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Taxonomic revision of the Poecilopsettidae and phylogenetic analysis of the Rhombosoleidae and Pleuronectiformes (Acanthopterygii)

Révision taxinomique des Poecilopsettidae et phylogénèse des Rhombosoleidae et des Pleuronectiformes (Acanthopterygii)

ANNIE-CHANTAL GUIBORD

Thèse soumise à la Faculté des études supérieures et postdoctorales
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Le savant dit
Si vous saviez mon ignorance
Le métier de la connaissance
Est mal connu et journalier

Gilles Vigneault

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These figures are original drawings made by François Chapleau : 59, 60a, 62, 63, 64a, 66, 67a,c, 68, 71, 73, 75, 78a and 81a.

Table of contents

Résumé: Les membres de la famille des Poecilopsettidae (Pleuronectiformes) se retrouvent dans les eaux des océans Atlantique, Pacifique et Indien. Dix-neuf espèces étaient considérées valides avant cette étude. Une révision taxinomique de toutes ces espèces a été réalisée. Cette révision est fondée sur l'examen du matériel type et de spécimens appartenant à chaque espèce selon la disponibilité. Une nouvelle espèce a été décrite (*Poecilopsetta dorsialta*) alors que deux espèces ont été mises en synonymie: *Nematops chui* est un synonyme junior de *N. macrochirus* et *Poecilopsetta megalepis* est un synonyme junior de *P. plinthus*. La famille des Poecilopsettidae est maintenant composée de 18 espèces valides: deux dans le genre *Marleyella*, trois dans le genre *Nematops* et 13 dans le genre *Poecilopsetta*. Les genres *Marleyella* et *Nematops* sont clairement monophylétiques. La monophylie du genre *Poecilopsetta* demeure incertaine puisqu'aucune caractéristique apomorphique qui unirait les 13 espèces du genre n'a été trouvée.

La famille des Rhombosoleidae (*sensu* Norman, 1934) (Pleuronectiformes) est formée de 19 espèces retrouvées dans les eaux au sud de l'Australie, de la Nouvelle-Zélande, dans l'Indo-Pacifique à l'ouest de l'Australie et de l'Amérique du Sud. Une matrice de 87 caractères morphologiques a été analysée selon la méthode cladistique afin de déterminer la monophylie des Rhombosoleidae et d'élaborer une hypothèse des relations phylogénétiques entre les espèces. Les Achiropsettidae et les Poecilopsettidae ont été utilisés comme hors-groupe. Les résultats de l'analyse (16 arbres équiparcimonieux; 118 pas; CI=0,669) indiquent que les Rhombosoleidae sont un groupe monophylétique. Huit apomorphies supportent cette monophylie. Les genres *Azygopus*, *Oncopterus* et *Psammodiscus* ont dû être enlevés de la famille. Ils ont été intégrés à une matrice globale de caractères des taxons de haut-rang de l'ordre des Pleuronectiformes afin d'élaborer une hypothèse concernant leur position phylogénétique. *Azygopus* fait maintenant partie des Achiropsettidae *Oncopterus* et

Psammodiscus forment une trichotomie avec un grand clade formé par les Rhombosoleidae, les Poecilopsettidae, les Achiropsettidae, les Samaridae, les Achiridae, les Soleidae et les Cynoglossidae (6 arbres équiparcimonieux ;109 pas; CI= 0,477). La famille Paralichthodidae (*sensu* Cooper et Chapleau, 1998a) est le groupe-frère d'un grand clade formé par les familles possédant un squelette caudal du type bothoïde (Scophthalmidae, Bothidae, Paralichthyidae and Pleuronectidae) et par le clade III (*Psammodiscus*, *Oncopterus*, Poecilopsettidae, Rhombosoleidae, Achiropsettidae, Samaridae, Achiridae, Soleidae et Cynoglossidae).

Abstract: The family Poecilopsettidae (Pleuronectiformes) occurs in the Pacific, Indian and Atlantic oceans. A taxonomic revision of all 19 species considered valid up to now was completed. Type specimens and additional material known for all these valid species were examined and measured. One new species is described (*Poecilopsetta dorsialta*), two species are synonyms of previously described species: *Nematops chui* is a junior synonym of *N. macrochirus* and *Poecilopsetta megalepis* is a junior synonym of *P. plinthus*. There are now 18 valid species in the family: two in the genus *Marleyella*, three in the genus *Nematops* and 13 in the genus *Poecilopsetta*. The genera *Nematops* and *Marleyella* are monophyletic. However, the monophyly of the genus *Poecilopsetta* remains doubtful because of the absence of unique characters for all 13 species of the genus.

The family Rhombosoleidae (Pleuronectiformes) (*sensu* Norman, 1934) is a group of 19 species distributed in Southern Australia, New Zealand, in the Indo-Pacific Ocean off Western Australia and South America. A data matrix of 87 morphological characters was analysed using cladistic methodology to assess the monophyly of the Rhombosoleidae and to determine the interrelationships within this family. Achiropsettidae and Poecilopsettidae were used as outgroups. The results (16 equally parsimonious trees; 118 steps; CI=0.669) found the family Rhombosoleidae to be monophyletic on the basis of eight apomorphies. The Rhombosoleidae was not monophyletic with the genera *Azygopus*, *Oncopterus* and *Psammodiscus* and they were removed from the family and added to a data matrix of of pleuronectiform families to assess their relationship within the order. *Azygopus* is placed in the Achiropsettidae. *Psammodiscus* and *Oncopterus* form a trichotomy with a large clade formed by Rhombosoleidae, Poecilopsettidae, Achiropsettidae, Samaridae, Achiridae, Soleidae and Cynoglossidae (6 equally parsimonious trees; 109 steps; CI= 0.477). The family Paralichthodidae (*sensu* Cooper and Chapleau, 1998a) is the sister-group of a large

clade formed by the families exhibiting a bothoid type of caudal skeleton (Scophthalmidae, Bothidae, Paralichthyidae and Pleuronectidae) and by clade III (*Psammodiscus*, *Oncopterus*, Poecilopsettidae, Rhombosoleidae, Achiropsettidae, Samaridae, Achiridae, Soleidae and Cynoglossidae).

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General Introduction

The Pleuronectiformes (flatfishes) are a group of 570 species (Nelson, 1994) distributed in 13 families. Chapleau (1993) found them to be monophyletic on the basis of three apomorphies: presence of a *recessus orbitalis*, the migration of one eye to the other side of the cranium during the larval stage and the forward position of the dorsal fin over the cranium. A review of the major changes in the classification of the Pleuronectiformes is discussed in chapter 2. Few phylogenetic analyses of the order Pleuronectiformes have been published. Lauder and Liem (1983) were the first to use cladistic methodology to hypothesise evolutionary relationships between families of the order, but their study included only a few characters. The first comprehensive cladistic analysis dealing only with the Pleuronectiformes was published by Chapleau (1993). In his analysis, Chapleau (1993) provided a first cladistic hypothesis of relationships between the families and a few historically problematical genera (see Appendix 1). Recently, Hoshino (2001) published a new phylogeny of the order Pleuronectiformes (Fig. 1). His hypothesis of relationships demonstrated the monophyly of the family Citharidae and provided a resolution to the relationships between the Rhombosoleidae and the Poecilopsettidae (see chapter 2).

Phylogenetic analyses at the familial level were done only for a few groups within the Pleuronectiformes. Sakamoto (1984) produced a phenetic analysis of one major family: the Pleuronectidae (see Appendix 1). At that time, the Pleuronectidae was a large group made up of five subfamilies. Two of those subfamilies were the Rhombosoleinae and Poecilopsettinae, the taxa that are studied in this thesis. Chapleau and Keast (1988), Chapleau (1993), and Cooper and Chapleau (1998a) proposed familial ranking for the subfamilies of the Pleuronectidae (Poecilopsettinae, Rhombosoleinae, Samarinae, Pleuronectinae and Paralichthodinae). Cooper and Chapleau's (1998b) phylogeny of the

Pleuronectidae is, until now, the only morphology-based hypothesis of intrarelationships of a family within the Pleuronectiformes.

Recently, Berendzen and Dimmick (2002) have published the first molecular phylogeny of the order Pleuronectiformes. Their study included 49 species belonging to 11 of 13 families of Pleuronectiformes. Unfortunately, this study provides very little insights into the intrafamilial relationships of flatfishes. Moreover, their study did not include rhombosoleids and included only one poecilopsettid species.

Chapter one deals with the revision of the family Poecilopsettidae. This taxonomic revision is necessary because the last one goes back to Norman (1934). In the last 70 years many species have been described. Furthermore, taxonomic revisions are necessary to clearly identify the number of valid species in a taxon before any phylogenetic analyses can be done. For this revision, species were recognised according to the phylogenetic species concept, namely that a species is the smallest monophyletic group sharing uniquely derived characters (Cracraft, 1983b).

The focus of chapter two is the elaboration of a hypothesis of interrelationships within the Rhombosoleidae. The cladistic methodology was used to hypothesise the relationships. The basic principles of the cladistic methodology are that: 1) natural (monophyletic) groups are defined by uniquely shared derived characters, also called synapomorphies and 2) only natural groups should be introduced in the Linnean classification (Cracraft, 1983a). Monophyletic groups should include all and only the descendants of a common ancestor. Based on these principles, the monophyly of the Rhombosoleidae was determined, the interrelationships between the species of the family were also hypothesised and a new classification is proposed to reflect the new intra- and interrelationships of the Rhombosoleidae.

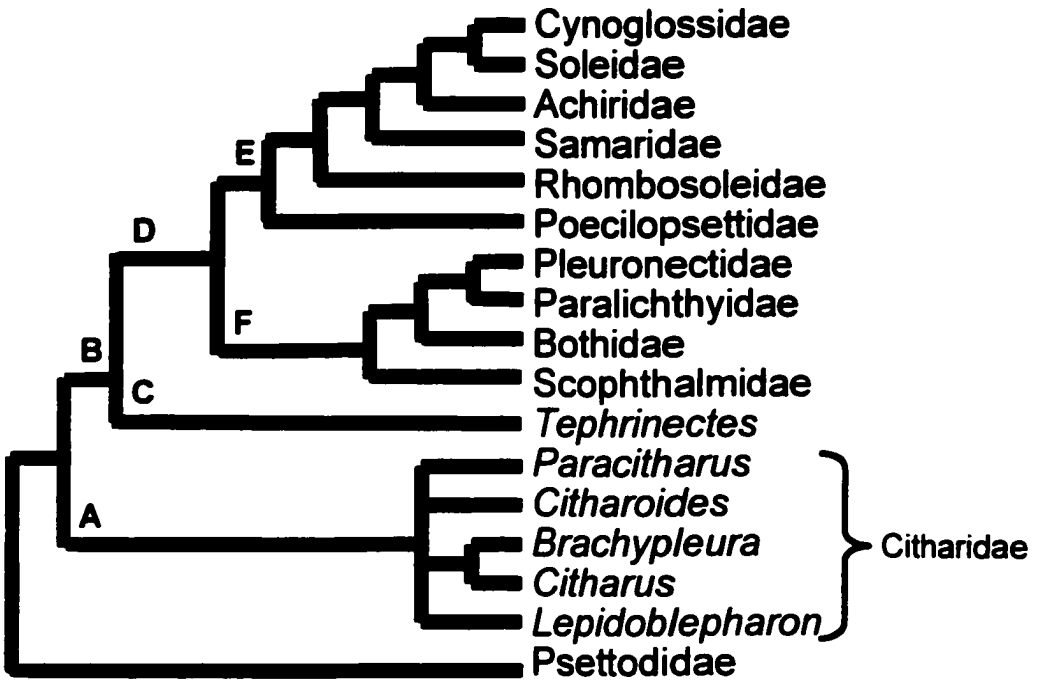

Fig. 1: Evolutionary relationships within the order Pleuronectiformes (modified from Hoshino, 2001).

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Chapter 1

Taxonomic revision of the family Poecilopsettidae (Pisces: Pleuronectiformes)

The family Poecilopsettidae includes three genera and 18 valid species (Eschmeyer *et al.*, 1998). Recently two new species were described (Hoshino *et al.*, 2001; Guibord and Chapleau, 2001) and two were placed in synonymy (this study), bringing the total to 18 valid species. The poecilopsettids are easily recognisable by their large eyes on the right side of the body, the absence of a lateral line on the blind side, a wide proximal pterygiophore zone without muscles and the absence of orbital and preorbital bones.

The first description of poecilopsettids was done by Günther (1880) when he classified *Poecilopsetta colorata* and *Nematops microstomus* in the Pleuronectidae. Shortly after, Goode (1881) described a species from the Atlantic Ocean, *Limanda beanii*, later recognised by Hubbs (1919) as *Poecilopsetta beanii*. Later, three more species were described, *P. praelonga* Alcock, 1894, *P. maculosa* Alcock, 1894 and *Boopsetta umbrarum* Alcock, 1896. Jordan and Starks (1904) described a poecilopsettid from the coast of Japan, *Alaeops plinthus*, later recognised as *Poecilopsetta plinthus* by Hubbs (1915). A species from Hawaii, *P. hawaiiensis* was described by Gilbert (1905).

Regan (1910) in a revision of the classification of order Heterosomata (Pleuronectiformes) recognised distinct groups within the Pleuronectidae. He created three subfamilies: Pleuronectinae, Samarinae and Rhombosoleinae. Species belonging to *Nematops*, *Poecilopsetta*, *Alaeops*, *Boopsetta* and *Limanda* (*sensu* Goode, 1881) remained within the Pleuronectinae. From 1922 to 1929, three species were described: *Poecilopsetta bicolorata* von Bonde, 1922, *Paralimanda inermis* Breder, 1927 and *Nematops grandisquamus* Weber and de Beaufort, 1929. Fowler (1925) recognised that von Bonde's species was different (elongated dorsal and pelvic fin rays) from the other

species of the genus *Poecilosetta* and erected the subgenus *Marleyella*. Norman (1931) described two new poecilopsettids: *Nematops macrochirus* and *Poecilopsetta natalensis*. In that same publication, Norman (1931) recognised *Boopsetta* Alcock, 1896 and *Paralimanda* Breder, 1927 as *Poecilopsetta*. Moreover, Norman (1931) elevated Fowler's subgenus *Marleyella* to the genus level, bringing the number of valid genera to three. Norman's (1931) publication represents the most important contribution to the classification of the Poecilopsettidae to date. However, since this first revision, ten species have been described: *Poecilopsetta albomarginata* Reid, 1934; *Nematops chui* Fowler, 1934; *P. megalepis* Fowler, 1934; *P. albomaculata* Norman, 1939; *Marleyella maldivensis* Norman, 1939; *P. zanzibarensis* Norman, 1939; *P. vaynei* Quéro, Hensley and Maugé, 1988; *P. normani* Foroshchuk and Fedorov, 1992; *P. macrocephala* Hoshino, Amaoka and Last, 2001; and *P. dorsialta* Guibord and Chapleau, 2001. Recently, Hoshino (2000) synonymised *P. albomarginata* Reid, 1934 with *P. inermis* (Breder, 1927). In the present study both species described by Fowler are synonymised, *Nematops chui* with *N. macrochirus* Norman, 1931 and *Poecilopsetta megalepis* with *P. plinthus* (Jordan and Starks, 1904) (Guibord and Chapleau, 2002).

We know very little about poecilopsettid intrarelationships. Sakamoto (1984) used the phenetic method to construct a tree of similarities between the subfamilies of the Pleuronectidae. His analysis included 5 poecilopsettines and the intrarelationships between the species were largely unresolved (see Appendix 1, Fig A1c). Chapleau (1993), in an article dealing with phylogeny of the order Pleuronectiformes, found the Poecilopsettinae to form a trichotomy with the Rhombosoleinae and a large clade formed by the samarines and the soles (Achiridae, Soleidae and Cynoglossidae) (see Appendix 1, Fig A1a). He suggested that the subfamilies Poecilopsettinae, Rhombosoleinae and Samarinae be raised to the family level (see also Cooper and Chapleau, 1998). In a recent phylogenetic analysis, the Poecilopsettidae were found to be the sister-group of a

clade including the Rhombosoleidae, Samaridae and the soles (Hoshino, 2001). No detailed analysis of the monophyly of the genera within the family nor the interspecific relationships within the genera has been done. Two genera are probably monophyletic: *Marleyella* (elongated dorsal and pelvic fin rays) and *Nematops* (usually with tentacles on the eyes and two nasal bones), but the monophyletic status of *Poecilopsetta* remains dubious at present. It includes all poecilopsettids that do not have the diagnostic traits of *Marleyella* and *Nematops*.

Before species relationships can be hypothesised, a taxonomic revision is necessary to assess the validity of the nominal species. Since the last taxonomic revision ten species have been described. This revision is the main goal of this study.

MATERIALS AND METHODS

Counts and measurements follow Hubbs and Lagler (1958). In *Poecilopsetta* and *Nematops*, the length of the first dorsal fin-ray is always shorter than the height of the dorsal fin. The first dorsal fin ray is measured from the base of the ray. Measurements were taken with a dial caliper to the nearest 0.1 mm. Counts of vertebrae, dorsal and anal fin rays were made from X-rays. Institutional abbreviations follow Leviton *et al.* (1985). When not indicated on museum labels or data, latitude and longitude of collections were determined using an international gazetteer.

The literature cited immediately follows this chapter.

RESULTS AND DISCUSSION

Genus *Marleyella*.-The genus *Marleyella* Fowler, 1925 has two nominal species (Eschmeyer et al., 1998). Apart from one species of *Nematops* (*N. macrochirus*), *Marleyella* is the only genus within the family Poecilopsettidae to exhibit sexual dimorphism. It is characterised by the presence of rostral spines in both sexes (stronger in males), elongated first few dorsal and pelvic fin rays (longer in males) and blue branchiostegal membranes (in males and females). Species of this genus are found in the Indian Ocean, near Africa and along the coast of the Maldive Islands in waters 55-229 m depth. Both nominal species are recognised as valid.

Etymology: named for Bell Marley (Fowler, 1925) principal fisheries officer of the Natal fisheries department. Marley collected and then gave specimens to Fowler who deposited them at the ANSP. Gender feminine.

Key of identification of the species of the genus *Marleyella*

1a Body depth (BD) 1.93-2.59 in standard length (SL), 10-12 gill rakers on first lower arch of ocular side, 10-12 ocular side pectoral fin rays.....*M. bicolorata*

1b BD 2.57-2.70 in SL, 15 gill rakers on first lower arch of the ocular side, 13-14 ocular side pectoral fin rays.....*M. maldivensis*

Marleyella bicolorata (von Bonde, 1922)

Figures 2, 3; Tables 1,2

Poecilopsetta bicolorata, von Bonde 1922, Rep. Fish. Mar. Biol. Surv. Union South Africa Rep. 2: 14-15. Barnard 1925, Ann. S. Afr. Mus., 21: 396.

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Common name: Comb flounder (Heemstra, 1986)

Syntypes.-**BMNH 1922.3.27:5-6**; Natal; 2: 136.4-149.8 mm SL.

Additional material: **ANSP 53428**; Indian Ocean, Natal coast, South Africa; 54.6-63.7 m (30-35 fm); 1924; female: 107.2 mm SL. **ANSP 55296**; Indian Ocean, Natal, South Africa; 1931; female: 137.9 mm SL. **ANSP 145373**; Indian Ocean, Somali coast; 11°24'N 51°35'E; 75-175 m; vessel Anton Bruun, Cr. 9, st. 463; 17 Dec. 1964; 2: 38.1-62.1 mm SL. **BMNH 1939.5.24:1794-1796**; Zanzibar area; Murray expedition, st. 106; 183-194 m; 3 (two females and one male): 97.4-98.0 mm SL.

Diagnosis.-A species of *Marleyella* with the following combination of characters: deep body (1.93-2.59 in SL), 10-12 gill rakers on ocular side first lower arch and 10-12 ocular side pectoral fin rays.

Description.-Data are presented for the male syntype and values for additional material are given in parentheses. A species of *Marleyella* with a rather deep body, eyes separated by a large scaly space, elongated ocular side dorsal and pelvic fin rays, rostral spine above ocular side premaxilla, non-confluent dorsal, caudal and anal fins, subsymmetrical pelvic fin bases and ocular side pectoral fin-rays longer than blind side rays. Body depth (BD) 51.9% in SL (38.7-50.3%), head length (HL) 24.2% in SL (24.7-29.8%). Snout scaleless with one rostral spine above the ocular side premaxilla. A rostral spine is found on the blind side of males. Interorbital space and maxilla with scales. Upper orbit 30.0% in HL (27.0-36.3%), very slightly encroaching on dorsal profile of head. Position of upper eye slightly anterior or equal to lower eye. Nostrils asymmetrical; those of blind side higher than those of ocular side. Both anterior nostrils with tubular opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla reaching to vertical through center of lower eye, 42.0 % in HL (39.1-42.8%). Blind side maxilla, 38.7% in HL (34.1-36.3%). Lower jaw almost symmetrical, ocular side 48.7% in HL (45.2-51.5%), blind side 46.8% in HL (44.5-48.4%). Conical teeth on premaxillae and dentaries. Teeth in multiple rows, inside and outside the mouth of the male syntype, (two to three) on blind side dentary and premaxilla. Multiple rows, inside and outside the mouth of the male syntype, (one or two rows) of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 7 (6-8) on upper limb and 11 (10-12) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 23.1% in SL (21.9-23.1%), height of arch 25.2% in BD (22.3-28.6%), 72 (67-80) ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 11 (10-12) rays, 8 (6-9) branched rays, length 63.9% in HL (59.5-66.8%). Blind side pectoral fin with 9 (8-10) unbranched rays, length 47.1% in HL (41.2-54.8%). Pelvic fins with 6 rays, the first three are elongated in both sexes. The first ray is the longest ray. Ocular side pelvic fin 200.4% in HL (127.1% in males) (83.4-91.7%

in females), blind side 53.3% in HL (38.4-45.0%). Unbranched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior half of upper eye. Dorsal fin with 57 (56-58) rays, first ray 72.8% in HL (41.6-55.8%). Elongated dorsal fin rays in males first to eighth, longest (sixth) 174.2% in HL (129.7%). Elongated dorsal fin rays in females and immature second to fourth, longest (third) 45.4-75.4% in HL. Anal fin with 47 (45-49) rays, longest ray 51.7% in HL (44.3-48.0%). Dorsal and anal fin rays unbranched. Pelvic fins with first three rays elongated. In males the first is the longest, 63.9% in HL, in females the second is the longest, 83.4-91.7% in HL. Origin of ocular side pelvic fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third ray of ocular side pelvic fin. Dorsal, anal, pectoral and pelvic fins scaleless. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 27 (26-27) caudal vertebrae. Ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin. The male syntype is the only mature male of the studied specimens. Six other specimens are females and two are juvenile specimens. Sexual dimorphism in this species is seen in the number and size of rostral spines on the snout. Males have two (one on each side) large rostral spines. Females have only one (ocular side) smaller rostral spine. Elongated fin rays are longer in males than females and interorbital space is wider in males.

