPUAN ARIID EVOLUTION

The turbulent tectonics and complex history of eastern Malesia (refer 7.3) is such that historical dispersal is impossible to trace. However, I am able to postulate the likely sequences of ariid dispersal and speciation in the Australian and New Guinea region, based on the known and conjectured, past and present physical events and environmental conditions which I have described in the previous sections.

No area cladogram (refer Humphries and Parenti, 1986) is proposed, for several reasons:

1) the paraphyletic nature of "*Arius*", and its global distribution;

2) the nature of the proposed phylogeny of the Australo-Papuan ariids (Chapter 5, 6.1) in which homoplasy is significant;

3) the probable close and unresolved relationships of several Australo-Papuan ariid taxa with extralimital taxa (e.g. *Cephalocassis* and "*Cathorops*" with *Nedystoma*; *Sciadeichthys* with "*Arius*" species 6) (refer 5.7); and

4) a number of taxa are distributed or have sister taxa outside of the study region (Genus 1, *Netuma* species group, *Hexanematichthys* and *Hemiarius*).

Despite these realities, generalised tracks (*sensu* Croizat, 1964) can be traced to illustrate the distribution of the endemic taxa *Nedystoma*, *Cinetodus*, *Brustiarius*, *Cochlefelis* and species group A (fig. 251). Furthermore, a study of ariid zoogeography in the Australian and New Guinea region is very worthwhile. It provides an understanding of the adaptability, modes of dispersal, speciation capacity and environmental tolerances inherent in this family. Knowledge of these can be applied in any subsequent zoogeographic studies of this and other catfish families.

7.4.1 Postulated general dispersal and speciation pattern of ariids in southern New Guinea and northern Australia

It is likely the ancestral Australo-Papuan ariid fauna moved into these waters no earlier than 15 mya - i.e. after the collision of Eastern and Western Sulawesi. Lowe-McConnell (1987) pointed out that in most tropical regions, long periods of relative stability prior to the sea level changes and rain periods of the Quaternary, would have permitted wide dispersal of species. Shallow water forms (such as Genus 1) may not have crossed until the Pleistocene, at times when sea levels were lowest. Ariids were not in Australia before the mid-Miocene (7.1, 7.2) despite the tropical Early Tertiary climate which then existed. I suggest therefore, that most extant members in this region are of "recent" origin.

Continued tectonic activity supplemented by widening sea distances since the last glacial maximum (approximately 20,000 years ago), would have isolated the populations here. It probably also eliminated the species' populations in the intervening Banda Sea-Moluccas region, where no brackish and freshwater ariids now occur. These vicariant events would have effectively promoted speciation to the east of the Sunda Shelf. As tectonic activity, plate convergence and periodic marine incursions affecting New Guinea and Australia have continued since the mid-Miocene, there would probably have been several ariid "waves" onto the Sahul Shelf - not all of them successful.

In their capacity as peripheral division freshwater fishes, the ariid ancestors were able to disperse into the "vacant" rivers in the absence of primary and secondary division fishes (these points were developed in 7.2) where "~~punctuational~~ punctuated" evolution took place (7.2.2). Either coastal ariid taxa evolved at the same time, or they represent subsequent "waves" of fishes which were excluded from the by then occupied rivers. The second "option" is more likely. These brackish-water and estuarine taxa frequently replaced freshwater ariids downstream (both in habitat and dietary preferences) and by so doing effectively and in turn, excluded those ariids from the lower rivers and estuaries. The direction of flow of the Digoel and Fly-Strickland Rivers, and probably the Roper, and the volume of water they discharged, suggests there could have been extensive ariid movement between southern New Guinea and northern Australia across the Arafura Sea-Carpentaria Basin; and no restrictions to dispersal would have been effected on the ariids by periodic high fresh- or salt-water levels (7.1.1). It is also probable that ariid movement west of the Sahul Shelf continued via the channels from the Bonaparte Lagoon and the Carpentaria Basin (7.3.1).

Climatic fluctuations contributed to speciation by dividing any possibly recombining fish populations and altering the water environments. The variable sea levels of the last 140,000 years (especially the dry period when Lake Carpentaria existed) and altered climatic regimes (7.3) would have led to the following event sequence: original and/or "second wave" ariids inhabiting the coasts and saline river sections would have survived in the brackish to saline Lake Carpentaria, where both they and the freshwater forms would probably have further diversified. After marine transgressions and the wetter climate experienced prior to the most recent submersion of Torres Strait, the "coastal" taxa dispersed again to New Guinea and Australian shores, and were able to inhabit the seasonally drying northern Australian rivers (possibly a consequence of their "experience" in the drying Carpentaria Basin). Distribution patterns of many southern New Guinea and Australian ariids reflect the recent palaeohistory of the Carpentaria Basin (refer Chapter 6).