Coloration in ethanol.-Ocular side sometimes with 1 faint broad transverse band located on posterior third of the body. Dorsal and anal fins with large dark brown spots along the length of the fins. Ocular side pectoral fin with multiple brown spots. Ocular side pelvic fin light brown. Branchiostegal membranes dark purple. Caudal fin with a triangular-shape spot on the middle rays. Blind side evenly brown or head with dark spots. Blind side pectoral and pelvic fins brown.

Etymology.-From the Latin *bicolorata* (*bi* meaning two and *colorata* meaning coloration). The specific name refers to the coloured blind side of this species. This is the type species of the genus.

Distribution.-*Marleyella bicolorata* is distributed along the eastern coast of Africa, from Natal (South Africa) to Somalia (Fig 3). This species is known to occur at depths between 54.6-194 m.

Remarks.-The male syntype was the only specimen found with teeth in multiple rows on premaxillae. More specimens of a wide range of sizes are needed to know if this condition is found only in males, or breeding males

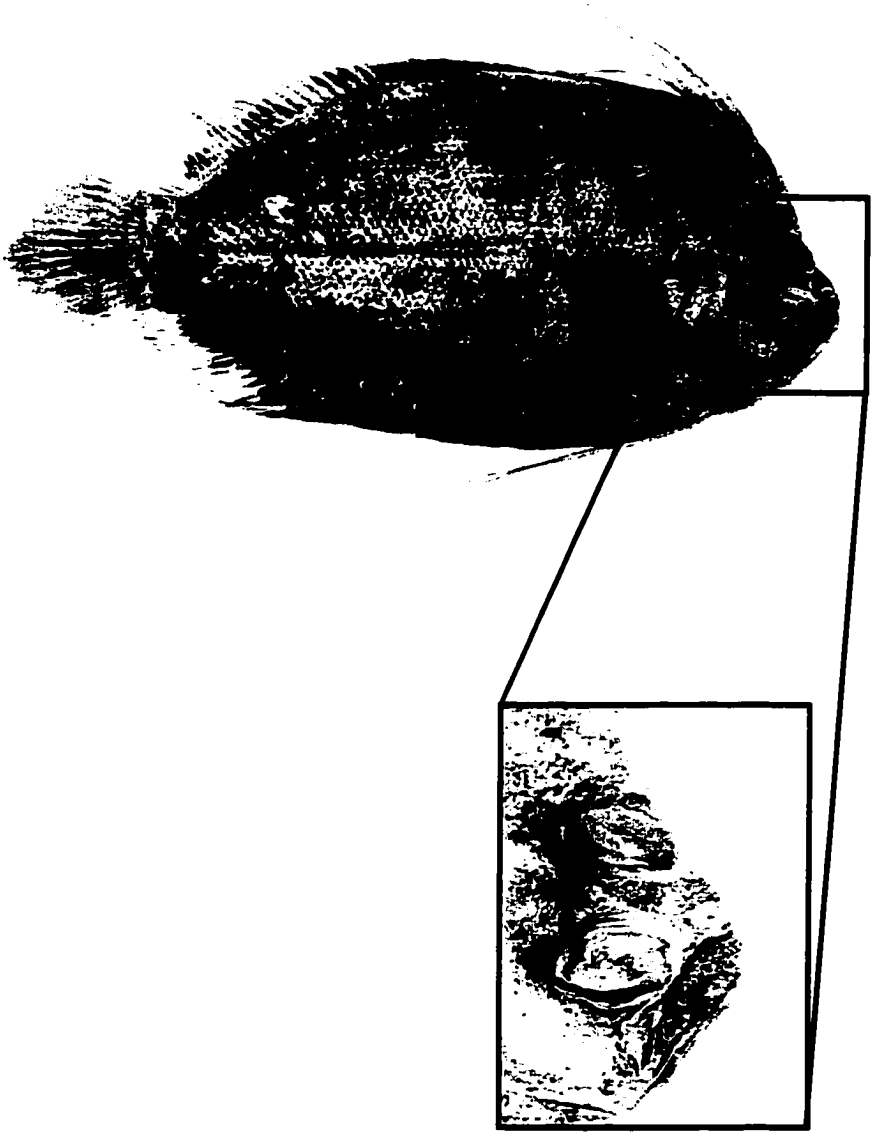


Fig. 2: *Marleyella bicolorata*, syntype: BMNH 1922.3.27:5-6; male: 149.8 mm SL. Inset is an enlargement of the head of the male syntype, showing the teeth on the ocular side premaxilla.

Table 1: Morphometric characters for two species of *Marleyella*. Ratios are expressed as proportion of the measurement in standard length (SL), in head length (HL) and in body depth (BD). In *M. bicolorata* the first number represents the data for the male syntype. The first series of numbers in parentheses represents the range for the non type material examined and the second set in parentheses, if given, indicates the number of specimens measured when different from the entire group. Juveniles were excluded from the values representing sexual dimorphism. For M. maldivensis the asterisk represents values for the holotype. BD, body depth; HL, head length; LLW, lateral line width; CPL, caudal peduncle length; UO, upper orbit diameter; UJO, length upper jaw ocular side; UJB, length upper jaw blind side; LJO, length lower jaw ocular side; LJB, length lower jaw blind side; LPectO, pectoral fin length ocular side; LPectB, pectoral fin length blind side; LPelOM, pelvic fin length ocular side in males; LPelOF, pelvic fin length ocular side in females; HDRM, highest dorsal fin-ray in males; HDRF, highest dorsal fin-ray in females; FDR, length of first dorsal fin-ray; HAR, highest anal fin-ray and LLH, lateral line height.

Measurements	*M. bicolorata*	*M. maldivensis*
	n=9	n=2
	Syntype (male)	Holotype
	BMNH 1922.3.27:5-6	BMNH 1939.5.24:1797-1798
SL (mm)	149.8 (38.1-138.4)	76.7-107.8*
In SL		
BD	1.93 (1.99-2.59)	2.57*-2.70
HL	4.13 (3.36-4.06)	3.42-3.57*
LLW	4.32 (4.33-4.56) (5)	4.60-4.96*

CPL	16.33 (14.71-20.16)	14.96*-15.66
In HL		
UO	3.33 (2.76-3.71)	2.77-2.84*
UJO	2.38 (2.34-2.55)	2.44*-2.65
UJB	2.59 (2.76-2.93)	2.92*-3.09
LJO	2.05 (1.94-2.21)	2.16*-2.17
LJB	2.14 (2.07-2.25)	2.23*-2.26
LPectO	1.56 (1.50-1.68) (8)	1.81*-2.04
LpectB	2.12 (1.82-2.43)	2.17-2.25*
LPelOM	0.50 (0.79) (2)	
LPelOF	1.09-1.20 (4)	0.93*-1.71
HDRM	0.57 (0.77) (2)	
HDRF	1.33-1.63 (5)	0.64*-0.81
FDR	1.37 (1.79-2.40)	2.31*-2.91
HAR	1.94 (2.08-2.26)	2.51-2.55*
In BD		
LLH	3.97 (3.50-4.37) (7)	3.84-3.92*

Table 2: Frequency distribution of meristic characters for *Marleyella bicolorata* and *M. maldivensis*. Asterisk represents values for the type.

Dorsal fin-rays									
	55	56	57	58	59	60	n	$\bar{x}$	s
M. bicolorata		2	4*	2			8	57.0	0.76
M. maldivensis			1*		1		2	58.0	1.41
Anal fin-rays									
	45	46	47	48	49	50	n	$\bar{x}$	s

M. bicolorata	1		3*	2	2					8	47.5	1.31
M. maldivensis						2*				2	50.0	0

Ocular side pectoral fin-rays

	10	11	12	13	14					n	$\bar{x}$	s
M. bicolorata	2	5*	2							9	11.0	0.71
M. maldivensis				1	1*					2	13.5	0.71

Blind side pectoral fin-rays

	8	9	10							n	$\bar{x}$	s
M. bicolorata	2	5*	2							9	9.0	0.71
M. maldivensis		1	1*							2	9.5	0.71

Caudal vertebrae

	26	27								n	$\bar{x}$	s
M. bicolorata	4	5*								9	26.6	0.53
M. maldivensis	1*	1								2	26.5	0.71

Lateral line scales

	67	70	71	72	75	76	78	80	83	n	$\bar{x}$	s
M. bicolorata	1	1		1*	1	1		1		6	73.3	4.63
M. maldivensis							1		1*	2	80.5	3.54

Gill rakers on first lower arch

	10	11	12	13	14	15				n	$\bar{x}$	s
M. bicolorata	1	6*	1							8	11.0	0.53
M. maldivensis						1*				1	15.0	0.00

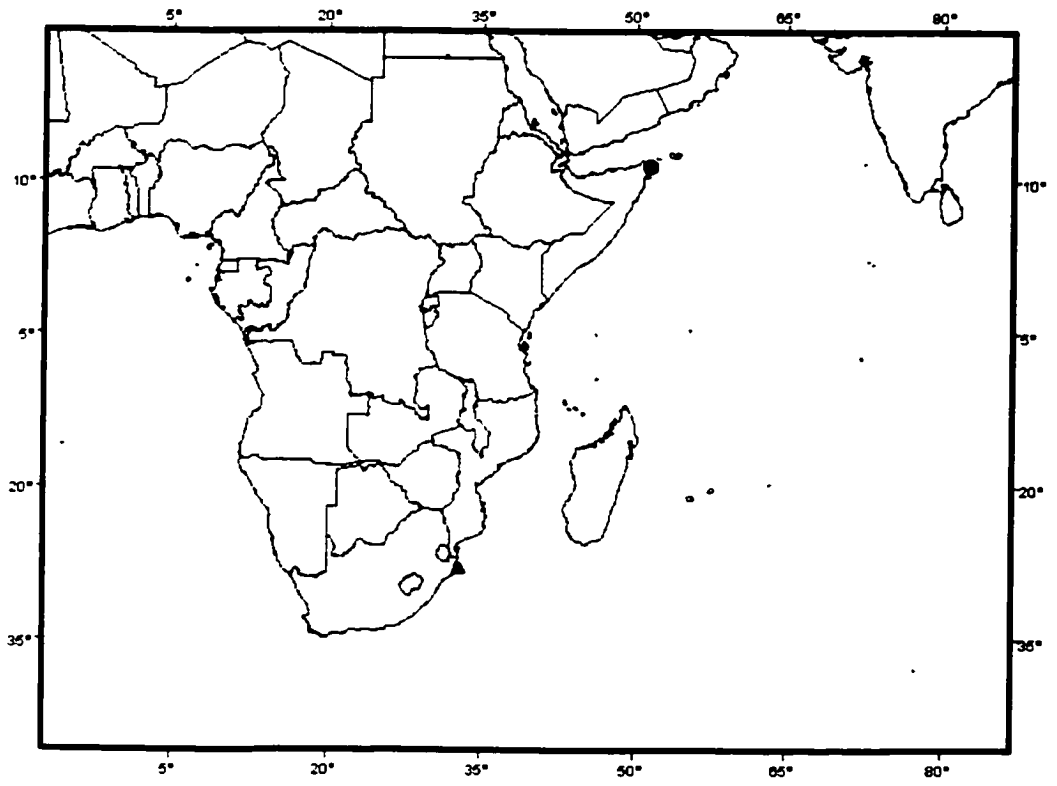


Fig. 3: Collection sites of *Marleyella bicolorata*. The triangle represents approximate collection site of syntypes and of two other lots (ANSP 53428 and 55296) off Natal.

***Marleyella maldivensis* Norman, 1939**

Figures 4, 5; Tables 1,2

Marleyella maldivensis Norman, 1939: The John Murray expedition 1933-1934 Scientific reports: 103-104. Adam *et al.* 1998, J.L.B. Smith Ichthyological Bulletin, 67: 15.

Common name: Maldives comb flounder

Holotype.-**BMNH 1939.5.24.1797-1798**; Maldive area, north of Ari Atoll, st. 157; 4°43'48"N 72°55'24"E to 4°44'00"N 72°54'18"E; 229 m; 6 Apr. 1934: 107.8 mm SL.

Paratype.-**BMNH 1939.5.24.1797-1798**; same as holotype; 76.7 mm SL.

Diagnosis.-A species of *Marleyella* with the following combination of characters: slender body (2.57-2.70 in SL), 15 gill rakers on ocular side first lower arch and 13-14 ocular side pectoral fin rays.

Description.-Data are presented for the holotype and value for the paratype is given in parentheses. A species of *Marleyella* with a rather elongated body, eyes separated by a narrow scaled space, elongated ocular side dorsal and pelvic fin rays, rostral spine above ocular side premaxilla, non-confluent dorsal, caudal and anal fins, subsymmetrical pelvic fin bases and ocular side pectoral fin-rays longer than blind side. Body depth (BD) 38.9% in SL (37.0%), head length (HL) 28.0% in SL (29.2%). Snout, eyes and maxilla scaleless. Upper orbit 35.2% in HL (36.1%), barely encroaching on dorsal profile of head. Position of lower eye slightly anterior or equal to upper eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with tubular opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through center of lower eye, 41.0 % in HL (37.7%). Blind side maxilla almost symmetrical, 34.2% in HL (32.3%). Lower jaw symmetrical, ocular side 46.4% in HL (46.1%), blind side 44.8% in HL (44.2%). Conical teeth present on premaxillae and dentaries. Teeth in three (two) distinct bands on blind side dentary and premaxilla. One row of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 6 on upper limb and 15 on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch

20.2% in SL (21.8%), height of arch 25.5% in BD (26.0%), 83 (78) cycloid scales on lateral line. Lateral line absent on blind side. Ocular side pectoral fin with 14 (13) rays, 9 (8) branched rays, length 55.3% in HL (49.1%). Blind side pectoral fin with 10 (9) unbranched rays, length 44.4% in HL (46.1%). Pelvic fins with 6 rays. Ocular side pelvic fin 107.6% in HL, blind side 32.8% in HL (27.1%). No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior half (third) of upper eye. Dorsal fin with 57 (59) rays, first ray 43.3% in HL (34.4%). First two to four (2 to 3) dorsal fin rays are elongated. Longest dorsal fin ray (second ray) 156.5% in HL (123.8%). Anal fin with 50 (50) rays, longest ray 39.2% in HL (39.8%). Dorsal and anal fin rays unbranched. Pelvic fins with first three rays elongated, second ray is longest. Origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third (fourth) ray of ocular side pelvic fin. Dorsal, anal, pectoral and pelvic fins scaleless. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 26 (27) caudal vertebrae. Cycloid scales on both sides. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

Coloration in ethanol.-Ocular side sometimes with 2 faint broad transverse bands. Dorsal and anal fins brown with white tips. Elongated rays of dorsal and pelvic fins white. Ocular side pectoral fin with brown lower margin and white spot at base. Ocular side pelvic fin brown and blind side pelvic fin light brown. Skin on the eyes is brown. Caudal fin with dark brown line along the length of the middle rays. Blind side uniformly brown. Blind side pectoral with faint brown pigmentation. Branchiostegal membranes dark brown.

Etymology.-From the latin *maldivensis*. The specific name refers to the type locality, the Maldives.

Distribution.-*Marleyella maldivensis* is known only from north of Ari Atoll, in the Maldives (Fig 5). This species is known to occur at a depth of 229 m.

Remarks.-Sexual dimorphism is not documented for this species. Of the two specimens known, the largest is a female and the smallest seems immature and perhaps a female. No obvious differences where found between these specimens. They, nonetheless, exhibit characters that are unique to the genus *Marleyella* (rostral spine, dark branchiostegal membrane and elongated dorsal and pelvic rays).

Fig. 4: *Marleyella maldivensis*, paratype: BMNH 1939.5.24:1797-1798; 76.7 mm SL.

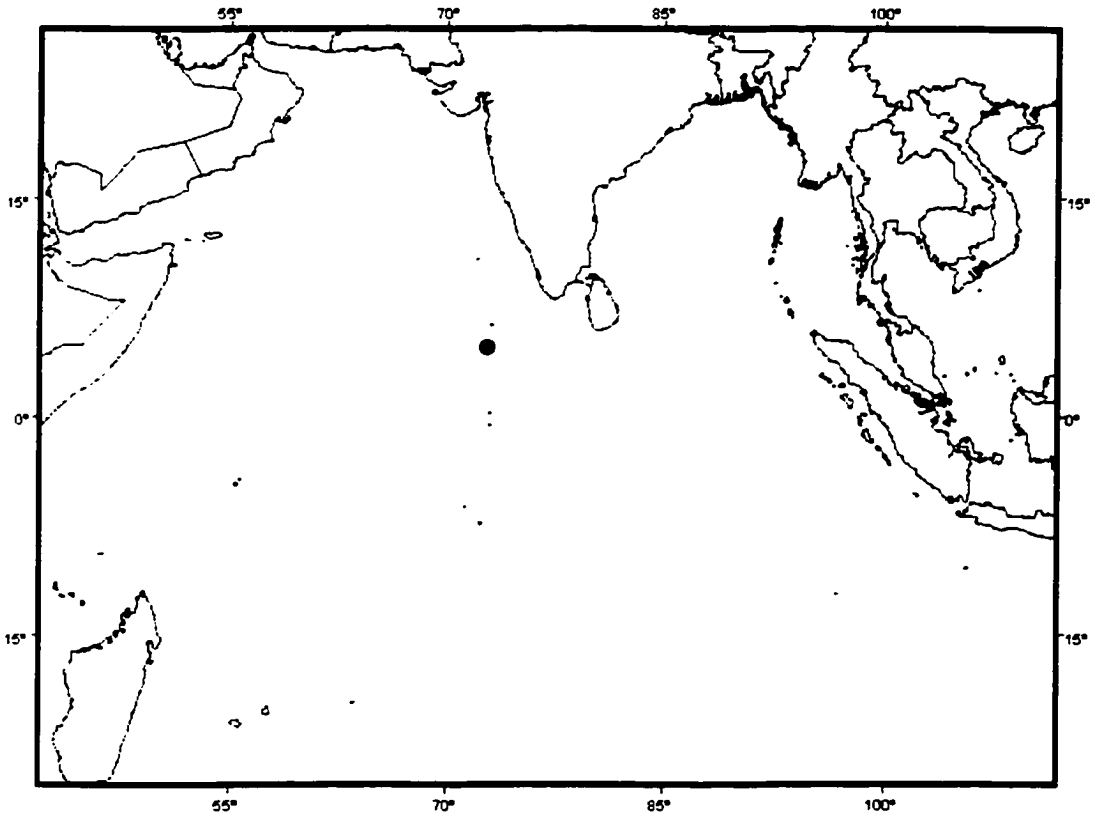


Fig 5: Collection site of *Marleyella maldivensis*.

Genus *Nematops*.-Four nominal species (Eschmeyer *et al.*, 1998) found mainly in the Philippines and from northwestern to southeastern Australia. One specimen was also caught in the Atlantic Ocean (Nielsen, 1961). They are found at depths of 146 to 520 m. Species of *Nematops* all have an ocular side nasal bone and three proximal radials of the anal fin found between the first enlarged pterygiophore of the anal fin and the hemal spine of the first caudal vertebra (Fig. 6). They often have a tentacle on the eyes but some specimens were found without tentacles. Most specimens have only one tentacle on the lower eye.

There are three valid species.

Etymology: from the Greek *nemat* meaning thread and *ops* for eye. Gender masculine.

Fig. 6: X-ray showing the number (3) of anterior anal fin pterygiophores supported by the first modified pterygiophore in the genus *Nematops*.

Key of identification of the species of the genus *Nematops*:

1a Body depth nearly 3 in SL, long ocular side pectoral fin in males (close to 1 in HL).....*N. macrochirus*

1b Body depth nearly 2 in SL, ocular side pectoral fin 2 in HL and same length for both sexes.....2

2a Lateral line scales 52-60.....*N. grandisquamus*

2b Lateral line scales 60-70.....*N. microstomus*

Nematops grandisquamus Weber and de Beaufort, 1929

Figures 7, 8; Tables 3,4

The species-group name was changed to agree with the gender of the generic name. *N. grandisquama* Weber & de Beaufort, 1929, The fishes of the Indo-Australian Archipelago, E.J. Brill Ltd., Leiden. Vol. 5, p. 134-136. Norman 1931, Treubia 13: 427. Norman 1934. A systematic monograph of the flatfishes (Heterosomata). Vol I: 395.

Common name: Large-scale righteye flounder (Hensley, 1997)

Syntype: **BMNH 1933.2.18:16**; St Nikolaas Bay; 1: 62.9 mm SL.

Additional material: **AMS I.20918-015**; 1-2 miles NNE of Raine Is., QLD; 11°35'S 144°02'E; 270-275 m; 12 Feb. 1979; 1: 81.6 mm SL. **CAS 46456**; Indo-West Pacific, Philippines, Luzon Is., Manila Bay; 18 May 1948; 1: 63.7 mm SL. **NTM S.13313-010**; Arafura Sea, NT; 09°18'S 133°12'E; 153 m; 6 Nov. 1990; 4: 67.6-84.3 mm SL. **USNM 93577**; Pacific Philippines Is., Mindanao; 07°03'N 125°39'E; 182 m (100 fm); vessel Albatross; 18 May 1908; 1: 77.1 mm SL.

Diagnosis.-A species of *Nematops* with the following combination of characters: 52-60 lateral line scales, dorsal fin rays 61-65 and anal fin rays 49-56.

Description.-Data are presented for the syntype and values for additional material are given in parentheses. A species of *Nematops* with a rather deep body, large eyes separated by a very narrow space, non-confluent dorsal, caudal and anal fins, subsymmetrical pelvic fin bases and blind side pectoral fin-rays usually longer than ocular side. Body depth (BD) 42.9% in SL (41.8-47.7%), head length (HL) 26.1% in SL (23.8-26.2%). Interorbital space, snout, eyes and maxilla scaleless. Upper orbit 38.9% in HL (39.2-44.0%), encroaching on dorsal profile of head. Position of upper eye slightly anterior or equal to lower eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through anterior fourth of lower eye, 26.2 % in HL (28.3-32.4%). Blind side maxilla, 25.4% in HL (24.7-29.2%). Lower jaw symmetrical, ocular side 36.9% in HL (37.7-40.8%), blind side 36.1% in HL (37.4-41.2%). Conical teeth present on premaxillae and dentaries. Gill rakers longer than wide and not serrated, 7 (6-7) on upper limb and 11 (5-12) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 18.9% in SL (22.9%), height of arch 22.6% in BD (21.9%), 52 (55-60) ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 8 (7-8) rays, 5 (3-4) branched rays, length 46.1% in HL (43.6-50.9%). Blind side pectoral fin with 7 (7) unbranched rays, length 47.0% in HL (47.1-56.5%). Pelvic fins with 6 rays. Ocular side pelvic fin 42.6% in HL (39.0-45.8%), blind side 45.2% in HL (39.6-45.1%). No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over approximately half of upper eye. Dorsal fin with 61 (61-65) rays, first ray 40.6% in HL (24.9-45.9%). Longest dorsal fin-ray 47.4% in HL (47.9-54.4%). Anal fin with 51 (49-56) rays, longest ray 42.9% in HL (48.3-55.1%). Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third or fourth

Fig. 7: *Nematops grandisquamus*, syntype: BMNH 1933.2.18:16; 62.9 mm SL.

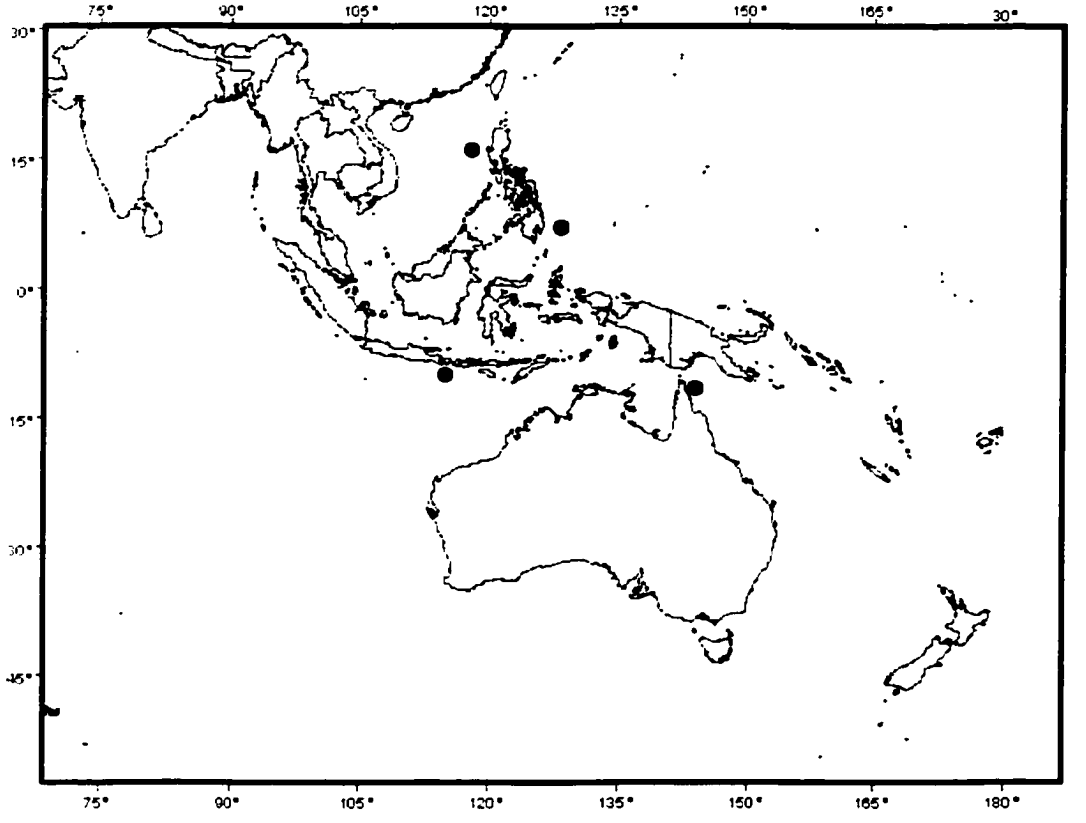


Fig. 8: Collection sites of *Nematops grandisquamus*.

ray of ocular side pelvic fin. Dorsal, anal, pectoral and pelvic fins scaleless. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 27 (27-29) caudal vertebrae. Large ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin. The holotype and two other specimens have a tentacle on both eyes, four specimens have a tentacle on the lower eye only and one specimen has no tentacles. Specimens without tentacles can be identified as *Nematops* on the basis of the presence of a nasal bone on the ocular side [absent in *Poecilopsetta* and *Marleyella* (Sakamoto, 1984)] and on the number of proximal pterygiophores found between the first anal fin pterygiophore and the hemal spine of the first caudal vertebra (three for *Nematops*; two for *Poecilopsetta* and *Marleyella* (this study see Fig. 6).

Coloration in ethanol.-Ocular side sometimes with two pairs of black spots at base of dorsal and anal fins, one pair near caudal peduncle, the other pair at 2/3 of body length. Dorsal and anal fins with black spots. Ocular side pectoral fin without pigment. Ocular side pelvic fin light brown. Caudal fin with two dark spots on upper and lower margins. Blind side creamy white with small dark spots.

Etymology.-From the Latin *grandisquamus* (*grandi* meaning large and *squamus* meaning scales). The specific name refers to the large scales found on this species.

Distribution.-*Nematops grandisquamus* is distributed along the coasts of the Philippine Islands to northern Australia (Queensland) (Fig. 8). This species is known to occur at depths between 153-275 m.

Remarks.-*Nematops grandisquamus* and *N. microstomus* are very similar and characters that were used by Weber and de Beaufort (1929) to distinguish between *N. microstomus* and specimens of *N. grandisquamus* are hard to see on specimens examined in this study. Lateral line scales are deciduous (i.e., easily lost) in the genus *Nematops* and are a defining character between these two species. According to Weber and de Beaufort (1929) and Norman (1934), another defining character is the number of dorsal fin rays, 52-59. Specimens of *N. grandisquamus* with as few as 52-59 dorsal fin rays were not found in this study. More over, most syntypes of *N. grandisquamus* were not available for measurement. The only syntype seen in this study had 61 dorsal fin rays, which is outside the range given by Weber and de Beaufort (1929). Also, the number of lateral line scales reported by Weber and de Beaufort (1929) for *N. grandisquamus* is ± 50 scales and not 44-48 reported by subsequent authors (Norman, 1931; Norman, 1934; Sakamoto, 1993).

Status of the type series.-In their description of *N. grandisquamus* Weber and de Beaufort (1925), do not seem to indicate that one of the five specimens they have examined is a holotype. The words type or holotype are never used and the proportions of the body parts are given without emphasis on one identified specimen. When they describe the coloration of the species, they clearly refer to multiple specimens: "Colour of alcohol specimens..." (p. 135), once again not referring to one specimen in particular. On the other hand, they represent by a drawing a specimen they examined but in the legend accompaniyng the drawing, there is no mention if this specimen is the type (= holotype). Also, at the end of the description, they mention the length of one (or multiple) specimen(s): 87 mm total length. This measurement is not associated with any lot number or any other specimen that could have the status of a holotype.

Regardless, Norman, in 1934, measured one specimen of *N. grandisquamus* kept in the collections of the British Museum of Natural History (BMNH 1933.2.18:16). He

labeled this specimen as being a paratype and mentions that the holotype is 87 mm in total length, citing Weber and de Beaufort (1925).

There is no convincing evidence to show that Weber and de Beaufort designated a holotype in their description of *Nematops grandisquamus*. Hence, the type series of *N. grandisquamus* is made of five syntypes.

Table 3: Morphometric characters of *N. microstomus* and *N. grandisquamus*. Standard length (SL), head length (HL), body depth (BD), length of curve in lateral line (CLL), length of the caudal peduncle (CPL), length of upper orbit (UO), length of lower orbit (LO), length of ocular side upper jaw (UJO), length of blind side upper jaw (UJB) length of ocular side lower jaw (LJO), length of blind side lower jaw (LJB), length of ocular side pectoral fin (LpectO), length of blind side pectoral fin (LpectB), length of ocular side pelvic fin (LpelvO), length of longest dorsal fin ray (LDR), length of longest anal fin ray (LAR), length of first dorsal fin ray (FDR), number of scales in the lateral line (LL scales), number of gill rakers on the first arch on the ocular side (Gill rakers) and number of caudal vertebrae including urostyle (Cvert). Numbers in parenthesis represent number of specimens surveyed for that character when it is different from the total number of specimens.

Measurements	*N. microstomus* Holotype BMNH 1879.5.14:91	*N. microstomus* n=8	*N. grandisquamus* Syntype BMNH 1933.2.18:16	*N. grandisquamus* n=7
SL	75.6	44.3-87.7	62.9	63.7-84.3
In SL				
HL	4.31	3.66-4.28	3.83	3.81-4.21

BD	2.37	2.13-2.50	2.33	2.10-2.39
CPL	17.90	19.58-25.91	36.56	17.98-24.94
LLW	5.65		5.29	4.37 (1)
In HL				
UO	2.29	2.41-2.50	2.57	2.27-2.55
UJO	3.53	3.17-3.51	3.82	3.09-3.54
UJB	4.03	3.60-3.86	3.94	3.42-4.05
LJO	2.55	2.48-2.65	2.71	2.45-2.65
LJB	2.63	2.51-2.68	2.77	2.43-2.68
LpectO		2.14-2.30	2.17	1.96-2.29 (5)
LpectB	2.07	1.83-2.63	2.13	1.77-2.12
LpelvO		2.22-2.96	2.35	2.18-2.57
LDR	1.84	1.92-2.33	2.11	1.83-2.10
LAR	2.07	1.81-2.35	2.33	1.81-2.19
FDR		3.38-5.13	2.46	2.76-4.02
Counts				
Caudal fin rays	22	20	20	20 (6)
LL scales	70	60-68 (3)	52	55-60 (2)
Gill rakers	8-12	6-7/10-12	7/11	6-7/5-12
Cvert	29	28	27	27-29

Table 4: Frequency distribution of meristic characters for *Nematops grandisquamus* and *N. microstomus*. Asterisk represents data for syntype and holotype.

	Dorsal fin rays											
	61	62	63	64	65	66	67	68	69	n	$\bar{x}$	s
N. grandisquamus	2*		2	2	2					8	63.3	1.58
N. microstomus					3	2	1	2*	1	9	66.6	1.51
	Anal fin rays											
	49	50	51	52	53	54	55	56	57	n	$\bar{x}$	s
N. grandisquamus	1		1*	1	2	2		1		8	52.8	2.12
N. microstomus						2	3	3*	1	9	55.3	1.00
	Ocular side pectoral fin rays											
	7	8								n	$\bar{x}$	s
N. grandisquamus	6	2*								8	7.3	0.46
N. microstomus	7*	2								9	7.2	0.44
	Blind side pectoral fin rays											
	7	8								n	$\bar{x}$	s
N. grandisquamus	8*									8	8.0	0.00
N. microstomus	7	2*								9	7.2	0.44
	Caudal vertebrae											
	27	28	29							n	$\bar{x}$	s
N. grandisquamus	3*	4	1							8	27.8	0.71
N. microstomus		8	1*							9	28.1	0.33

Nematops macrochirus Norman, 1931

Figures 9-12; Tables 5,6

Nematops macrochirus Norman, 1931, Treubia, 13: 421-427. Norman 1934, A systematic monograph of the flatfishes (Heterosomata). Vol I: 396. Nielsen 1961, Atlant. Rep., 6: 124-126.

Nematops chui Fowler, 1934: this study.

Common name: Long-fin righteye flounder (Hensley, 1997)

Holotype.-**BMNH 1931.7.23:1**; Bali Strait; 8°29'S 114°40'E; 200 m; 15 Apr. 1929; male: 85.5 mm SL.

Holotype.-*N. chui*: **USNM 93087**; Pacific, Philippine Is; Cebu Market; vessel Albatross; 5 Apr. 1908; male: 65.5 mm SL.

Additional material: **AMS I.22641-001**; E of Sydney, NSW; 33°45'S 151°59'E; 440-448 m; vessel Kapala; 8 May 1981; 2 females: 55.3-70.0 mm SL. **AMS I.22821-044**; Indian Ocean, Northwest shelf, 200 km NW of Port Hedland; 18°16'S 118°12'E; 298-320 m; vessel Soela; 10-11 Apr. 1982; 5 (3 males and 2 females): 82.2-98.0 mm SL. **AMS I.22825-003**; Indian Ocean, Northwest shelf, 200 km NW of Port Hedland; 18°59'S 117°10'E; 300-326 m; vessel Soela; 13 Apr. 1982; 6 (3 males and 3 females): 79.7-91.8 mm SL. **AMS I.23386-001**; Sydney, Jervis Bay; 34°21'S 151°21'E; 270-281 m; vessel Kapala; 13 Dec. 1978; 3 (1 male and 2 females): 80.5-87.0 mm SL. **AMS I.23999-001**; SE of Yamba, NSW; 29°40'S 153°47'W; 475 m; vessel Kapala; 7 Nov. 1978; 3 (1 male and 2 females): 71.5-91.4 mm SL. **AMS I.24420-004**; Off Port Kembla, NSW; 34°27'S 151°19'E; 329-402 m; vessel Kapala; 18 May 1983; 1 female: 95.0 mm SL. **AMS I.24494-001**; Off

Sydney, NSW; 33°40'S 151°54'E; 439 m; vessel Kapala; 26 Jun. 1979; 2 (1 male and 1 female): 67.0-76.8 mm SL. **AMS I.25932-005**; E of Port Jackson, NSW; 33°44'S 151°57'E; 439-466 m; vessel Kapala; 19 Dec. 1985; male: 71.7 mm SL. **WAM P.25401-019**; Browse Is., WA; 13°47'S 123°18'E; 242 m; vessel Umitaka Maru; 23 Dec. 1969; male: 77.4 mm SL. **ZMUC P853081**; Jamestown, St. Helena; Feb. 1930; male: 80.1 mm SL.

Paratypes of *P. megalepis* identified as *N. macrochirus*: **USNM 93571**; Pacific Philippines, between Cebu and Bohol; 10°10'30"N 123°51'15"E; 265 m (145 fm); vessel Albatross, Sta. 5411; 23 Mar 1909; female: 68,3 mm SL. **USNM 93573**; Pacific Philippines, between Cebu and Bohol; 10°08'50"N 123°52'30"E; 291 m (159 fm); vessel Albatross, Sta. 5418; 25 Mar 1909; 3 males: 59,6-83,9 mm SL. **USNM 93574**; Pacific Philippines, between Cebu and Bohol; 10°09'15"N 123°52'E; 296 m (162 fm); vessel Albatross, Sta. 5412; 23 Mar 1909; 2 females: 78,8-81,6 mm SL. **USNM 93575**; Pacific Philippines, between Cebu and Bohol; 10°10'N 123°53'15"E; 302 m (165 fm); vessel Albatross, Sta. 5417; 25 Mar 1909; 3 (2 males et 1 female): 71,6-81,4 mm SL. **USNM 93576**; Pacific Philippines, Balabac Strait; 07°50'45"N 116°43'15"E; 271 m (148 fm); vessel Albatross, Sta. 5353; 1 Jan 1909; 1 male: 66,3 mm SL. **USNM 93578**; Pacific Philippines, China Sea, vicinity southern Luzon, Malavatuan Is.; 13°57'30"N 120°22'15"E; 214 m (117 fm); vessel Albatross, Sta. 5279; 17 July 1908; 1 female: 70,5 mm SL.

Diagnosis.-A species of *Nematops* with the following combination of characters: body depth nearly 3 in HL and long ocular side pectoral fin in males (nearly 1 in HL).

Description.-Data are presented for the holotype and values for additional material are given in parentheses. A species of *Nematops* with a rather elongated body, large eyes separated by a very narrow space, non-confluent dorsal, caudal and anal fins,

subsymmetrical pelvic fin bases and tentacles on eyes. Body depth (BD) 36.4% in SL (27.8-41.0%), head length (HL) 23.9% in SL (19.5-25.6%). Interorbital space, snout, eyes and maxilla scaleless. Upper orbit 46.2% in HL (37.9-48.5%), encroaching on dorsal profile of head. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through anterior third of lower eye, 27.6% in HL (26.7-38.9%). Blind side maxilla, 25.4% in HL (24.6-32.4%). Lower jaw symmetrical, ocular side 38.0% in HL (35.5-47.3%), blind side 38.1% in HL

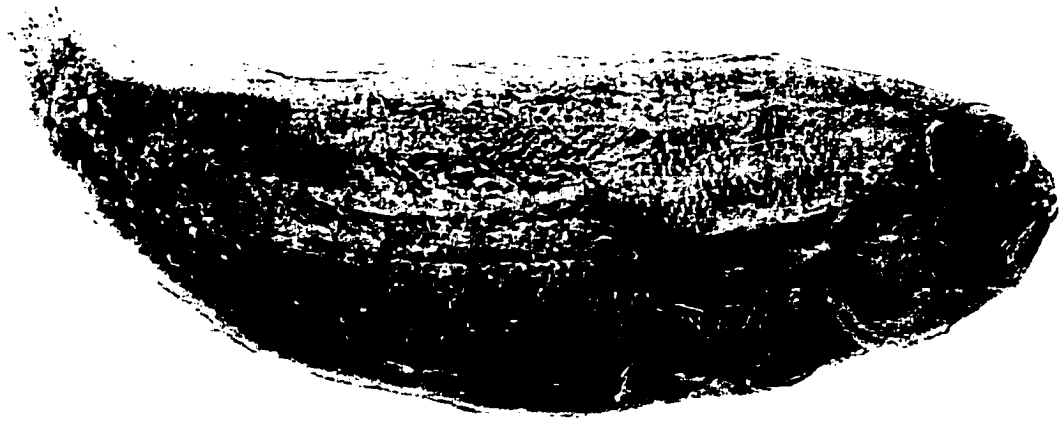


Fig. 9: *Nematops macrochirus*, holotype: BMNH 1931.7.23:1; 85.5 mm SL.

Fig. 10: *Nematops chui* holotype a) USNM 93087; 65.5 mm SL.

(36.5-47.1%). Conical teeth present on premaxillae and dentaries. Teeth in three (two to four) distinct bands on blind side dentary and premaxilla. Two rows (one to three) of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 7 (5-7) on upper limb and 11 (8-12) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 20.3% in SL (16.2-20.6%), height of arch 23.4% in BD (22.9-33.9%), 62 (53-65) ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 8 (6-9) rays, 7 (5-8) branched rays, length 111.8% in HL (75.7-121.6%) for males, (45.5-64.4%) for females. Blind side pectoral fin with 7 (6-8) unbranched rays, length 45.4% in HL (47.6-65.7%) for males, (40.9-60.2%) for females. Pelvic fins with 6 rays. Ocular side pelvic fin 36.1% in HL (33.1-45.4%), blind side 38.7% in HL (34.6-48.6%). Rays sometimes branched in both pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior half of upper eye. Dorsal fin with 64 (59-68) rays, first ray 26.8% in HL (17.6-36.3%). Longest dorsal fin ray 49.6% in HL (41.4-63.2%). Anal fin with 53 (45-58) rays, longest ray 45.5% in HL (40.6-65.6%). Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third (third or fourth) ray of ocular side

pelvic fin. Dorsal, anal, and pelvic fins scaleless. Ocular side pectoral scaled. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 29 (27-30) caudal vertebrae. Large ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin. The holotype of *N. macrochirus* has two tentacles, in the 36 other specimens examined, 2 specimens had no tentacles, 16 only had one (on the lower eye) and 18 had two tentacles.

Coloration in ethanol.-Ocular side sometimes light brown, sometimes lighter. Dorsal and anal fins with dark spots. Ocular side pectoral fin with black spot at posterior tip. Ocular side pelvic fin light brown. Caudal fin with dark triangular spot. Blind side creamy white.

Etymology.-From the Greek *macrochirus* (*macro* meaning long and *chirus* referring to pectoral fin). The specific name refers to the long ocular side pectoral fin in males.