The alternative scenario - that the coastal ariids became extinct with the drying of the Carpentaria Basin, a second wave of marine taxa moved in with re-inundation 14,000 to 8,000 year ago, thence speciated in coastal waters only because the rivers were still "occupied" - has problems. The main ones are the very short period for the often high levels of adaptive radiation to occur (e.g. in "Arius" species 4), and the lack of support from known phylogenies (e.g. in Species Group B, which includes berneyi, graeffei and species 3).

Several times in this thesis, I have pointed out the importance of habitat and diet in the distribution of ariids, factors which cannot be underestimated in reconstructing the pattern of ariid speciation in this region. For example, the ariids which earlier radiated into the "vacant" rivers of New Guinea diversified in response to the habitat and the food those waters provided. As these items were (and are) largely absent from northern Australia, the southern New Guinea freshwater species did not move into those rivers, even in the pluvial period of 8,000 years ago. Allen and Hoese (1980) suggested that water temperature could have also been important. Haines (1983) provided a very good summary of the interrelationship of diet, habitat and ariid taxa in the Purari River system. Mud and detritus form the basis of the food chain in the southern rivers. Decapods (prawns and yabbies) and molluscs are particularly numerous, diverse, and very important sources of food, and insects, their larvae and plant material abound in the swiftly-flowing, permanent rivers. The freshwater ariids in southern New Guinea exhibit varying degrees of morphological specialisations associated with diet, and occupy most available trophic niches (Table 3; Chapter 4.4). The importance of diet (and water clarity) as a dictator of distribution pattern, is best displayed in Cinetodus froggatti (7.2), in which distribution is closely linked with the distribution and abundance of gastropod molluscs. The disjunct distribution patterns of ariids which feed on insects and higher plants (e.g. macrorhynchus and latirostris) may be a reflection of the vegetation type and its thickness along rivers, river flow rate, and the extent of the mid and upper river sections.

The two freshwater taxa which survived in northern Australian rivers during the dry glacial period, are adapted to a different climatic regime than that of most freshwater southern New Guinea taxa. Interestingly, "Arius" berneyi populations in New Guinea are only located in the area where similar conditions occur (fig. 188); and it is possible that these disjunct populations are actively evolving (refer Discussion, 6.6.9.2). In the case of "Arius" midgleyi, the one taxon was probably widely distributed in northern Australian rivers before the last glacial maximum when the drying Arafura Sea isolated the Timor and Gulf of Carpentaria drainage systems. Interriverine movement via the coast or connecting streams became impossible, hence the evolution of subspecies in each drainage (vicariant speciation).

7.4.2 Postulated general dispersal and speciation pattern of ariids in northern New Guinea

The ariids would have moved into this region from the west at the same time as southern ariids. Similarly, they occupied the "vacant" rivers and speciated.

That is the simple explanation. The northern rivers are younger than those in the south, there are affinities with southern ariids (e.g. Species Group A, of "Arius" taylori, velutinus and species 7) and the coastal shelf is narrow. It is possible the fresh and brackish water ariids in these river systems shared ancestors with the southern ariids, and some vicariant event(s), such as tectonic uplift along the several faultlines (7.3.1), interrupted common distribution and promoted speciation (in both regions). The higher altitude habitat preference and phenotypic similarity of taylori and velutinus tends to support this hypothesis, but not (necessarily) the phenotypic similarity of "Arius" leptaspis and "Arius" species 2 - taxa which do not appear to be closely related phylogenetically (refer Chapter 5.6, 5.7). A less likely explanation is that the coastal descendants of the "first wave" ancestors in the north became extinct after adaptive radiation into the rivers had occurred. I favour the view that they were not there in the first place. The absence of ariids in the Gogol River would tend to support this.

7.4.3 Hexanematichthys and Hemiarius

I suggest that the ancestral taxa of these subgenera followed the pattern of other ariids and moved onto the Sahul Shelf from S.E. Asia sometime after the mid-Miocene Plate collision. Population divergence occurred on both Shelves, facilitated by the various vicariant events. When sea level rose after the last glacial maxima, descendant taxa had less chance of recolonising each area because their predecessor was better adapted to local conditions (Woodland, 1986), i.e. competitive exclusion by each species of its congener has occurred.