Distribution.-*Nematops macrochirus* is distributed along the coasts of the Philippine Islands to the north-western coast of Australia in the Indian Ocean and to Sydney in the Pacific Ocean. One specimen was collected off the coast of St-Helena (Fig. 11). Possible explanations for the presence of *N. macrochirus* in the Atlantic Ocean are water currents (Fig. 12; Lincoln *et al.*, 1998). A cold water current flowing north along the western coast of Australia (Fig. 12: 1- West Australian current) meets a warm current from Indonesia and flows through the Indian Ocean (2- Indian equatorial current). This current reaches the eastern coast of Africa and flows south along the coast (3- Mozambique current). The specimen would have reached, through the Agulhas current (Fig. 12; 4), the Benguela current (Fig. 12; 5) flowing north along the western coast of Africa. This a possible way that the specimen would have made its way to St Helena Island. A larva of *N. macrochirus* could travel to the Atlantic following this route if it has a long larval life. Long larval stage is

known for some species of the genus *Poecilopsetta* but no larvae are known for the genus *Nematops*. Another possible explanation is a much wider distribution than known today. These small flatfishes have no commercial value and are not very well known, two factors that could explain why they have not been reported on a broader geographical scale. This species is known to occur at depths between 200-475 m.

Status of *N. chui* Fowler, 1934.- *Nematops chui* was described based on a single specimen (male) collected in the South China Sea, off Luzon (Fowler, 1934). Fowler provided three characteristics that separated the holotype of *N. chui* from other known *Nematops*: body depth nearly 3 times in standard length, 48 lateral line scales and a tentacle only on the lower orbit.

The holotype of *N. chui* has a body depth similar to *N. macrochirus* (Table 5). In the comparison section, Fowler (1934) compares the holotype of *N. chui* with only two of the three other species of *Nematops* (*N. microstomus* and *N. grandisquamus*, two species with deep bodies). Seemingly, *N. macrochirus* was not known to Fowler (1934) because he did not mention it in the comparison section of his description.

Fowler (1934: p. 340) stated that the holotype of *chui* had "Scales 48 in lateral line to caudal base (...)". Generally, lateral line scales are easily lost in *Nematops* and empty pockets of lateral line scales are difficult to delimit. This renders this particular character difficult to use in species identification. There are 43 lateral line scales remaining on the holotype of *N. chui*. Most missing scales were situated on the curve of the lateral line just dorsal to the pectoral fin. In other species of *Nematops* (including *N. macrochirus*) nearly 20 scales are found on the lateral line curve (Guibord and Chapleau, pers. obs). I estimate at 15 the number of scales that can be added to the count of the holotype of *N. chui*, bringing the total of lateral line scales to approximately 58. This total is within the range observed for *N. macrochirus* (Table 6) (see also Sakamoto, 1993).

The third character used by Fowler is the presence of a tentacle only on the lower eye. This characteristic is variable within species of *Nematops*. For example, in 37 specimens of *N. macrochirus* examined, two had no tentacles, 16 had one (on the lower eye) and 19 had two tentacles (including the holotype). Specimens without tentacles can be identified as *Nematops* on the basis of the presence of a nasal bone on the ocular side (absent in *Poecilopsetta* and *Marleyella*) and on the number of proximal pterygiophores found between the first anal fin pterygiophore and the hemal spine of the first caudal vertebra (three for *Nematops*; two for *Poecilopsetta* and *Marleyella*; Guibord and Chapleau, pers. obs.). Furthermore, they can be assigned to the species *N. macrochirus* because of the length of the ocular side pectoral fin in males and because of the slender body shape.

Moreover, when comparing Tables 5 and 6, complete overlap is seen in the meristic and morphometric characters between *N. chui* and *N. macrochirus*. Thus, I conclude that *N. chui* is a junior synonym of *N. macrochirus* Norman, 1931.

The holotype of *Nematops chui* falls within the geographic range of *N. macrochirus* which is distributed along the coasts of the Philippine Islands to Northwest Australia in the Indian Ocean and south to Sydney, Australia, in the Pacific Ocean.

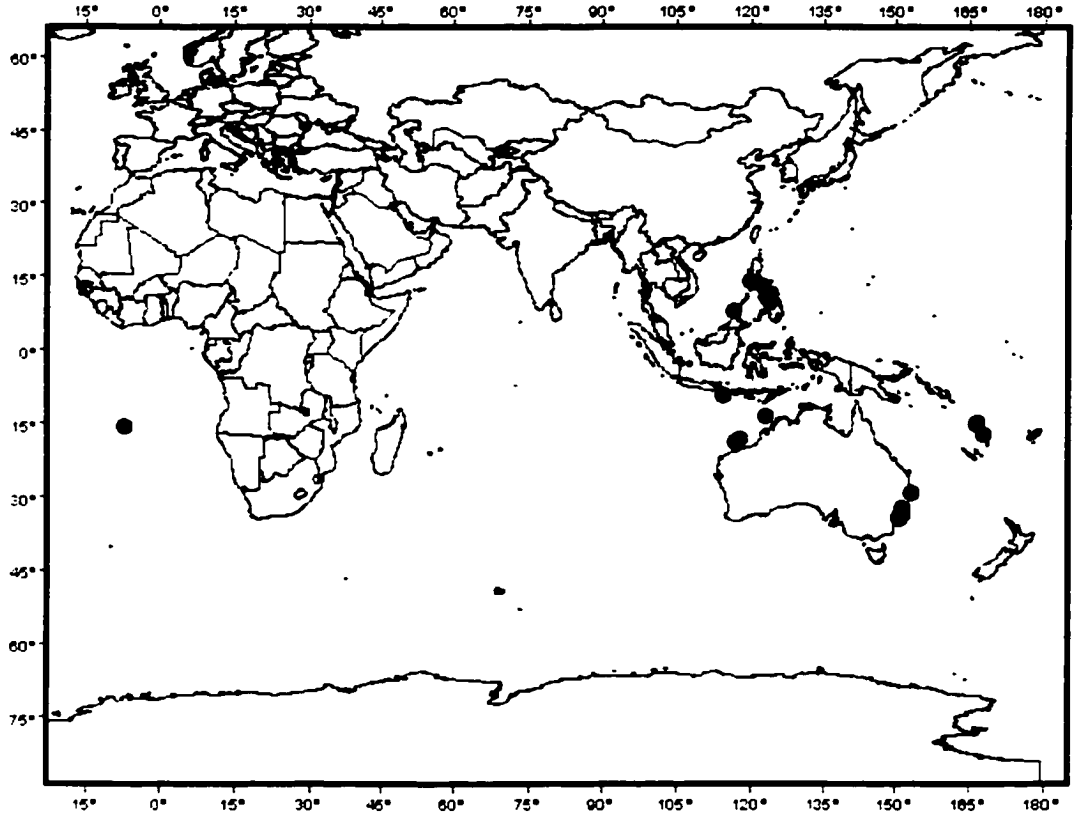


Fig. 11: Collection sites of *Nematops macrochirus*.

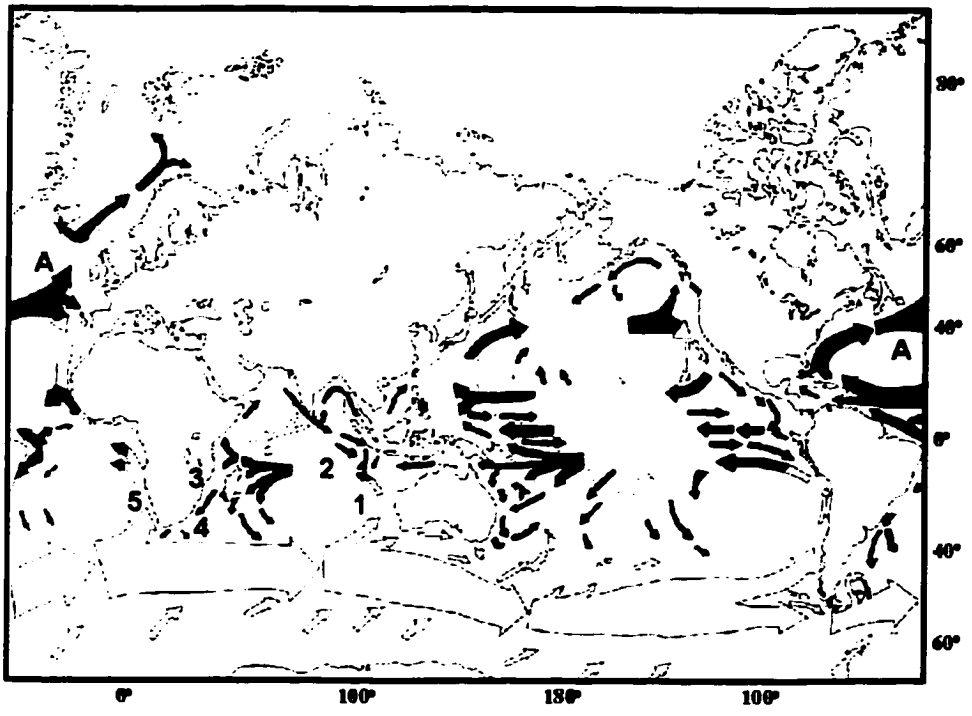


Fig. 12: Water currents at the surface of the Oceans. Black arrows represent warm water currents, white arrows represent cold water currents and the dashed arrows represent a warm winter current. **1** is the West Australian current; **2** is the Indian Equatorial current; **3** is the Mozambique current; **4** is the Agulhas current; **5** is the Benguela current; and **A** represents the North Atlantic gyre. (Modified from Lincoln *et al.*, 1998)

Table 5: Morphometric characters of *Nematops chui* and *N. macrochirus*. For abbreviations see Table 3. LPectOM: length of the pectoral fin on the ocular side in males; LpectOF: length of the pectoral fin on the ocular side in females; LPectBM: length of the pectoral fin on the blind side in males; LPectBF: length of the pectoral fin on the blind side in females.

Measurements	*Nematops chui* Holotype USNM 93087	*N. macrochirus* Holotype BMNH 1931.7.23:1	*N. macrochirus* N=36
SL	65.5	85.5	55.3-98.0
In SL			
HL	4.14	4.18	3.90-5.14
BD	3.00	2.74	2.44-3.60
LLC		4.93	4.86-6.17 (11)
CPL	21.99	18.23	15.83-34.85
In HL			
UO	2.34	2.17	2.06-2.64
LO	2.23	2.47	2.02-2.67
UJO	3.49	3.66	2.57-3.75
UJB	3.85	3.94	3.08-4.07 (35)
LJO	2.48	2.63	2.12-2.81
LJB	2.63	2.62	2.12-2.74
LPectOM	1.08	0.89	0.82-1.32 (19)
LPectOF			1.55-2.20 (17)
LPectBM	1.81	2.20	1.52-2.10 (19)
LPectBF			1.66-2.44 (17)

LPelvO	2.67	2.77	2.20-3.03 (35)
LDR	1.97	2.02	1.58-2.41
LAR	2.18	2.20	1.52-2.46
FDR	3.33	3.73	2.75-5.67 (34)

Table 6: Frequency distribution of meristic characters for *Nematops macrochirus*. Numbers in bold corresponds to data for holotype of *N. chui*. For *N. macrochirus* the asterisk represents data for holotype. Mean and standard deviation represent values for *N. macrochirus*, excluding value for *N. chui*.

Dorsal fin rays	59	60	62	63	64	65	66	67	68		n	$\bar{x}$	s
	1	2	4	4*	**7**	7	5	6	2		38	64.5	2.24
Anal fin rays	45	50	51	52	53	54	55	56	57	58	n	$\bar{x}$	s
	1	1	2	4	**4***	11	5	6	2	2	38	54.0	2.43
Ocular side pectoral fin rays	6	7	8	9							n	$\bar{x}$	s
	2	14	**18***	4							38	7.6	0.76
Blind side pectoral fin rays	6	7	8								n	$\bar{x}$	s
	10	**23***	5								38	6.9	0.63
Caudal vertebrae	27	28	29	30							n	$\bar{x}$	s
	2	**10**	25*	1							38	28.7	0.63
Lateral line scales	53	54	56	58	60	61	62	64	65		n	$\bar{x}$	s
	1	1	2	**2a**	1	2	2	1	2		14	59.8	4.04

a: estimated number of lateral line scales for *N. chui*.

Nematops microstomus Günther, 1880

Figures 13, 14; Tables 3,4

The species-group name was changed to agree with the gender of the generic name. *Nematops microstoma* Günther, 1880: Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873-1876. Zoology 1 (pt 6): 1-82. Norman 1931, Treubia, 13: 427. Norman 1934, A systematic monograph of the flatfishes (Heterosomata). Vol I: 394. Munro, I. S. R. 1955: The marine and fresh water fishes of Ceylon: 132.

Common name: Small-mouth righteye flounder (Hensley, 1997)

Holotype.-**BMNH 1879.5.14:91**; Admiralty Island, outside Nares Harbour; 278 m (152 fm); 1: 75.6 mm SL.

Additional material: **AMS I.22805-029**; Northwest Shelf, 170 km N of Port Hedland, Indian Ocean; 18°28S 118°15E; 150-156 m; vessel Soela; 5: 49.2-87.8 mm SL. **NTM S.12904-016**; NNE of Cape Don, Arafura Sea, NT; 09°18'S 133°25'E; 146 m; 7 Nov. 1990; 2: 102.1-104.3 mm SL. **NTM S.12904-017**; NNE of Cape Don, Arafura Sea (NT); 09°18'S 133°25'E; 146 m; 7 Nov. 1990; 1: 44.3 mm SL.

Diagnosis.-A species of *Nematops* with the following combination of characters: lateral line scales 60-70, dorsal fin rays 65-69 and anal fin rays 54-57.

Description.-Data are presented for the holotype and values for additional material are given in parentheses. A species of *Nematops* with a rather deep body, large eyes separated by a very narrow space, non-confluent dorsal, caudal and anal fins, subsymmetrical pelvic fin bases. Body depth (BD) 42.2% in SL (40.0-47.0%), head length (HL) 23.2% in SL (23.4-27.3%). Interorbital space, snout, eyes and maxilla scaleless. Upper orbit 43.6% in HL (40.0-44.2%), encroaching on dorsal profile of head. Position of lower eye slightly anterior to upper eye (lower eye equal or slightly posterior to upper eye). Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through anterior quarter of lower eye, 28.3 % in HL (28.5-31.6%). Blind side maxilla 24.8% in HL (25.9-27.8%). Lower jaw symmetrical, ocular side 39.2% in HL (37.7-40.4%), blind side 38.0% in HL (37.3-39.8%). Conical teeth present on premaxillae and dentaries. Gill rakers longer than wide and not serrated, 8 (6-7) on upper limb and 12 (10-12) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 17.7% in SL, height of arch 23.3% in BD, 70 ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 7 (7-8) rays, (3-5) branched rays, one specimen had no branched ocular side pectoral fin rays, length (43.5-46.7%) in HL. Blind side pectoral fin with 8 (7-8) unbranched rays, length 48.3% in HL (38.0-54.6%). Pelvic fins with 6 rays. Ocular side pelvic fin (33.8-45.9%) in HL, blind side 46.5% in HL (37.8-46.1%). No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over approximately half of upper eye. Dorsal fin with 68 (65-69) rays, first ray (19.5-29.6%) in HL. Longest dorsal fin-ray 54.5% in HL (43.0-52.0%). Anal fin with 56 (54-57) rays, longest ray 48.4% in HL (42.6-55.3%). Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third (third or fourth) ray of ocular side pelvic fin.

Dorsal, anal, pectoral and pelvic fins scaleless. Twenty-two caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 29 (28) caudal vertebrae. Large ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin. The holotype has a tentacle on both eyes, seven specimens have a tentacle on the lower eye only and one specimen has no tentacles. Specimens without tentacles can be identified as *Nematops* on the basis of the presence of a nasal bone on the ocular side [absent in *Poecilopsetta* and *Marleyella* (Sakamoto, 1984)] and on the number of proximal pterygiophores found between the first anal fin pterygiophore and the hemal spine of the first caudal vertebra (three for *Nematops*; two for *Poecilopsetta* and *Marleyella* (this study, see Fig.5).

Coloration in ethanol.-Ocular side sometimes with one black spot at the base of the dorsal fin 2/3 of the body length. Dorsal and anal fins with black spots all along the fins, sometimes with black spot on dorsal and anal at the base of caudal peduncle. Ocular side pectoral fin with blackish tip. Caudal fin with a black triangular marking. Blind side creamy white.

Etymology.-From the Greek *microstomus* (*micro* meaning small and *stomus* referring to the mouth). Referring to the small mouth of this species. This is the type species of the genus.

Distribution.-*Nematops microstomus* is distributed from Nares Harbour to the north-western coast of Australia (Fig 14). This species is known to occur at depths between 146-278 m.

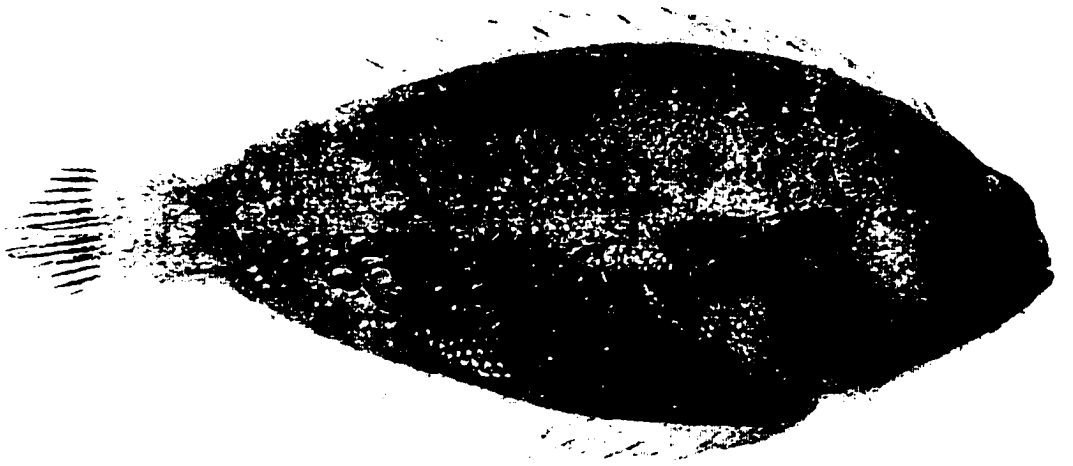


Fig. 13: *Nematops microstomus*, holotype: BMNH 1879.5.14:97, 75.6 mm SL.

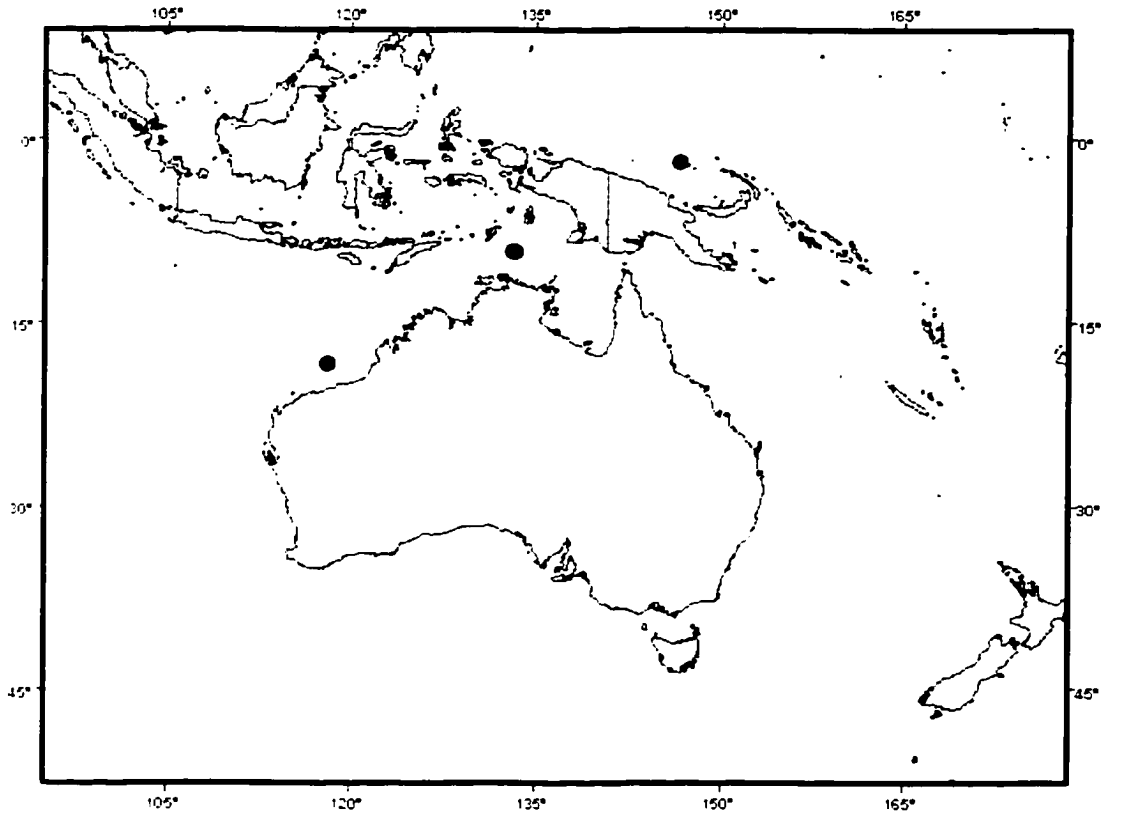


Fig. 14: Collection sites of *Nematops microstomus*.

Genus *Poecilopsetta*.-The genus *Poecilopsetta* comprises 13 valid species. They are found in the Atlantic, Indian and Pacific Oceans in temperate and tropical waters. This genus is also mostly found in deep waters, with three species (*P. colorata*, *P. plinthus* and *P. hawaiiensis*) found in relatively shallow waters.

This genus is not monophyletic because it is defined by the fact that it lacks the apomorphies found in the other genera of the family: absence of tentacles and only one nasal bone (tentacles and two nasal bones found in *Nematops*) and no elongated dorsal and pelvic fin rays (found in *Marleyella*). As such, it includes all the species that cannot be placed into a well defined genus but that share the characteristics of the family.
Etymology: *Poecilo* is from the Greek, *poikilo*, meaning spotted or mottled, and *psetta*, also from the Greek, meaning flatfish. Most species within this genus have spots on the ocular side and on the dorsal and anal fins. Some only have spots on the fins. Gender feminine.

Key of identification of the species of the genus *Poecilopsetta*.

1a Scales on the ocular side pectoral fin-rays, large, flat and scaly interorbital space, scales sometimes present on ocular side maxilla.....2

1b No scales on ocular side pectoral fin-rays, interorbital space small or absent and scaleless, no scales on the ocular side maxilla 5

2a 10 or less blind side pectoral fin rays, 13 or fewer ocular side pectoral fin rays.....3

2b More than 10 blind side pectoral fin rays, 13 or more ocular side pectoral fin rays.....***P. normani***

3a 98-131 lateral line scales, fewer dorsal fin rays (55-62), not in Hawaii.....4

3b 75-101 lateral line scales, high number of dorsal fin rays (59-70; 90% have 64 +), endemic to Hawaii.....***P. hawaiiensis***

4a White spots along the body, cycloid scales on the ocular side.....***P. albomaculata***

4b No white spots along the body, ctenoid scales on the ocular side, blind side sometimes light brown.....***P. colorata***

5a Long first dorsal fin ray (1.79-2.01 in HL), long ocular side pelvic fin (1.56-1.95 in HL).....***P. dorsialta***

5b Normal first dorsal fin ray, normal ocular side pelvic fin length.....6

6a Dark shadow around the postero-lateral edge of the eyes, 77-94 lateral line scales.....***P. natalensis***

6b Absence of a dark shadow around the eyes.....7

7a Small scales, 90 or more in the lateral line.....8

7b Big scales, less than 90 in the lateral line 9

8a 32-33 caudal vertebrae, large band of muscles along the body, dark spots at the base of hypural plates near the edges of the caudal skeleton (most easily seen in

juveniles), dark spots along the body on the ES in juveniles, with a well defined edge.....***P. zanzibarensis***

8b 30-32 (usually 30-31) caudal vertebrae, smaller band of muscles along the body (large area without muscles between dorsal and anal fins and body musculature), dark spots at the base of hypural plates near the mid-line of the body (seen even in larger specimens), dark spots along the body on the ES in juveniles, with a fainting edge, not well defined .....***P. praelonga***

9a 31-33 (usually 32-33) caudal vertebrae, 70-87 lateral line scales, 6-13 branched rays in the ocular side pectoral fin.....***P. beanii***

9b 28-32 (usually 28-31) caudal vertebrae, 0-9 branched rays in ocular side pectoral fin.....10

10a Ocular side pectoral fin shorter than blind side pectoral fin.....11

10b Ocular side pectoral fin longer than blind side pectoral fin.....12

11a Long head (3.52-3.96 in SL).....***P. macrocephala***

11b Short head (3.97-4.33 in SL).....***P. vaynei***

12a 54-68 lateral line scales, dorsal and anal fin rays with numerous small black spots, caudal fin rays with two or four black spots.....***P. plinthus***

12b 64-80 lateral line scales, dorsal and anal fin rays with creamy white edges, caudal fin with two black circles on its edges.....***P. inermis***

***Poecilopsetta albomaculata* Norman, 1939**

Figures 15, 16; Tables 7, 8

Poecilopsetta albomaculata, Norman, 1939, The John Murray expedition 1933-1934 Scientific reports, p. 101-102. Quéro *et al.* 1988, Cybium, 12(4): 328. Adam *et al.*, 1998, J.L.B. Smith Ichthyological Bulletin, 67:15.

Common name: White-spotted mottled flounder

Holotype.-**BMNH 1939.5.24:1774-1776**; southwest of Baa Atoll; 4°45'36"N 72°52'12"E to 4°42'36"N 72°50'24"E; 275 m; 4 Apr. 1934; 101.7 mm SL.

Paratypes.-**BMNH 1939.5.24:1774-1776;** same as holotype, 2: 97.1-110.9 mm SL.

Diagnosis.-A species of *Poecilopsetta* with the following combination of characters: white spots on the ocular side of body, cycloid scales on both sides of the body and a high (13-14) number of gill rakers on the first lower arch on the ocular side.

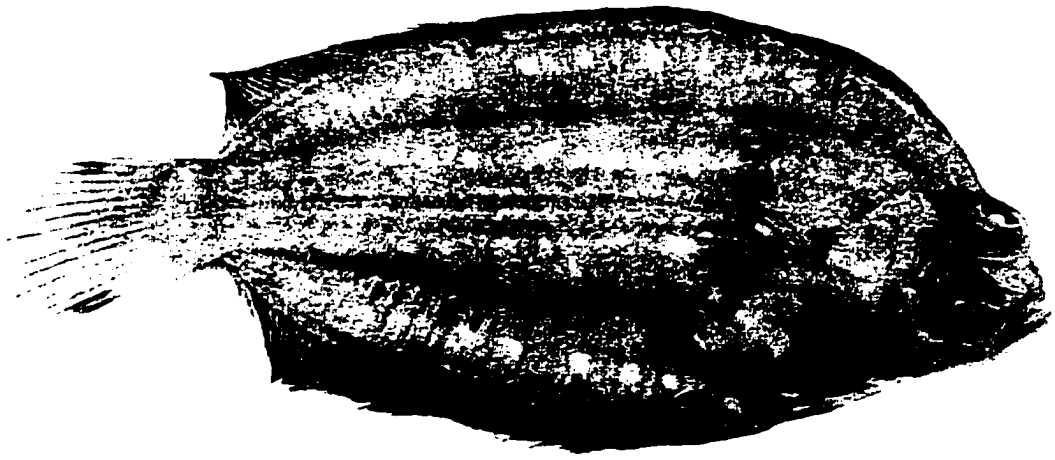
Description.-Data are presented for the holotype and values for paratypes are given in parentheses. A species of *Poecilopsetta* with a rather deep body, large eyes separated by a scaled interorbital space, non-confluent dorsal, caudal and anal fins, subsymmetrical pelvic fin bases and cycloid scales on both sides. Body depth (BD) 47.4% in SL (45.2-

46.0%), head length (HL) 24.2% in SL (23.1-25.7%). Interorbital space, snout and maxilla with scales. Eyes scaleless. Upper orbit 38.7% in HL (37.4-41.2%), encroaching on dorsal profile of head. Position of lower eye slightly anterior or equal to upper eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through anterior third of lower eye, 27.8 % in HL (26.9-27.1%). Blind side maxilla almost symmetrical, 26.6% in HL (27.4-28.0%). Lower jaw symmetrical, ocular side 37.0% in HL (34.9-36.9%), blind side 36.3% in HL (37.4-38.4%). Conical teeth present on premaxillae and dentaries. Teeth in three (three to four) distinct bands on blind side dentary and two (two to three) on blind side premaxilla. Two (two to three) rows of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 8 (8-9) on upper limb and 13 (13-14) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 17.2% in SL (18.8-19.6%), height of arch 21.6% in BD (20.2-21.8%), 118 (116-131) cycloid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 12 (12-13) rays, 8 (9-11) branched rays, length 61.4% in HL (59.9-60.5%). Blind side pectoral fin with 10 (8-10) unbranched rays, length 40.8% in HL (39.0-44.2%). Pelvic fins with 6 rays. Ocular side pelvic fin 37.2% in HL (37.0-39.2%), blind side 37.2% in HL (35.9-37.0%). No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior third of upper eye. Dorsal fin with 60 (61) rays, first ray 34.4% in HL (24.8-32.0%). Longest dorsal fin-ray 39.8% in HL (40.7-41.0%). Anal fin with 51 (50-51) rays, longest ray 39.3% in HL (39.9-43.3%). Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third ray of ocular side pelvic fin. Dorsal, anal and pelvic fins scaleless. Both pectoral fins have scales. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae,

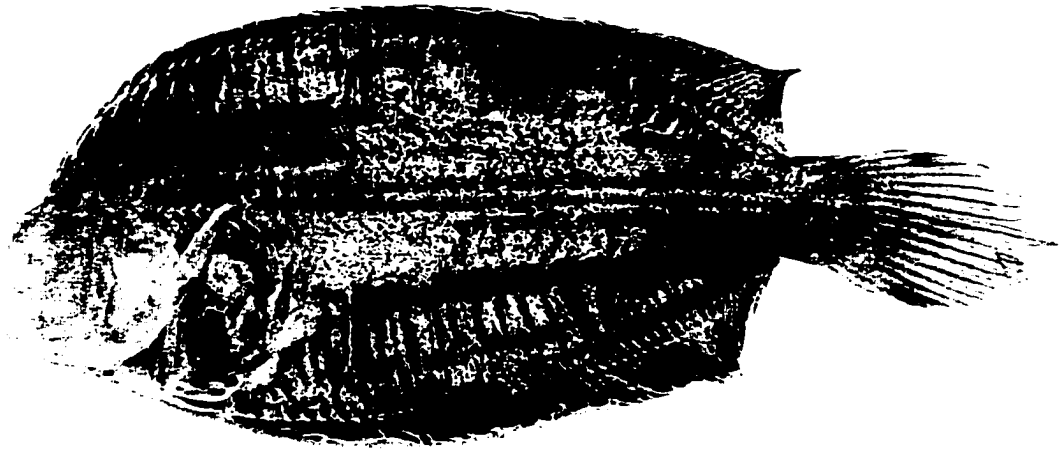
30 caudal vertebrae. Small cycloid scales on both sides. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

Coloration in ethanol.-Ocular side with four rows of white spots. Two rows near the origin of the dorsal and anal fins and one row on each side of the lateral line. Dorsal and anal fins brown with white tips. Ocular side pectoral fin with dark spot at the ventro-posterior tip. Both pelvic fins light brown. Caudal fin with two dark spots on upper and lower margins. Blind side evenly brown with head lighter.

Etymology.-From the Latin *albomaculata* (*albus* meaning white and *maculata* meaning spotted). The specific name refers to the white spots along the body.



A



B

Fig. 15: *Poecilopsetta albomaculata*, A) holotype: BMNH 1939.5.24:1774-1776; 101.7 mm SL, B) blind side.

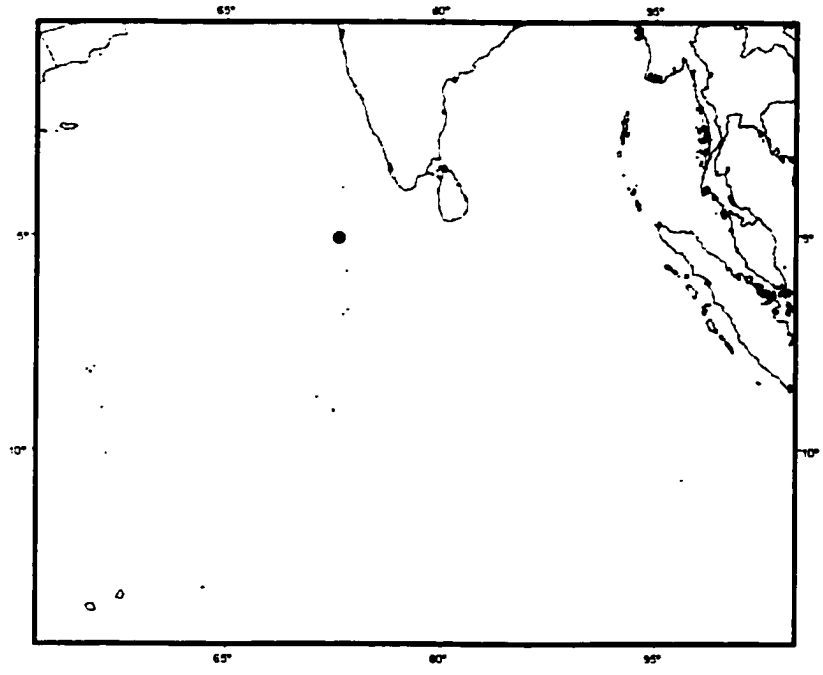


Fig. 16: Collection site of *Poecilopsetta albomaculata*.

Distribution.-*Poecilopsetta albomaculata* is only known from off Baa Atoll in the Maldive Islands (Fig. 16). This species is known to occur at a depth of 275 m.

Remarks.-*Poecilopsetta albomaculata* is similar to *P. colorata*, *P. hawaiiensis* and *P. normani*. These species all have scales on their interorbital space, maxilla and ocular side pectoral fins. *P. albomaculata* is easily distinguishable from the other "scaly" species by its white spots along the body and cycloid scales on the ocular side.

Table 7: Morphometric characters of *Poecilopsetta albomaculata*, *P. normani*, *P. natalensis*, *P. zanzibarensis*, *P. praelonga*, *P. colorata*, *P. vaynei* and *P. macrocephala* from the waters of the Indian Ocean. For abbreviations see Table 3.

Measurements	*P. albomaculata* n=3 Holotype BMNH 1939.5.24.1774-1776	*P. normani* n=8	*P. natalensis* n=17 Holotype BMNH 1922.3.27:7	*P. zanzibarensis* n=28 Holotype BMNH 1939.5.24:1785-1792	*P. praelonga* n=65	*P. colorata* n=28 Holotype BMNH 1879.5.14:97	*P. vaynei* n=20 Holotype MNHN 1986-653	*P. macrocephala* n=12 Holotype CSIRO H5213-01
SL (mm)	101.7 (97.1-110.9)	84.9-121.7	116.7 (77.9-128.9)	101.7 (68.9-125.9)	66.0-152.6	115.7 (67.2-150.2)	103.1 (68.6-107.7)	95.3 (70.1-103.5)
In SL								
BD	2.11 (2.18-2.21)	2.22-2.51	2.40 (2.41-2.80)	2.28 (2.42-3.22)	2.21-2.96	2.20 (2.01-2.64)	2.57 (2.38-2.99)	2.50 (2.47-2.85)
HL	4.13 (3.90-4.32)	3.96-4.38	4.46 (4.18-5.12)	4.30 (3.93-4.70)	3.65-4.48	3.75 (3.61-4.38)	3.97 (4.01-4.33)	3.52 (3.57-3.96)
LLW	5.82 (5.09-5.33)	5.18-6.01	5.48 (5.31-5.91) (6)	5.77 (5.20-6.44) (9)	4.84-6.19 (41)	4.78 (4.23-5.48) (21)	(5.31-6.24) (14)	5.53 (4.96-5.27) (6)
CPL	14.93 (16.43-16.60)	14.65-20.35	21.38 (16.37-27.03) (14)	24.38 (18.17-27.13) (27)	19.90-36.97	17.74 (15.58-23.26)	23.53 (18.23-45.68)	23.77 (17.04-40.78)
In HL								
UO	2.58 (2.43-2.67)	2.51-2.72	2.38 (2.16-2.48)	2.42 (2.14-2.77)	2.20-3.02	2.83 (2.38-3.04)	2.50 (1.95-2.51)	2.21 (1.96-2.25)
UJO	3.60 (3.69-3.71)	3.43-4.22	3.84 (3.14-4.00)	4.30 (3.26-4.41)	2.99-4.00	3.04 (2.69-3.79)	3.30 (2.38-3.65)	2.99 (2.61-2.99)
UJB	3.76 (3.57-3.65)	3.67-4.63	4.30 (3.16-4.23)	4.38 (3.50-5.03) (27)	2.97-4.07	3.26 (2.90-4.59)	3.71 (2.58-3.46)	3.23 (2.80-3.44)
LJO	2.71 (2.71-2.87)	2.64-3.17	2.70 (2.36-2.60)	2.68 (2.35-2.80)	2.37-3.05 (62)	2.50 (2.27-2.92) (26)	2.39 (2.06-2.53)	2.31 (2.26-3.44)
LJB	2.75 (2.60-2.68)	2.58-3.21	2.65 (2.44-2.68)	2.70 (2.31-2.77) (27)	2.26-3.07 (62)	2.43 (2.27-3.04)	2.34 (2.09-2.52)	2.30 (2.14-2.37)
LpectO	1.63 (1.65-1.67)	1.43-1.75	1.95 (1.60-2.36)	2.31 (1.92-5.02) (23)	1.62-2.77 (59)	1.87 (1.63-2.05) (24)	2.95 (2.77-3.66) (19)	3.12 (2.34-3.31)
LPectB	2.45 (2.26-2.56)	2.24-2.88	2.22 (1.90-2.70)	2.24 (2.09-5.85) (23)	1.55-3.20 (60)	2.47 (2.04-3.44) (24)	2.67 (2.06-2.57) (19)	2.23 (1.87-2.47)

LPelO	2.69 (2 55-2 71)	2 25-2 58	2 13 (1 82-2 85)	2 24 (2.19-3 09) (25)	1 94-2.79 (54)	2 64 (2.15-3 05)	2.43 (1 83-2.43) (18)	(2 32-2.77) (10)
HDR	2.51 (2.44-2 46)	2 07-2 49	2.00 (1 59-2 21)	2 28 (1 95-2 43) (23)	1.63-2 51 (60)	2 71 (2.01-2.66)	2.31 (1 82-2.48) (19)	2.22 (1.99-2 51)
FDR	2.90 (3.12-4 03)	2.82-3.92	2.78 (2.21-3.55)	2.82 (2.22-5.28)	2.23-4 45 (62)	4.16 (2.67-4.29)	3.37 (2.23-3.21)	3.31 (2.71-3.48)
HAR	2.55 (2 31-2.51)	1.97-2.61	2.20 (1 69-2 27)	2.28 (1.90-2.59) (24)	1.73-2 54 (60)	2.54 (2.14-2.66)	2 27 (1.92-2.48) (19)	2.96 (1.97-2.62)
In BD								
LLH	4.63 (4.59-4.96)	4 01-5 43	(4.02-4 69) (6)	4.08 (3.71-5.32) (10)	2.55-5.45 (42)	4.69 (3.71-5.07) (23)	3.62 (3.45-4.10) (10)	3.97 (3.47-4.38) (6)
Counts								
LL scales	118 (116-131)	110-133	77 (79-94) (6)	97 (90-101) (8)	91-111 (42)	97 (98-124) (21)	79 (70-81) (12)	75 (75-80) (5)
Cvert	30	30 (31-32)	31 (27-33)	32 (32-33) (26)	29-32	29 (26-29)	30 (28-31)	29 (28-30)

Table 8: Frequency distribution of meristic characters for *P. albomaculata*, *P. normani*, *P. natalensis*, *P. zanzibarensis*, *P. praelonga*, *P. colorata*, *P. vaynei* and *P. macrocephala*. The asterisk represents data for the holotype.

Dorsal fin-rays

	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	n	$\bar{x}$	s
P. albomaculata						1*	2									3	60.7	0.58
P. normani					1		2	1	1	3*	4	1				13	63.4	2.13
P. natalensis			1					5*	7	4						17	62.6	1.62
P. zanzibarensis					1	2	3	8*	7	5						26	62.3	1.34
P. praelonga			1	2	2	6	11	24	10	6	1					63	61.7	1.55
P. colorata	2			1	5	8	6*	6								28	60.0	1.82
P. vaynei								1	3	4	5	3	7*	5	1	29	65.8	1.89
P. macrocephala									2	5	2	1*	2			12	64.6	1.37

Anal fin-rays

	47	48	49	50	51	52	53	54	55	56	57	58	n	$\bar{x}$	s
P. albomaculata				1	2*								3	50.7	0.58
P. normani					1	1	4	1	4*	2			13	53.9	1.55
P. natalensis			1			1	8	7*					17	53.1	1.22
P. zanzibarensis		1		2	5*	6	7	4	1				26	52.2	1.55
P. praelonga		1	1	1	14	23	17	5	1				63	52.1	1.19
P. colorata		2	7	5*	4	5	5						28	50.6	1.64

P. vaynei					1		3	3	5	6*	9	2	29	55.6	1.76
P. macrocephala							3	2	5*	1	1		12	54.6	1.24

Ocular side pectoral fin-rays

	6	7	8	9	10	11	12	13	14	15	16	17	n	$\bar{x}$	s
P. albomaculata							2*	1					3	12.3	0.58
P. normani								3	3		1	1	8	14.3	1.49
P. natalensis			2	9	6*								17	9.2	0.66
P. zanzibarensis			1	5	12	7*							25	10.0	0.82
P. praelonga	1		14	33	12	1							61	9.0	0.80
P. colorata				2	7	13*	4						26	10.7	0.83
P. vaynei		3	7*	4	10	3	1						28	9.2	1.34
P. macrocephala		4*	7	1									12	7.8	0.62

Blind side pectoral fin-rays

	5	6	7	8	9	10	11	12	13	14	15	n	$\bar{x}$	s
P. albomaculata				1		2*						3	9.3	1.15
P. normani							3	2	2		1	8	12.3	1.39
P. natalensis				12	3*	2						17	8.4	0.71
P. zanzibarensis				1	16*	4	2					23	9.3	0.70
P. praelonga		3	18	33	6							60	7.7	0.72
P. colorata	1			4*	11	11						27	9.1	1.09
P. vaynei		2*	10	11	5							28	7.7	0.86

P. macrocephala			9*	3																							12	7.3	0.45

Caudal vertebrae

	26	27	28	29	30	31	32	33	n	$\bar{x}$	s
P. albomaculata					3*				3	30.0	0.00
P. normani					1*	10	2		13	31.1	0.49
P. natalensis		1			1	14*		1	17	30.8	1.13
P. zanzibarensis							4*	22	26	32.8	0.37
P. praelonga					11	44	8		63	30.9	0.55
P. colorata	1		3	24*					28	28.8	0.63
P. vaynei			1	9	17*	2			29	29.7	0.66
P. macrocephala			1	10*	1				12	29.0	0.43

Lateral line scales

	70	73	74	75	77	78	79	80	81	83	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
P. albomaculata																										
P. normani																										
P. natalensis					1*		1	1	1	1					1											
P. zanzibarensis											1					2	1	1	1		1	1				
P. praelonga												1	4	2		1		1		2	2	4	3	5	1	2
P. colorata																		1*	1		2			1	1	2
P. vaynei	1	1	1	3		3	2*	2	2																	

P. macrocephala				2*		1	1	1														

Lateral line scales

	106	107	108	109	110	111	112	116	117	118	120	122	123	124	125	127	131	133	n	$\bar{x}$	s
P. albomaculata								1		1*							1		3	122	8.14
P. normani					1				1		2	1			1	1		1	8	122	6.88
P. natalensis																			6	82	6.06
P. zanzibarensis																			8	97	3.40
P. praelonga	2	4	3	1	3	1													42	102	5.79
P. colorata		2				1	6		1		1		1	1					21	109	7.72
P. vaynei																			15	77	3.24
P. macrocephala																			5	77	2.30

Poecilopsetta beanii (Goode, 1881)

Figures 12, 17-21; Tables 9-11

Limanda beanii: Goode, 1881, Proceedings of the United States Museum 3: 467-474. Goode and Bean 1896, U.S. National Museum Special Bull. No 2: 428.