7.4.4 The Netuma species group

The marine taxa thalassinus and bilineatus are the most widely dispersed of all Indo-Australian ariids. They have a streamlined morphology and semi-demersal habit as adults. Active and wide-ranging fish, they are captured in moderate to large numbers from the Arabian Gulf (Al-Hassan *et al.*, 1988), through the Java Sea (Anon., 1980) to northern Australia. The ancestral taxa(on), having evolved in warm seas off Africa-India, moved into the warmed Australian Plate waters. The apparent ability of *thalassinus* and *bilineatus* to traverse long distances and the dietary independence by adults of benthic organisms, would permit movement between populations across and through features forming effective barriers to other taxa (e.g. deep ocean trenches, large distances between "hospitable" habitats, limited dietary and water requirements). I suggest that the *Netuma* ancestor which moved onto the Sahul Shelf evolved into the group member *proximus* during the Pleistocene and/or, that the *thalassinus* and *bilineatus* members moved away off the Shelf as sea waters declined in extent. These two taxa moved back onto the Shelf (including northern New Guinea) with the subsequent sea level rise and marine incursions.

The absence of *thalassinus* and *bilineatus* from the Pacific Plate partly contradicts their ability to distribute widely in marine waters. Springer (1982) discussed this phenomenon with respect to many widely distributed Indo-West Pacific fishes. He concluded that the deep-sea trenches along the western margin of the Plate would form a physical barrier, which may or may not have been subducted during frequent tectonic activity. Coleman's (1980) view, that there were more islands in the Melanesian Pacific Plate 2 mya than there now are, supports this. The expanses of sea which existed (and still do) would have been greater than any in eastern Malesia, effectively prohibiting the dispersal of ariids - even *thalassinus*. Furthermore, the western Pacific Plate islands would probably not have offered a suitable environment for colonisation by ariids (Kailola, 1983): e.g. no substantial estuaries but few and short rivers; streams with fast currents and steep gradients without gravel or sand beds, hence a limited food supply.

As no ariids inhabit the Pacific Plate (except marginally, on northern New Guinea), it is likely they were never there - an hypothesis more reasonable than that they were once present yet are now extinct (Springer, 1982).

It is worth considering the paradox that the sophisticated reproductive strategy of parental care imposes on dispersal (refer 7.2.2). Whereas the dispersal of fish whose eggs and young are planktonic components or pelagic, is not affected by great ocean depth (Woodland, 1983), that of fish exhibiting high levels of parental care is. In the case in point, the act of oral incubation ensures that the species will not freely disperse across "inhospitable" water as juveniles, simply because the parent doesn't!

This statement is equally applicable to the following group of taxa:

7.4.5 Genus 1

Although tempting, the *Netuma* scenario is not as clear-cut for the three Genus 1 representatives in Australia-New Guinea, largely because of insufficient information. This problem extends from the taxonomic level to life histories (refer 6.5 Biology and Discussion sections). Two taxa (*argyropleuron*, *polystaphylodon*) mature at a small to moderate size and at all stadia, inhabit turbid, coastal waters and feed on soft-bottom, benthic organisms (at least, *argyropleuron*). Their external morphology is not that of an active swimmer, and the fish do not inhabit outer continental shelf waters. These features suggest that the ancestral form(s) dispersed onto the northern Australian Plate at some time when more or less continuous, suitable habitats existed from Asia to (at least) northwestern Australia, perhaps 8-2 mya (refer 7.3). Although juvenile Genus 1 *nella* also feed on benthic biota, the adults may consume fish and crustacea taken above the sea floor. This species' apparently extensive migrations and large size may enhance dispersal across wider ocean tracts (e.g. it has been trawled off NW Australia).

Even so, allopatric distribution patterns within this genus (e.g. between northern and southern New Guinea and between *dussumieri* [western Asia] and its likely sister-species *nella*) suggests that vicariance has been significant in promoting intrageneric speciation. Furthermore, assuming S.E. Asian and Australo-Papuan populations of *nella*, *argyropleuron* and *polystaphylodon* still exchange mature cohorts (or individuals) across the Timor Trough, the Banda Sea or the shallower waters between New Guinea and the north Moluccas, why isn't sympatric distribution in evidence around New Guinea (as there appears to be on the Sunda Shelf)? It is possible that Australo-Papuan and S.E. Asian populations of these three taxa are *not* conspecific, and the emergence of ecological and physical barriers over the past 15 my could be effecting slow and gradualistic evolutionary change (refer 7.2.2). For example, individual morphology of my *argyropleuron* material is very variable (6.5.3, Discussion). This situation may be comparable to that of *Congrogadus subducens* (cited in Woodland, 1986), in which Sunda and Sahul Shelf populations exhibit morphological differences but gene flow appears to be sufficient between the two areas to prevent speciation. The relative paucity of material and observations (especially from S.E. Asia) and the systematic techniques applied in my study, preclude a "finer" resolution of the zoogeography and speciation in this group of Genus 1 taxa. Whereas gene flow between populations of thalassinus and bilineatus is apparently sufficiently large, and life-styles vagarious enough to inhibit speciation (Woodland, 1983; Vari, 1988: 7.2.2), such may not be true in Genus 1.