Poecilopsetta beanii: Hubbs 1919, Proceedings of the Biological Society of Washington 32: 163-164. Norman 1931, Treubia 13: 425. Norman 1934, Monograph of the flatfishes, p 388. Boschung 1992, Bulletin Alabama Museum of Natural History, 14: 177.

Common name: Deepwater dab (Nelson *et al.*, 2002 draft)

Lectotype and paralectotype.-**USNM 26102**; Atlantic Ocean, off Martha's Vinyard; 39°57'N to 70°56'W-70°57'W; 219-230 m (126-120 fm); vessel Fish Hawk; 13 Sep. 1880; 99.2 and 107.5 mm SL.

Additional material: **BMNH 1931.8.19:10**; 28°41'N 86°07'W, 309 m (169 fm); 1: 67.1 mm SL. **BMNH 2000.8.1:1**; 49°31'14"N 11°5'42"W; 201-203 m; Sta. 39, CIRO voyage 3/95; 26 March 1995; 1: 81.7 mm SL. **CAS 117431**; Gulf of Mexico; 27°50'N 91°11'W; 375 m (205 fm); 11 Nov. 1951; 2: 101.6-106.0 mm SL. **CAS 117432**; Gulf of Mexico; 29°15'5"N 87°53'W; 320 m (175 fm); 27 Apr. 1951; 1: 60.8 mm SL. **CAS 117433**; Gulf of Mexico, U.S.A.; 27°51'N 91°32'30"W; 402 m (220 fm); 11 Nov. 1951; 5: 88.0-100.8 mm SL. **CAS 149898**; Gulf of Mexico, U.S.A., Florida, Hillsborough, off Egmont Key; 27°49'N 84°59'W; 366 m (200 fm); 29 Sept. 1951; 5: 95.2-110.1 mm SL. **UF 40082**; Gulf of Mexico, U.S.A., Texas; 27°45'36"N 95°6'46"W; 384 m (210 fm); 15 Aug. 1983; 7: 71.9-107.4 mm SL. **UF 100947**; Atlantic Ocean, U.S.A., Florida Keys; 24°20'5"N 82°53'4"W to 24°20'4'N

82°52.32'W; 182-185 m; 25 Apr. 1995; 12: 55.5-118.6 mm SL. **UF 100948**; Atlantic Ocean, Florida Keys; 24°19'10"N 82°58'10"W to 24°18.90'N 82°55.61W; 282-295 m; 25 Apr. 1995; 7: 90.4-100.3 mm SL. **UF 100959**; Atlantic Ocean, Florida Keys; 24°20'13"N 82°56'4"W to 24°20,07'N 82°53.53'W; 187-200 m; 25 Apr. 1995; 10: 53.5-112.4 mm SL. **UF 108278**; Atlantic Ocean, Florida Keys; 24°20'33"N 83°6'31"W; 308-306 m; 14 May 1996; 6: 60.3-104.2 mm SL. **UF 108889**; Atlantic Ocean, Florida Keys; 24°18'34.2"N 82°37'3"W; 188-183 m (103-100 fm); 1 May 1998; 4: 86.2-117.3 mm SL. **USNM 157820**; Gulf of Mexico, W. of Florida Keys; 24°28'N 83°25'W; 366 m (200 fm); vessel Oregon, sta. 1011; 14 Apr. 1954; 1: 113.4 mm SL. **USNM 158302**; Gulf of Mexico, S. W. of New Orleans, LA.; 27°50'N 91°11'W; 375 m (205 fm); vessel Oregon, sta. 500; 11 Nov. 1951; 1: 87.4 mm SL. **USNM 158362**; Gulf of Mexico, Pensacola, Florida; 29°38'N 87°16'30"W; 205 m (112 fm); vessel Oregon, sta. 281; 25 Feb. 1951; 4: 69.0-114.1 mm SL. **USNM 158496**; Gulf of Mexico, Florida; 29°15'30"N 87°53'W; 320 m (175 fm); vessel Oregon, sta. 314; 27 Apr. 1951; 3: 67.7-104.0 mm SL. **USNM 164142**; Gulf of Mexico, Tortugas Is, W of Key West; 24°20'N 83°20'W; 347 m (190 fm); vessel Oregon, sta. 1005; 13 Apr. 1954; 9: 49.3-91.5 mm SL. **USNM 217976**; Gulf of Mexico, Mississippi, off Mississippi delta; 29°00'N 88°38'30"W; 338-347 m (185-190 fm); vessel Oregon, sta. 4034, cr. 82; 2 Nov. 1962; 4: 95.3-108.7 mm SL. **USNM 286560**; Atlantic, Florida; 31°02'N 79°48'W; 256 m (140 fm); vessel Oregon II, sta. 11710, cr. 33; 20 Jan 1972; 1: 113.1 mm SL.

Diagnosis.-A species of *Poecilopsetta* with the following combination of characters: a rather elongated body (2.45-3.33 in SL) with a high number of caudal vertebrae (31-33).

Description.-Data are presented for the lectotype and values for the additional material are given in parentheses. A species of *Poecilopsetta* with an elongated body, eyes separated

by a very narrow space, non-confluent dorsal, caudal and anal fins, subsymmetrical pelvic fin bases and ocular side pectoral fin-rays longer than blind side. Body depth (BD) 39.1% in SL (30.1-40.8%), head length (HL) 18.6% in SL (19.4-24.6%). Interorbital space, snout, eyes and maxilla scaleless. Upper orbit 41.6% in HL (35.7-47.5%), encroaching on dorsal profile of head. Position of lower eye equal or slightly anterior to upper eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through anterior third of lower eye, 30.4% in HL (25.4-35.1%). Blind side maxilla almost symmetrical, 27.4% in HL (23.3-32.9%). Lower jaw symmetrical, ocular side 40.7% in HL (36.7-47.5%), blind side 40.2% in HL (35.6-47.2%). Conical teeth present on premaxillae and dentaries. Teeth in two (two to three) distinct bands on blind side dentary and premaxilla. Two rows of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 7 (6-9) on upper limb and 10 (9-12) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 15.8% in SL (13.9-23.4%), height of arch 21.0% in BD (18.6-26.0%), 84 (70-87) ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 7 (6-13) rays, 6 (3-8) branched rays, length 49.7% in HL (19.0-54.6%). Blind side pectoral fin with 7 (5-10) unbranched rays, length 42.5% in HL (22.7-48.6%). Pelvic fins with 6 rays. Ocular side pelvic fin 50.2% in HL (37.4-50.9%), blind side 46.2% in HL (37.4-49.8%). No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior third of upper eye, sometimes over posterior half. Dorsal fin with 64 (61-67) rays, first ray 33.5% in HL (27.4-41.1%). Longest dorsal fin-ray 50.5% in HL (38.3-64.4%). Anal fin with 54 (51-57) rays, longest ray 48.7% in HL (38.0-63.7%). Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third (second to fourth) ray of ocular

side pelvic fin. Dorsal, anal, pectoral and pelvic fins scaleless. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 32 (31-33) caudal vertebrae. Ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

Coloration in ethanol.-Evenly brown with black spots on dorsal and anal fins. Caudal fin with two black spots. Ocular side pectoral fin with dark spot at its distal end. Black peritoneum on the ocular side only. Blind side creamy white.

Etymology.-Named in the honour of T. H. Bean (Goode 1881), a colleague of Goode.

Distribution.-*Poecilopsetta beani* is distributed from the Gulf of Mexico to the eastern coast of the United States. The type locality, off New England, is the northernmost distribution point in the western Atlantic. There is one record off the southwestern coast of England (J. Nielsen, pers. comm.) (Fig. 18). Water currents can be responsible for the presence of a specimen on the other side of the Atlantic (Fig. 12). This specimen could have followed the North Atlantic gyre (Fig. 12; A) flowing along the coast of North America towards western Europe. This species is known to have a long larval stage (see below) which would have followed the water currents to the other side of the Atlantic. This species is known to occur at depths between 182-402 m.

Fig. 17: *Poecilopsetta beanii*, paralectotype :USNM 26102; 99.2 mm SL.

Remarks.-*Poecilopsetta beanii* is very similar to *P. inermis* and *P. zanzibarensis* of the Indian Ocean. *P. zanzibarensis* has a higher number of lateral line scales (90-101 *vs* 70-87 for *P. beanii*). *P. beanii* and *P. inermis* are the only species known from the Atlantic Ocean. They can be distinguished by their number of caudal vertebrae. Seventy-eight percent of all *P. beanii* measured had 32 caudal vertebrae. For *P. inermis*, 96% have 30 and 31 caudal vertebrae. *P. beanii* also has a slightly narrower body than *P. inermis* (Fig. 19). When the three diagnostic characters are used (caudal vertebrae, BD and LL scales), 89% of all fishes from the Atlantic Ocean can be identified. Another five percent can be added to the 89% identified when the geographical information is incorporated. The two species do not completely overlap geographically.

Larvae.-In *Poecilopsetta*, very little is known about the larval stage. So far, only six species have larvae that have been described (*P. beanii*, this study), *P. inermis* and *P. colorata* (Evseenko and Suntsov, 1993), *P. hawaiiensis* (Ahlstrom *et al.*, 1984; Bray and Leis, 2000), *P. plinthus* (Minami, 1988; Evseenko and Suntsov, 1993; Uyeda and Sasaki,

2001) and *P. praelonga* (Hoshino *et al.*, 2000). Others have described larvae but have been unable to assign them to a species (Quéro *et al.*, 1986; Evseenko and Suntsov, 1993; Bray and Leis, 2000; this study, see after *P. zanzibarensis*).

For *P. beanii*, no larvae have been previously described. Five specimens where found in lots studied for this work (Fig. 20, 21). The main difference between larvae and adults is the coloration. Also, in the two smaller specimens (49.3-60.3 mm SL) the scales on the ocular side are cycloid. In the three longer specimens (60.8-70.3 mm SL) the scales have ctenii, which is the condition found in the adults. In addition, in larvae, both pelvic fins are closer together, the fin on the blind side being equal to or slightly behind that of ocular side. In the adult, the blind side fin is slightly more posterior than the fin on the ocular side. The larvae described here represent transformation larvae (*sensu* Kendall *et al.*, 1984) for they have all the characteristics of a juvenile but do not have fully formed pectoral fin rays.

General larva.-Larvae of the genus *Poecilopsetta* are easily recognizable with their narrow body musculature and broad pterygiophore zone without muscles between the body musculature and dorsal and anal fins. They also have black spots found in lines on the body. These lines are always found in the same regions. On the ocular side there are four distinct lines with black spots. From the dorsal portion of the fish they are: line 1) at the base of the dorsal fin rays, line 2) on the dorsal edge of the body musculature, line 3) at the ventral edge of the body musculature and line 4) at the base of the anal fin rays. In all larvae there is a single spot at the base of the caudal peduncle exactly on the vertebral column. On the head and abdominal region the pattern of spotting is more variable and will be described separately for the different species.

On the blind side, we also find spots arranged in lines. The lines are more numerous, six are found on the blind side. They are located: line A) at the base of the

dorsal fin rays, line B) on the dorsal edge of the body musculature, line C) on the epaxial musculature immediately above the vertebral column, line D) on the hypaxial musculature immediately below the vertebral column, line E) at the ventral edge of the body musculature and line F) at the base of the anal fin rays. As seen on the ocular side, a single spot is found at the base of the caudal peduncle on the vertebral column. Once again the head and abdominal region are highly variable and will be described separately for the different species.

On the fins, two spots are usually found on the caudal fin. The dorsal and anal fins have spots. The tip of the pelvic fins are also pigmented.

Coloration of the larvae of *P. beanii*.-On the ocular side, line 1 has six spots, line 2 has five or six spots, line 3 has five spots and line 4 has five spots (Fig. 20). Line 2 and 3 are more visible in the smallest larvae and seem to be the first to disappear as the fish reaches the juvenile stage because they are less distinguishable in the longest larvae. The single black spot on the vertebral column is followed by two spots at the base of the caudal skeleton near the level of hypural five and parhypural. These three spots are also seen on the blind side.

On the head, the snout and lower jaw are the only pigmented areas. These spots are observed on both sides of the body. One on the snout is found over the upper jaw (close to the nasal organ) while the other is situated on the tip of the snout.

On the abdominal region spots are seen in the smaller specimens only.

The caudal fin shows the same coloration as for the adults: two black spots on the last rays of the upper and lower lobes. Some larvae also have a black spot on the middle rays, on the distal end of the fin. In the smallest larvae the tip of the pelvic fin rays are pigmented. This spot is lost in longer specimens.

On the ocular side of the larva from the UF 108272 lot (Fig. 20 b) there is some faint coloration all along the body. These markings do not form distinct spots and may be the beginning of the coloration found in the adult.

On the blind side (Fig. 21), line A has six or seven spots, line B has six spots, line C has five spots, line D has five spots, line E has five spots and line F also has five spots.

Three spots are found on the abdominal region. One in the middle of the region, one near the pelvic fins and one at the beginning of the anal fin. On the head, spots are found on the snout, under the lower jaws and on the branchiostegal membrane. On the snout, there is one spot just above the upper jaw. Two spots are found on the lower jaw, one at the tip of the dentary and one at the other extremity. One last spot is found at the base of branchiostegal rays, on the body mid-line.

Evseenko and Suntsov (1993) described larvae from the Atlantic Ocean. They identified these larvae as *P. beanii*. After examining these larvae (ZMUC 853468-472), I conclude that these larvae belong to *P. inermis* (see section under *P. inermis*).

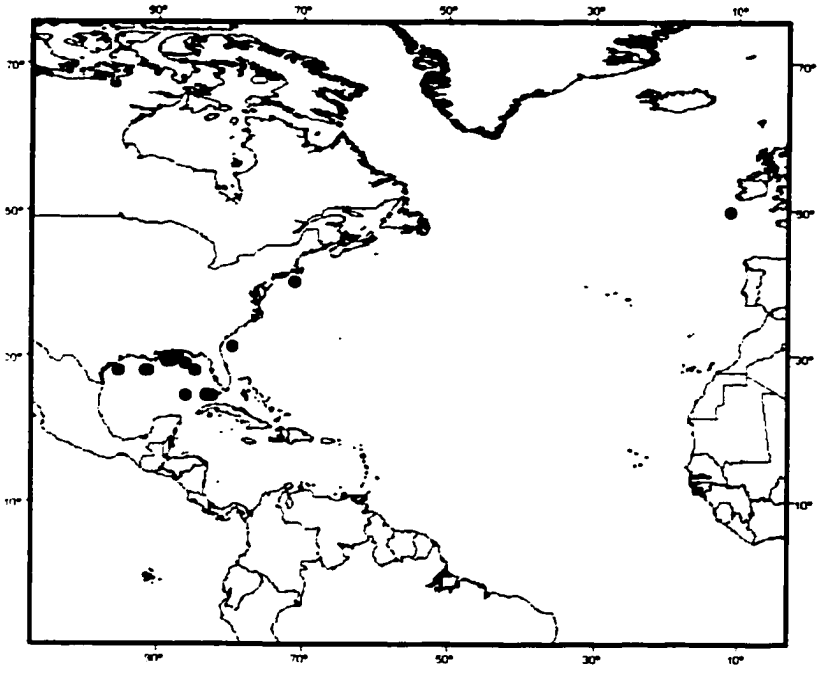


Fig. 18: Collection sites of *Poecilopsetta beanii*.

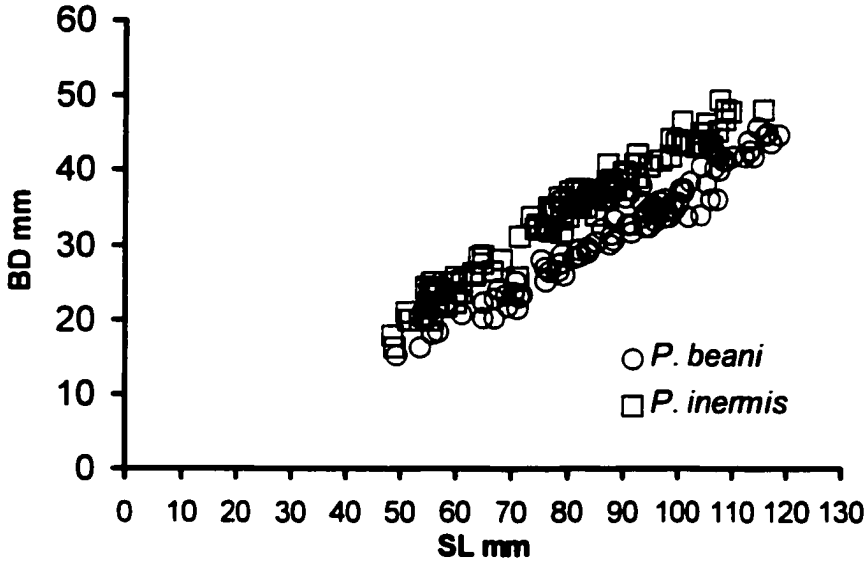


Fig. 19: Body depth in millimetres in relation to standard length (in mm) in *Poecilopsetta beanii* and *P. inermis*.

Table 9: Morphometric characters of *Poecilopsetta beanii* and *P. inermis* from the Atlantic Ocean. For abbreviations see Table 3.

Measurements	*P. beanii* n=86 Lectotype USNM 26102	*P. inermis* n=101
SL (mm)	107.5 (49.3-118.6)	54.5-115.7
ln SL		
BD	2.56 (2.45-3.33)	2.13-3.01
HL	5.39 (4.04-5.16)	3.57-4.73
LLW	(4.27-7.22)	4.91-7.79 (50)
CPL	16.62 (14.50-31.66) (85)	16.71-33.52 (100)
ln HL		
UO	2.41 (2.10-2.80)	2.18-2.99
UJO	3.29 (2.85-3.93) (85)	2.96-4.47 (99)
UJB	3.65 (3.04-4.29)	3.27-4.48 (99)
LJO	2.46 (2.10-2.73)	2.26-3.00
LJB	2.49 (2.12-2.81)	2.28-2.85
LPectO	2.01 (1.83-5.25) (81)	1.96-3.52 (80)
LpectB	2.35 (2.06-4.41) (82)	1.86-3.39 (94)
LPelO	1.99 (1.96-2.68)	1.79-2.95 (99)
HDR	1.98 (1.55-2.61) (85)	1.64-2.71 (99)
FDR	2.99 (2.43-3.66) (85)	2.13-3.94 (98)
HAR	2.06 (1.57-2.63) (85)	1.57-2.41 (99)
ln BD		
LLH	4.76 (3.85-5.37) (81)	3.68-5.47 (54)

Table 10: Frequency distribution of meristic characters for *Poecilopsetta beanii* and *P. inermis*. The asterisk represents data for the lectotype.

Dorsal fin-rays

	56	57	58	59	60	61	62	63	64	65	66	67	n	$\bar{x}$	s
P. beanii						4	16	13	27*	17	6	2	85	64	1.4
P. inermis	1	1		4	8	18	21	23	15	7		1	99	62	1.8

Anal fin-rays

	49	50	51	52	53	54	55	56	57	58	n	$\bar{x}$	s
P. beanii			2	9	15	24*	20	12	2		84	54	1.4
P. inermis	2	5	13	18	27	25	6	3			99	53	1.5

Ocular side pectoral fin-rays

	6	7	8	9	10	11	12	13	n	$\bar{x}$	s
P. beanii	1	5*	19	40	16	2		1	84	8.9	1.0
P. inermis		2	31	30	22	3			88	8.9	0.9

Blind side pectoral fin-rays

	4	5	6	7	8	9	10	11	n	$\bar{x}$	s
P. beanii		1	1	11*	49	18	4		84	8.1	0.8
P. inermis	1			14	44	32	4	2	97	8.3	1.0

Caudal vertebrae

	28	29	30	31	32	33	n	$\bar{x}$	s
P. beanii				18	67*	1	86	31.8	0.4
P. inermis	1	1	54	42	1		99	30.4	0.6

Lateral line scales

	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	n	$\bar{x}$	s
P. beanii							1	1	3	3	7	7	7	5	5	5	9	8	10	1	4*	3	1	1	81	78.5	3.9
P. inermis	1		1	2	3	4	6	8	10	5		8	2		1		1								52	71.7	3.0

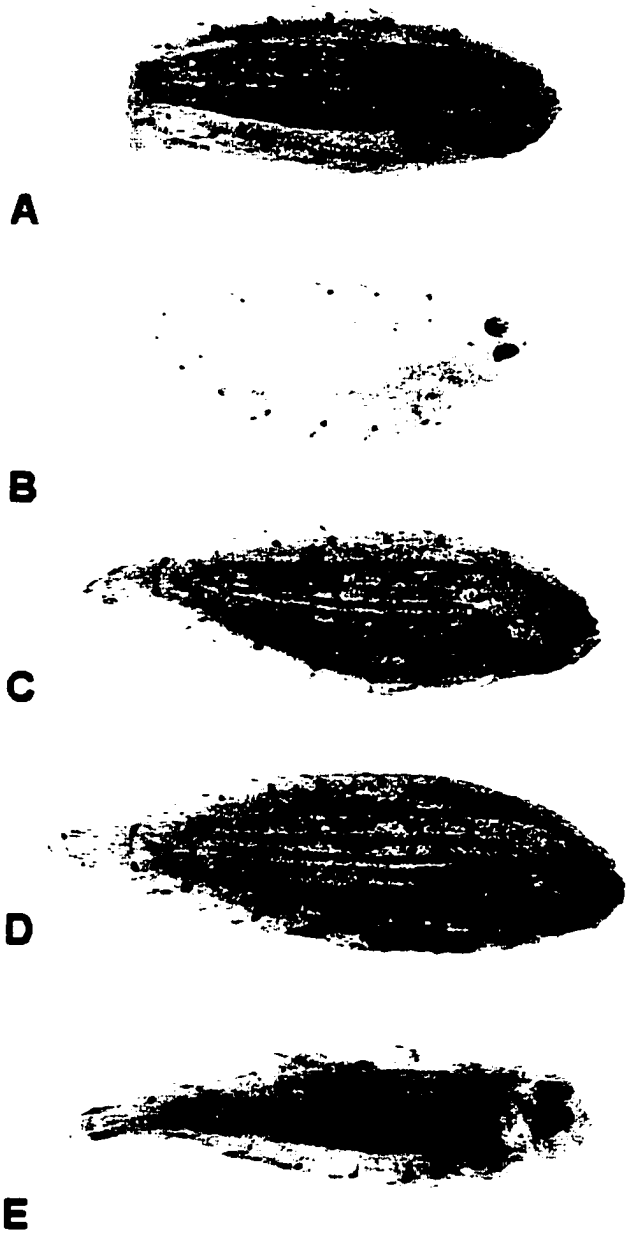


Fig. 20: Ocular side of larvae of *Poecilopsetta beanii*. A) CAS 117432: 60.8 mm SL, B) UF 108278; 60.3 mm SL, C) USNM 158496; 70.3 mm SL, D) USNM 158496; 67.7 mm SL, E) USNM 164142; 49.3 mm SL.

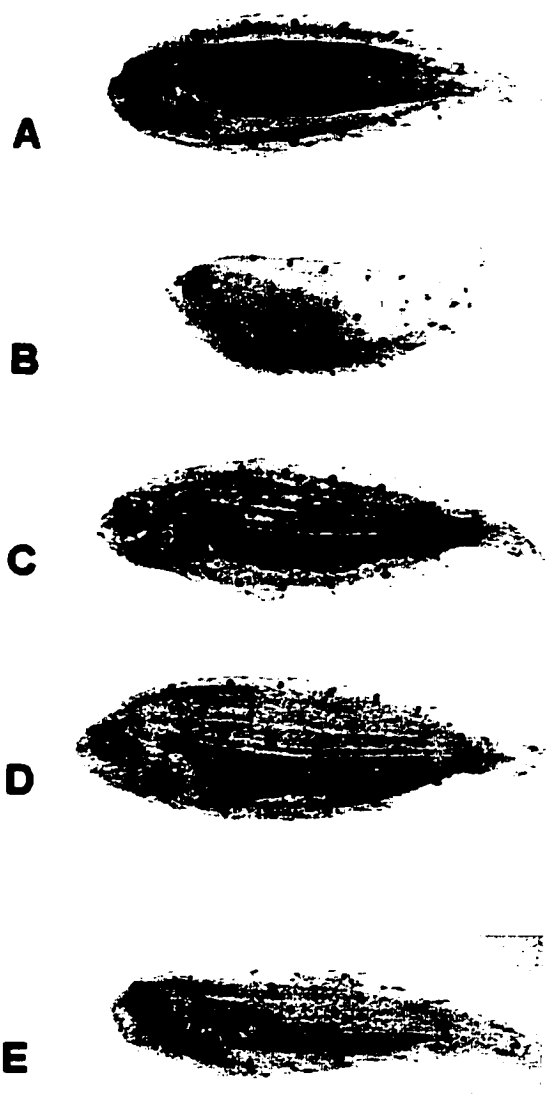


Fig. 21: Blind side of larvae of *Poecilopsetta beanii*. A) CAS 117432: 60.8 mm SL, B) UF 108278; 60.3 mm SL, C) USNM 158496; 70.3 mm SL, D) USNM 158496; 67.7 mm SL, E) USNM 164142; 49.3 mm SL.

Table 11: Measurements of larvae, juveniles and adults of *Poecilopsetta beanii*. For abbreviations see Table 3. LPelBS: length of the pelvic fin on the blind side.

Measurements	Larvae n=5	Juveniles and adults n=81
SL	49.3-70.3 mm SL	53.5-118.6 mm SL
In SL		
BD	2.58-3.24	2.45-3.33
HL	4.04-4.66	4.18-5.39
In HL		
UO	2.66-2.80	2.10-2.74
UJO	3.04-3.34	2.85-3.93
UJB	3.04-3.59	3.04-4.29
LJO	2.27-2.53	2.10-2.73
LJB	2.13-2.55	2.12-2.81
LPectOS		1.83-5.25
LPectBS		2.01-4.41
LPelOS	2.23-2.68	1.96-2.62
LPelBS	2.13-2.55	2.01-2.92
HDR	2.22-2.61	1.55-2.52
FDR	2.56-3.51	2.43-3.66
HAR	2.02-2.63	1.57-2.42

***Poecilopsetta colorata* Günther, 1880**

Figures 22-25; Tables 7, 8, 12-14

Poecilopsetta colorata: Günther, 1880, Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873-1876. Zoology 1 (pt 6):1-82. (Reprinted in 1963 by J. Cramer). Norman 1931, Treubia 13: 425. Norman 1934, Monograph of the flatfishes, p 390. Gloerfelt-Tarp and Kailola 1984, Trawled fishes of Southern Indonesia and Northwestern Australia: 276-277 (Picture of page 276 is misidentified as *Psammodiscus ocellatus*). Quéro *et al.* 1988 Cybium 12(4): 329. De Bruin, Russell and Bogusch 1994, FAO species identification field guide for fishery purposes. The marine fishery resources of Sri Lanka. FAO, Rome. 400p.

Common name: Coloured righteye flounder (Gloerfelt-Tarp and Kailola, 1984)

Holotype: **BMNH 1879.5.14:97**; Kei Is., vessel Challenger; 1: 115.7 mm SL.

Additional material: **BMNH 1927.1.6:62-63**; Andaman sea; 338 m (185 fm); 2: 69.9-84.6 mm SL. **NTM S.10760-008**; Southeast Lombok, Indonesia; 8°58'S 116°34'E; 150-280 m; July 1981; 1: 99.7 mm SL. **NTM S.11351-016**; South of Teluk Goembang, Lombok, Indonesia; 9°00'S 116°19'E; 180 m; 21 Aug 1984; 1: 94.0 mm SL. **NTUM 02495**; Hongkong; 20°4'N 114°37'E; 6 Mar. 1960; 1: 136.0 mm SL. **USNM 137392**; Pacific Philippines, China sea vicinity Southern Luzon, Malavatuan Id.; 13°55'55"N 120°10'15"E; 214 m (117 fm); vessel Albatross, Sta. 5275; 16 July 1908; 1: 90.0 mm SL. **USNM 286556**; Pacific Philippines, Macclesfield bank, South China sea; 16°10'6"N 114°29'12"E

to 16°11'42"N 114°27'42"E; 307-311 m (167-170 fm); vessel Cape St. Mary; 12 June 1964; 1: 117.9 mm SL. **WAM P.29729-012**; 60km West of Bernier Is., WA; 25°2'S 112°9'E; 383 m; 28 Feb. 1988; 11: 116.8-151.1 mm SL. **WAM P.29730-002**; 60km west of Dorre Is.; 25°20'S 112°9'E; 380-420 m; 28 Feb 1988; 6: 120.9-136.3 mm SL. **WAM P.29732-024**; 24°40'S 112°10'E; 500 m; 3 Apr 1988; 1: 144.3 mm SL. **WAM P.29862-001**; Joseph Bonaparte Gulf, WA; 13°43'S 128°38'E; 62 m; 26 Dec 1969; 1: 131.3 mm SL. **WAM P.30586-003**, WA, 19°20S 115°40E, 348-352 m, vessel Soela, 29 Jan 1984; 1: 67.2 mm SL.

Diagnosis.-A species of *Poecilopsetta* with the following combination of characters: scales on the ocular side maxilla, ocular side pectoral and interorbital space, fewer than 30 caudal vertebrae, ctenoid scales on the ocular side and 9-12 ocular side pectoral fin rays.

Description.-Data are presented for the holotype and values for additional material are given in parentheses. A species of *Poecilopsetta* with a rather deep body, large eyes separated by a large scaly space, non-confluent dorsal, caudal and anal fins and subsymmetrical pelvic fin bases. Body depth (BD) 45.5% in SL (37.9-49.8%), head length (HL) 26.7% in SL (22.8-27.7%). Interorbital space, snout, eyes and maxilla scaleless. Upper orbit 35.3% in HL (32.9-42.0%), encroaching on dorsal profile of head. Position of lower eye slightly anterior or equal to upper eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through anterior third of lower eye, 32.9% in HL (26.4-37.2%). Blind side maxilla almost symmetrical, 30.7% in HL (21.8-34.5%). Lower jaw symmetrical, ocular side 40.0% in HL (34.2-44.0%), blind side 41.1% in HL (32.9-44.1%). Conical teeth present on premaxillae and dentaries.

Teeth in three (two to four) distinct bands on blind side dentary and premaxilla. Two (one to three) rows of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 8 (6-9) on upper limb and 11 (11-13) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 21.3% in SL (18.2-23.6%), height of arch 21.3% in BD (19.7-27.0%), 97 (98-124) ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 11 (9-12) rays, 8 (3-8) branched rays, length 53.6% in HL (48.8-61.2%). Blind side pectoral fin with 8 (5-10) unbranched rays, length 40.5% in HL (29.1-49.0%). Pelvic fins with 6 rays. Ocular side pelvic fin 37.9% in HL (32.8-46.4%), blind side 44.2% in HL (32.4-49.3%). No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior half of upper eye. Dorsal fin with 61 (55-62) rays, first ray 24.0% in HL (23.3-37.5%). Longest dorsal fin-ray 36.9% in HL (37.5-49.8%). Anal fin with 50 (48-53) rays, longest ray 39.3% in HL (37.6-46.8%). Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of second to fourth ray of ocular side pelvic fin. Dorsal, anal and pelvic fins scaleless, ocular side pectoral fin with scales. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae (one with eleven precaudal vertebrae), 29 (26-29) caudal vertebrae. Small ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

Coloration in ethanol.- Dorsal and anal fins light brown. Ocular side pectoral fin with a dark spot on the mid-portion of the fin. Ocular side pelvic fin light brown. Caudal fin with two dark spots on upper and lower margins. Blind side mostly creamy white with small dark spots sometimes with light brown coloration with head creamy white.

Etymology.-From the Latin *colorata* (referring to the coloration of this species). This is the type species of the genus.

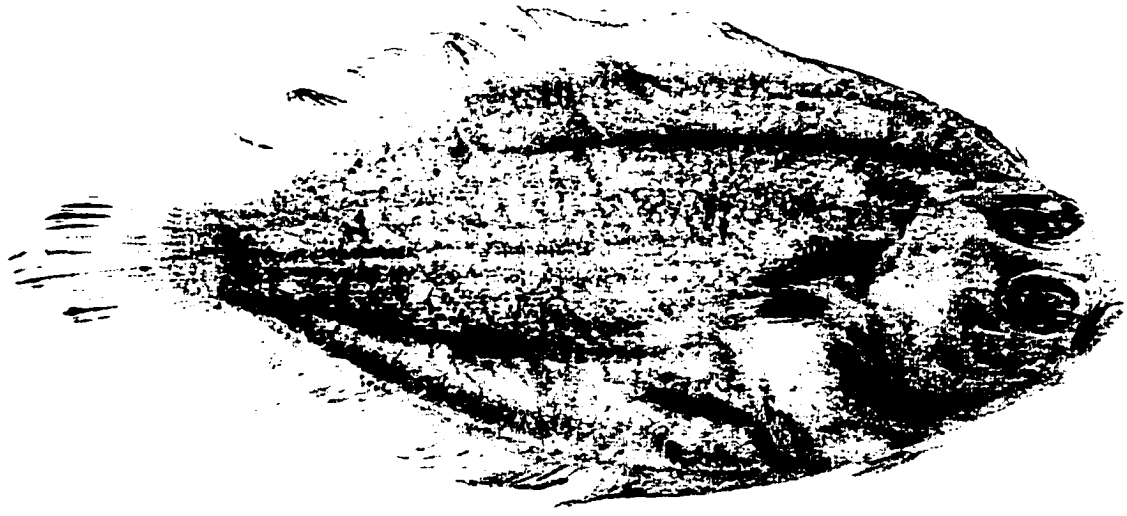


Fig. 22: *Poecilopsetta colorata*, holotype: BMNH 1879.5.14:97; 115.7 mm SL.

Distribution.-*Poecilopsetta colorata* is distributed in the Indian Ocean from Kei Island in Andaman Sea to Western Australia (Shark Bay) and in the South China Sea (Pacific Ocean) (Fig. 23). This species is known to occur at depths between 150-500 m.

Remarks.-*P. colorata* is similar to *P. hawaiiensis* and *P. praelonga*. *P. hawaiiensis* is endemic to Hawaii and has more dorsal and anal fin rays than *P. colorata*. *P. praelonga* does not have scales in the interorbital region and on the ocular side pectoral fin.

Larvae of *P. colorata*.-Larvae of *P. colorata* have previously been described by Evseenko and Suntsov (1993) based on two specimens. The specimens are transformation larvae (Kendall *et al.*, 1984) from the Indian Ocean off of Sri Lanka. Two other specimens were examined for this study. They are also transformation larvae but were collected in the

Andaman sea near Indonesia and off Western Australia, also in the Indian Ocean. The larvae are similar to juveniles and adults (Table 14) except for the pelvic fins that are almost symmetrical in larvae (subsymmetrical in adults) and the pigmentation pattern. See the general description of larvae in the section on *P. beanii* for the location of the different pigmented lines on the ocular and blind sides.

Coloration of the larvae of *P. colorata*.-On the ocular side, line 1 has seven spots, line 2 has six or seven spots, line 3 has five or six spots and line 4 has five spots (Fig. 24). In *P. colorata*, the pterygiophore zone is wide and in larvae, we can see faint circles along the body muscles in this area. One larva has lost most of its coloration (BMNH) but in the other specimen we can clearly see that six darker blotches are found above line 2. Immediately under line 2 there is a second row of darker blotches (Fig. 24 A). Under line 3 five darker blotches can be seen. Immediately above line 3 two smaller blotches can be seen. The spot at the base of the caudal peduncle is followed by two spots at the base of the caudal skeleton. These spots can also be seen on the blind side.

Two spots are found on the caudal fin, as in the adults. The ocular and blind side pelvic fin rays have a darker spot on their distal tips.

In the abdominal region, there are two spots, one approximately in the middle of this section of the body and one near the base of the pelvic fins. There is a faint spot near the anus.

Few spots are found on the head of the larvae. One is found on top of the upper eye, two others are found on the snout, one at the tip of the snout and another just over the upper jaw, at the level of the nasal organ. The last spots on the head are found on the retroarticular bone and two are found on the branchiostegal membranes, one at the proximal end of the branchiostegal rays and the other slightly behind.

On the blind side (Fig. 25), line A and line B have seven spots, line C has six spots, line D and line E have four or five spots, and line F has five spots.

Two spots can be found on the abdominal portion of the body, one in the middle of the section and one near the base of the pelvic fins.

There are few spots on the head. One is found over the upper eye, one is on the dorsal margin of the blind side maxilla and the others are found on the lower jaw and branchiostegal membranes. These last spots correspond to the ones found in the same area on the ocular side.

The larvae of *P. colorata* show almost the same coloration pattern as in *P. beanii* except for the presence of larger circular spots on the ocular side of *P. colorata* larvae.

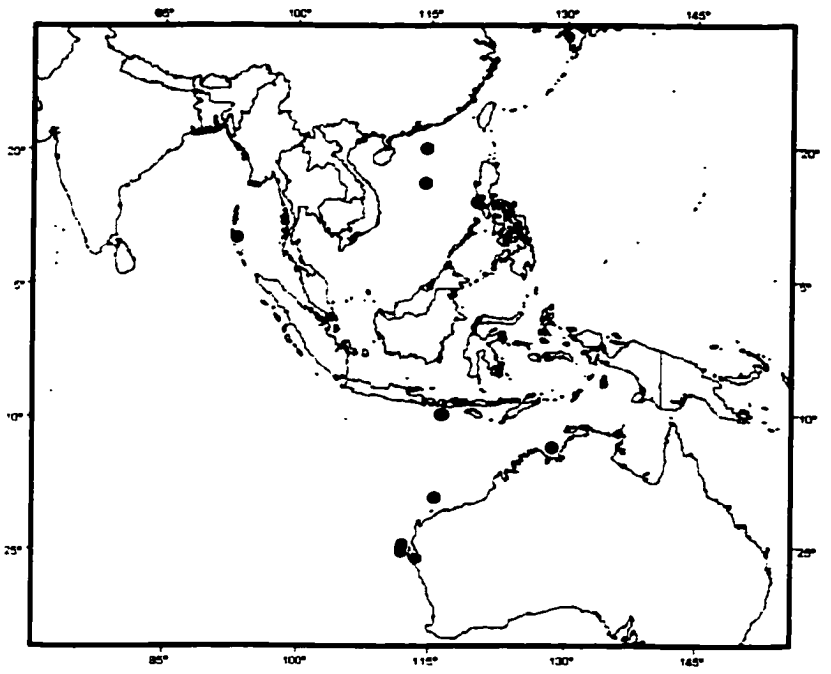


Fig. 23: Collection sites of *Poecilopsetta colorata*.

Table 12: Morphometrics for larvae, juveniles and adults of *Poecilopsetta colorata*. For abbreviations see Tables 3 and 11.

Measurements	Larvae n=2	Juveniles and adults n=26
SL	67.2-84.6	69.9-150.2
ln SL		
HL	4.11-4.38	3.61-4.38
BD	2.01-2.06	2.02-2.64
ln HL		
UO	2.95-3.01	2.38-3.04
UJO	3.09-3.59	2.69-3.79
UJB	3.34-3.75	2.90-4.59
LJO	2.33-2.83	2.27-2.92
LJB	2.27-2.70	2.27-3.04
PectOS		1.63-2.05
PectBS		2.04-3.44
PelOS	2.29-2.57	2.15-3.05
PelBS	2.23-2.33	2.03-3.09
HDR	2.01-2.40	2.28-2.66
FDR	2.67-3.72	2.72-4.29
HAR	2.17-2.38	2.14-2.66

A)

B)

Fig. 24: Ocular side of larvae of *Poecilopsetta colorata*, A) WAM P.30586-003; 64 mm SL, B) BMNH 1927.1.6:62-63; 84.6 mm SL.