7.5 WALLACE'S LINE?

Powell et al.'s (1981) tectonic model of S.E. Asian and Australian Plate interaction in the Cretaceous provided an understanding of the evolution and significance of the zoogeographic lines of Wallace and Lydekker (the "lines of faunal contrast") and Weber (the "line of faunal balance"). These authors suggested that although Weber's Line may migrate depending on the ecological success of various groups, the lines of contrast remain along the edges of their respective continental margins, the Sunda and Sahul Shelves.

Several examples of fish distributions influenced by Wallace's and Lydekker's Lines are given by Woodland (1986). He pointed out that, where closely related taxa have complementary distributions to the east and west of Wallace's Line, a barrier promoting speciation exists (or has existed) in that region.

Historical geography and climate (refer 7.3) have also played a role in creating these zoogeographic zones. The seas of the Sunda and Sahul Shelves are today characterised by low salinity, high turbidity, mud bottoms (because of river discharge) and poor coral development (Woodland, 1983; this chapter). The intermediate more oceanic and coralline area therefore, effectively creates an environmental isolating mechanism between populations and faunas of inshore fishes.

The distribution and speciation of Australo-Papuan ariid catfishes, as outlined in this chapter, supports the existence of these biogeographic lines and Whitmore's (1987) observation that they are "very real boundaries". In summary, these are the high complement of endemic Sahul Shelf taxa (29 of the total of 34 species), the exclusion of sibling species in the subgenera *Hexanematichthys* and *Hemiarius*, and the morphological variation in some Genus 1 taxa.

8. CONCLUSION

I have achieved the five major objectives of this study, which were: to revise the taxonomy of the Australo-Papuan ariids; to describe the osteology and morphological variation within them; to reconstruct the phylogeny of the Ariidae in Australia and New Guinea whilst at the same time considering homologous character states in extralimital ariid taxa; and to analyse and explain the zoogeography of the family in this region. ~~The results are a significant contribution to our global knowledge of the Ariidae and offer new information for developing concepts of ostariophysan evolution and zoogeography.~~

The monophyly of the Ariidae is established by the habit of oral incubation. The family is holistic in nature and distinct from all other siluroids. It is conservative for many characters which differentiate other catfish families yet possesses a variety of states for "ariid only" characters (autapomorphies within the suborder). The present disjunct distribution patterns of many species do not coincide with patterns of dissimilarity between genera.

The phylogenetic study revealed few yet significant clades within the Australo-Papuan Ariidae, even with the number of species analysed and the high representation of nominal genera among them. Groupings with extralimital taxa, often from widely separated geographical regions, were also revealed. This may well reflect a real phenomenon, i.e. most ariids may belong to a single, highly variable genus ("Arius"?) that underwent "explosive" morphological, ecological and geographical radiation following acquisition of its highly advantageous reproductive strategy. Ariids are shown to have the ability to diversify from a relatively ancient and conservative morphotype. Furthermore, the capacity of many extant species to live in both marine and freshwater environments suggests that the ancestral species also enjoyed the range of habitat thus made available, and that rapid geographical expansion is an "expectation" of the Ariidae.

The high level of homoplasy encountered in reconstructing a phylogeny for the Australo-Papuan ariids has created some small difficulties in proposing a classification. In it, "Arius" is presently shown to be paraphyletic. Nonetheless, I am confident that a future phylogenetic reconstruction of the whole family, will not greatly alter the classification I have put forward.

The evolution of Australo-Papuan ariids is an expression of a combination of dispersal and vicariant events. The Australian Plate's mid-Miocene and subsequent association with S.E. Asia, the historical absence of ostariophysans from the Plate, and the changing sea levels and climate of the last 2 million years, have enabled the family to undertake diverse and rapid speciation in Australia and New Guinea.

I concur with William A. Gosline (UMMZ) in "respect" for this fish family; and I challenge successors to prove that the ariids deserve the category of pariahs among catfishes.

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