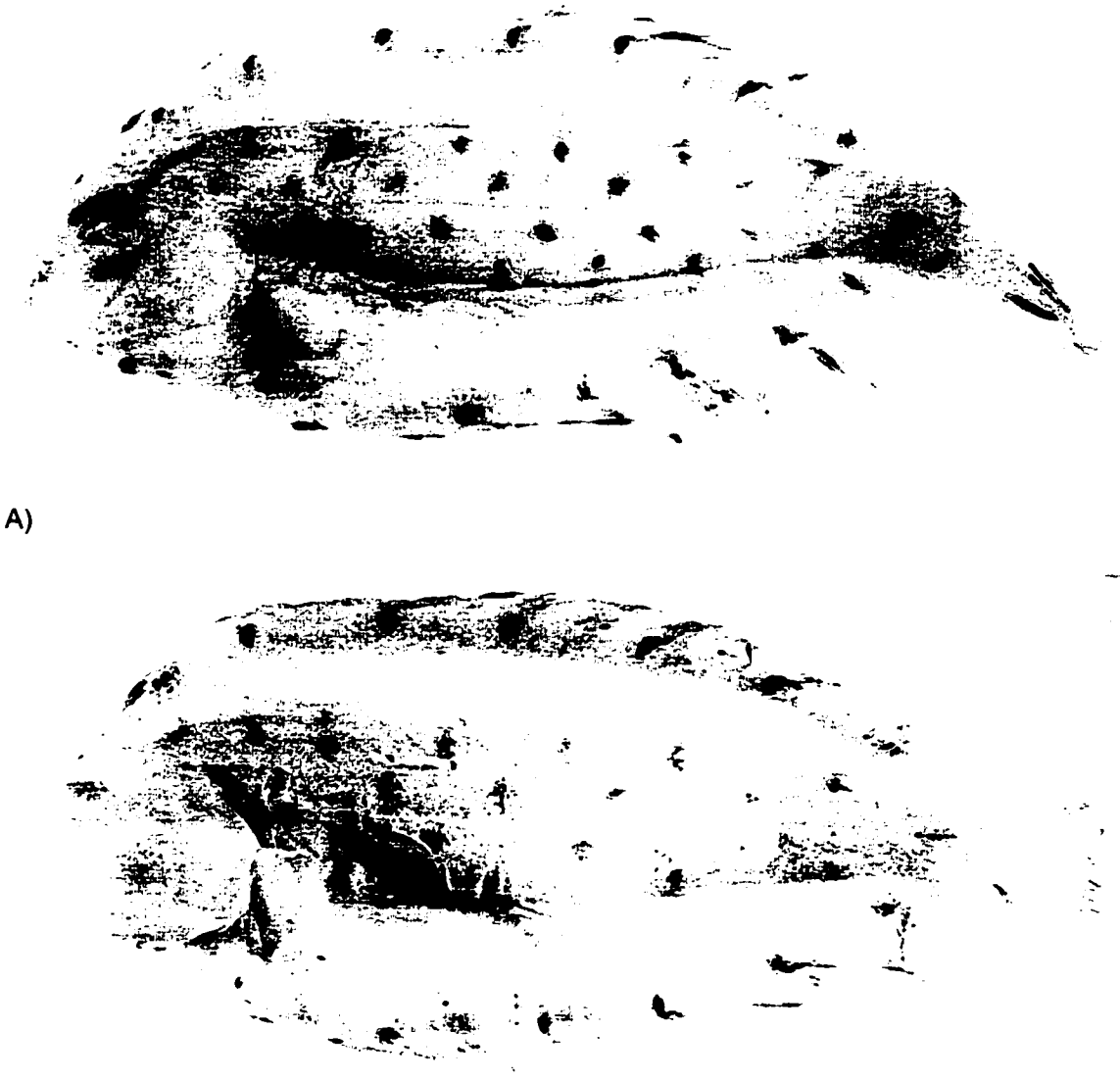


Fig. 25: Blind side of larvae of *Poecilopsetta colorata*, A) WAM P.30586-003; 64 mm SL, B) BMNH 1927.1.6:62-63; 84.6 mm SL.

Poecilopsetta dorsialta Guibord and Chapleau, 2001

Figures 26, 27; Tables 13, 14

Poecilopsetta dorsialta Guibord and Chapleau, 2001 Copeia 2001(4): 1081-1086.

Holotype.-**USNM 150696**; Philippines, between Panay and Guimaras, Lusaran Pt.; 10°33'30"N 122°26'E; 250 m (137fms); R.V. Albatross, Sta. 5421; 30 Mar 1909; 1: 98.8 mm SL.

Paratypes.-**USNM 363487**; same as holotype; 1: 103.9 mm SL. **USNM 361865**; Philippines; 8°46'N 123°32'30"E; 320 m (175 fm); R.V. Albatross, Sta. 5516; 9 Aug 1909; 1: 96.6 mm SL; formerly USNM 138005. **USNM 138008**; Philippines, Gulf of Davao, Dumulag Is.; 7°2'N 125°38'45"E; 247 m (135 fm); R.V. Albatross, Sta. 5247; 18 May 1908; 1: 96.8 mm SL. **USNM 138013**; Philippines, Marinduque Is. and vicinity, Tabayas; 13°49'12"N 121°36'9"E; 275 m (150 fm); R.V. Albatross, Sta. 5372; 24 Feb 1909; 1: 111.6 mm SL. **USNM 138015**; Philippines, southern Mindanao, eastern Illana bay, Utara Pt., Bongo Is.; 7°21'45"N 124°7'15"E; 289 m (159 fm); R.V. Albatross, Sta. 5256; 22 May 1908; 2: 75.4-79.3 mm SL.

Common name: High fin mottled flounder

Fig. 26: *Poecilopsetta dorsialta*, holotype: USNM 150696; 98.8 mm SL.

Diagnosis.-A species of *Poecilopsetta* with the following combination of characters: long first dorsal fin-ray (1.79-2.01 in HL) (Table 13), fewer (73-83) lateral line scales and long ocular side pelvic fin rays (1.56-1.95 in HL).

Description.-Data are presented for the holotype and values for paratypes are given in parentheses. A species of *Poecilopsetta* with a rather elongated body, large eyes separated by a very narrow space, non-confluent dorsal, caudal and anal fins, subsymmetrical pelvic fin bases and blind side pectoral fin-rays longer than eyed side. Body depth (BD) 37.8% in SL (37.1-40.6%), head length (HL) 23.9% in SL (22.8-25.0%). Interorbital space, snout, eyes and maxilla scaleless. Upper orbit 40.0% in HL (37.7-45.2%), encroaching on dorsal profile of head. Position of lower eye slightly anterior to upper eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through center of lower eye, 29.5 % in HL (29.0-32.5%). Blind side maxilla almost symmetrical, 28.2% in HL (29.1-30.4%). Lower

jaw symmetrical, ocular side 43.0% in HL (40.3-44.0%), blind side 41.8% in HL (41.1-43.7%). Conical teeth present on premaxillae and dentaries. Teeth in four (three to four) distinct bands on blind side dentary and premaxilla. Two rows of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 6 (6-8) on upper limb and 11 (10-11) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 20.0% in SL (16.6-18.9%), height of arch 23.8% in BD (20.6-27.6%), 75 (73-83) ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 10 (9-10) rays, 8 (5-8) branched rays, length 36.0% in HL (34.8-40.2%). Blind side pectoral fin with 8 (8-9) unbranched rays, length 46.0% in HL (40.4-50.1%). Ocular side pectoral fin 78% (79%-98%) the length of blind side pectoral fin. Pelvic fins with 6 rays. Ocular side pelvic fin 56.3% in HL (51.3-64.2%), blind side 44.2% in HL (39.8-45.3%). No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior 1/3 of upper eye. Dorsal fin with 58 (59-62) rays, first ray 53.7% in HL (49.8-55.8%). Longest dorsal fin-ray 56.9% in HL (51.0-61.2%). Anal fin with 48 (45-52) rays, longest ray 50.6% in HL (50.4-60.3%). Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third ray of ocular side pelvic fin. Dorsal, anal, pectoral and pelvic fins scaleless. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 29 (29-30) caudal vertebrae. Large ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

Coloration in ethanol.-Ocular side sometimes with 5-6 faint broad transverse bands. Dorsal and anal fins light brown. Ocular side pectoral fin without pigment. Ocular side pelvic fin light brown. Caudal fin with two dark spots on upper and lower margins. Blind side creamy white with small dark spots.

Etymology.-From the Latin *dorsialta* (*dorsi* referring to dorsal fin and *alta* meaning high). The specific name refers to the long first dorsal fin-ray and the height of the dorsal fin.

Table 13: Comparison of morphometric characters for *Poecilopsetta dorsialta*, *P. praelonga*, *P. plinthus*, *P. megalepis*, *P. colorata*, *P. hawaiiensis*, *P. natalensis* and *P. macrocephala*. For abbreviations see Table 3.

Measurements	*P. dorsialta* n=7 Holotype USNM 150696	*P. praelonga* n=65	*P. plinthus* n=63 Holotype USNM 51406	*P. megalepis* n=2 Holotype (*) USNM 93094	*P. colorata* n=28 Holotype BMNH 1879.5.14:97	*P. hawaiiensis* n=159 Holotype USNM 51638	*P. natalensis* n=16 Holotype BMNH 1922.3.27:7
SL (mm)	98.8 (75.4-122.8)	66.0-152.6	126.2 (36.1-109.5)	85.4-98.8*	115.7 (67.2-150.2)	99.0 (48.1-136.9)	116.7 (77.9-128.9)
In SL							
BD	2.64 (2.46-2.69)	2.21-2.96	2.35 (2.06-2.95)	2.51-2.57*	2.20 (2.01-2.64)	1.87 (1.74-2.26)	2.40 (2.41-2.80)
HL	4.18 (3.99-4.39)	3.65-4.48	4.30 (3.80-5.01)	3.72*-3.88	3.75 (3.61-4.38)	4.44 (3.49-4.51)	4.46 (4.18-5.12)
LLW	5.01 (5.30-6.01)	4.84-6.19 (41)	6.36 (4.88-6.83) (40)	5.52-6.07*	4.78 (4.23-5.48) (21)	5.36 (4.36-6.32) (137)	5.48 (5.31-5.91) (6)
CPL	21.25 (19.71-26.58)	19.90-36.97	24.79 (20.40-33.36) (60)	24.09*-25.50	17.74 (15.58-23.26)	(16.66-37.91) (148)	21.38 (16.37-27.03) (14)
In HL							
UO	2.50 (2.21-2.66)	2.20-3.02	2.73 (2.25-3.10)	2.76-2.95*	2.83 (2.38-3.04)	2.79 (2.57-3.71)	2.38 (2.16-2.48)
UJO	3.39 (3.08-3.45)	2.99-4.00	3.90 (2.90-3.94)	3.74*-3.77	3.04 (2.69-3.79)	3.51 (3.04-4.06)	3.84 (3.14-4.00)
UJB	3.54 (3.29-3.44) (5)	2.97-4.07	(3.43-4.46)	3.43-4.15*	3.26 (2.90-4.59)	3.34 (2.91-4.08) (157)	4.30 (3.16-4.23)
LJO	2.33 (2.27-2.48)	2.37-3.05 (62)	2.67 (2.31-2.87)	2.64-2.84*	2.50 (2.27-2.92) (26)	2.43 (2.37-2.93)	2.70 (2.36-2.60)
LJB	2.39 (2.29-2.44)	2.26-3.07 (62)	2.86 (2.34-2.82)	2.66-2.84*	2.43 (2.27-3.04)	2.54 (2.34-2.86)	2.65 (2.44-2.68)
LPectO	2.78 (2.49-2.87)	1.62-2.77 (59)	2.26 (1.75-2.87) (60)	2.01*-2.19	1.87 (1.63-2.05) (24)	1.61 (1.30-5.66) (150)	1.95 (1.60-2.36)
LPectB	2.17 (2.00-2.47) (5)	1.55-3.20 (60)	(1.87-2.65) (61)	2.05-2.24*	2.47 (2.04-3.44) (24)	2.25 (1.83-6.52) (157)	2.22 (1.90-2.70)

LPelO	1.77 (1.56-1.95)	1.94-2.79 (54)	2.28 (1.98-2.97) (59)	2.19-2.48*	2.64 (2.15-3.05)	2.06 (1.88-3.40) (149)	2.13 (1.82-2.85)
HDR	1.76 (1.63-1.96)	1.63-2.51 (60)	2.42 (1.86-3.07)	1.97-2.22*	2.71 (2.01-2.66)	2.10 (1.97-3.10) (157)	2.00 (1.59-2.21)
FDR	1.86 (1.79-2.01)	2.23-4.45 (62)	3.86 (1.76-4.57)	2.92-3.33*	4.16 (2.67-4.29)	2.33 (2.36-4.41) (157)	2.78 (2.21-3.55)
HAR	1.98 (1.66-1.99)	1.73-2.54 (60)	2.43 (1.73-2.72)	2.05-2.30*	2.54 (2.14-2.66)	2.05 (1.94-2.86) (157)	2.20 (1.69-2.27)
In BD							
LLH	4.20 (3.63-4.85)	2.55-5.45 (42)	4.21 (3.44-5.06) (41)	4.14*-4.90	4.69 (3.71-5.07) (23)	4.61 (3.79-5.37) (139)	(4.02-4.69) (6)
Counts							
LL scales	75 (73-83)	91-111 (42)	60 (57-68) (39)	54-57*	97 (98-124) (21)	84 (75-101) (133)	77 (79-94) (6)
Cvert	29 (29-30)	29-32	31 (30-32)	30	29 (26-29)	29 (28-30)	31 (27-33)

Table 14: Frequency distribution of meristic characters for *Poecilopsetta dorsialta*, *P. praelonga*, *P. plinthus*, *P. megalepis*, *P. colorata*, *P. hawaiiensis*, *P. natalensis* and *P. macrocephala*. The asterisk represents data for the holotype.

Dorsal fin-rays

	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	n	$\bar{x}$	s
P. dorsialta				1*	1	4		1									7	59.9	1.21
P. praelonga			1	2	2	6	11	24	10	6	1						63	61.7	1.55
P. plinthus					1	1	1	3	7	7	11*	8	11	7	6		63	65.5	2.33
P. megalepis					1							1*					2	62.5	4.95
P. colorata	2			1	5	8	6*	6									28	60.0	1.82
P. hawaiiensis					1		1	4	10	23	40*	44	22	12	1	1	159	65.4	1.60
P. natalensis			1					5*	7	4							17	62.6	1.62

Anal fin-rays

	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59		n	$\bar{x}$	s
P. dorsialta	1			1*	1	2	1	1									7	49.3	2.29
P. praelonga				1	1	1	14	23	17	5	1						63	52.1	1.19
P. plinthus								5	4	10	12	13*	9	7	3		63	55.5	1.87
P. megalepis								1				1*					2	54.0	2.83
P. colorata				2	7	5*	4	5	5								28	50.6	1.64
P. hawaiiensis								2	8	19*	40	46	33	8	3		159	55.7	1.37
P. natalensis					1			1	8	7*							17	53.1	1.22

Ocular side pectoral fin-rays

	6	7	8	9	10	11	12	n	$\bar{x}$	s
P. dorsialta				3	4*			7	9.6	0.53
P. praelonga	1		14	33	12	1		61	9.0	0.80

P. plinthus	1	4	48*	8	2				63	8.1	0.52
P. megalepis		1*	1						2	7.5	0.71
P. colorata				2	7	13*	4		26	10.7	0.83
P. hawaiiensis			7	29	81*	39	1		157	10.0	1.08
P. natalensis			2	9	6*				17	9.2	0.66

Blind side pectoral fin-rays

	5	6	7	8	9	10			n	$\bar{x}$	s
P. dorsialta				3*	4				7	8.6	0.53
P. praelonga		3	18	33	6				60	7.7	0.72
P. plinthus		5	45*	12					62	7.1	0.52
P. megalepis			2						2	7.0	0.00
P. colorata	1			4*	11	11			27	9.1	1.09
P. hawaiiensis	1	1	11	84*	56	5			158	8.3	0.98
P. natalensis				12	3*	2			17	8.4	0.71

Caudal vertebrae

	26	27	28	29	30	31	32	33	n	$\bar{x}$	s
P. dorsialta				2*	5				7	29.7	0.49
P. praelonga					11	44	8		63	30.9	0.55
P. plinthus					28	33*	2		63	30.6	0.56
P. megalepis					2*				2	30.0	0.00
P. colorata	1		3	24*					28	28.8	0.63
P. hawaiiensis			6	128*	25				159	29.1	0.43
P. natalensis		1			1	14*		1	17	30.8	1.13

Distribution.-*Poecilopsetta dorsialta* is distributed along the coasts of the Philippine Islands, from Dumulag Island in the Gulf of Davao to Marindique Island (Fig. 27). This species is known to occur at depths between 247-320 m.

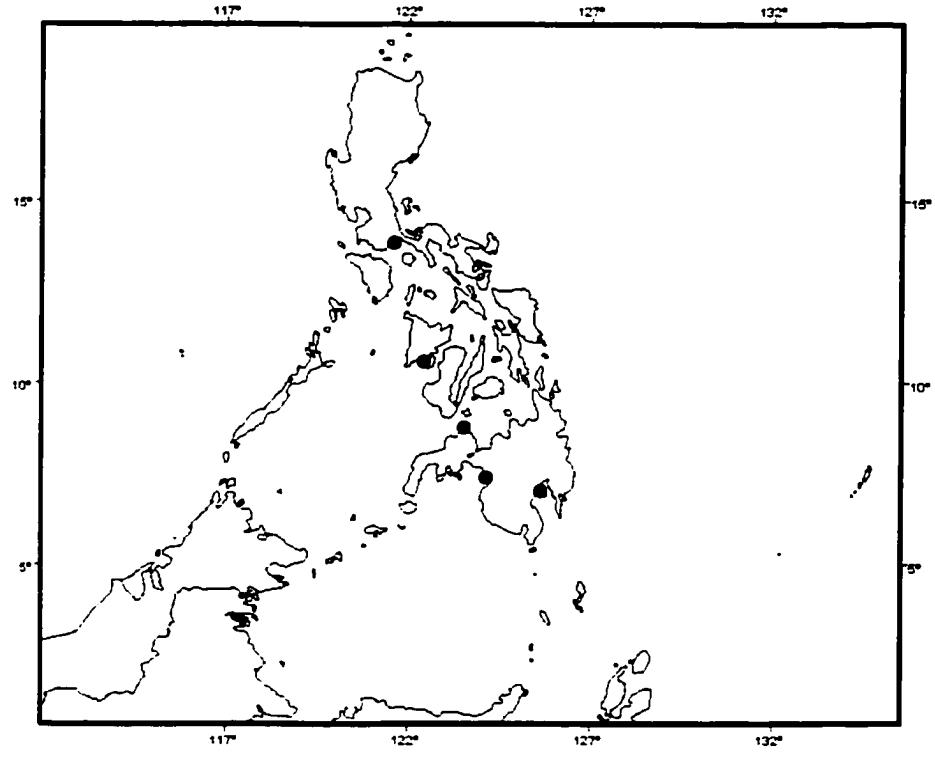


Fig. 27: Collection sites of *Poecilopsetta dorsialta*.

Remarks.-*Poecilopsetta dorsialta* was identified as *P. praelonga* in USNM collections. These two species have different lateral line scale counts (73-83 for *P. dorsialta* and 91-111 for *P. praelonga*). *P. dorsialta* can be distinguished from 9 of 11 species of *Poecilopsetta* by its long first dorsal fin-ray. In the remaining species, *P. zanzibarensis* (90-

101) and *P. plinthus* (57-68), the number of lateral-line scales allows a clear separation from *P. dorsialta*.

***Poecilopsetta hawaiiensis* Gilbert, 1905**

Figures 28-32; Tables 13-15

Poecilopsetta hawaiiensis: Gilbert, 1905, The deep sea fishes of the Hawaiian Islands, Bull. U.S. Fish. Comm. Vol 23: 679-680, Plate 95. Norman 1931, Treubia13: 425. Norman 1934, A systematic monograph of the flatfishes (Heterosomata). Vol I: 391.Tinker 1978, Fishes of Hawaii: 456-457. Quéro, Hensley and Maugé 1988, Cybium 12(4): 329.

Common name: Hawaiian right-eyed flounder (Tinker, 1978)

Holotype.-**USNM 51638**; Pacific,Hawaiian Is., south coast of Oahu Is., Honolulu light; 0-386 m (0-211 fm); vessel Albatross, Sta. 3810; 27 Mar 1902; 1: 99.0 mm SL. Paratypes.-**USNM 51690**; same as holotype; 8: 80.4-119.1 mm SL. **USNM 227796**; Pacific Hawaiian Is., Hawaii; vessel Albatross; Jan 1902; 1: 99.7 mm SL. **USNM 231811**; Pacific Hawaiian Is., Hawaii; vessel Albatross; Mar. to Apr. 1902; (not included in the data). **BMNH 1931.8.19:7**; Hawaiian Is.; 1: 99.2 mm SL.

Additional material: **ANSP 176079**; Western Pacific, Hawaiian Is, Hawaii; 21°3'30"N 156°29'6"W; 274-318 m; vessel Townsend Cromwell, Cr. 40, Sta. 92; 25 Nov 1968; 13: 57.3-79.0 mm SL. **ANSP 176105**; Western Pacific, Hawaiian Is, Hawaii; 20°47'42"N 156°39'48"W; 260-292 m; vessel Townsend Cromwell, Cr. 33, Sta. 37; 9 Nov 1967; 12:

88.2-124.1 mm SL. **ANSP 176110**; Western Pacific, Hawaiian Is, Hawaii; 20°59'6"N 157°3'W; 254-278 m; vessel Townsend Cromwell, Cr. 35, Sta. 37; 8 Apr 1968; 10: 97.1-128.1 mm SL. **BPBM 10011**; Oahu, Hawaiian Is., off Haleiwa; 180-195 m; 20 June 1970; 11: 48.1-78.4 mm SL. **BPBM 24277**; Hawaiian Is., northwest of Maui; 21°4'N 156°31'W; 322-337 m; vessel Townsend Cromwell, Cr. 40, Sta. 73; 21 Nov 1968; 23: 85.0-121.0 mm SL. **CAS 30137**; Northwestern & Central Pacific, USA, Hawaii, Molokai Is., off southeast coast of Molokai, Pailolo Channel; 30 Oct 1973; 4: 113.1-136.9 mm SL. **CAS 30146**; Northwestern & Central Pacific, USA, Hawaii, Molokai Is., off southeast coast of Molokai, Pailolo Channel; 30 Oct 1973; 6: 94.3-117.8 mm SL. **CAS 31054**; Northwestern & Central Pacific, USA, Hawaii, Molokai Is., off southeast coast of Molokai, Pailolo Channel; 30 Oct 1973; 5: 88.1-108.6 mm SL. **CAS 89546**; Northwestern & Central Pacific, USA, Hawaii; 27 Apr 1968; 10: 85.0-131.5 mm SL. **CAS 89547**; Northwestern & Central Pacific, USA, Hawaii; 27 Apr 1968; 10: 81.3-101.9 mm SL. **CAS 89548**; Northwestern & Central Pacific, USA, Hawaii; 28 Apr 1968; 10: 80.8-111.3 mm SL. **HUMZ 145585**; Hawaiian Is.; 24°4'N 156°32'W; 344-348 m; 22 Nov 1968; 1: 91.6 mm SL. **HUMZ 145586**; Hawaiian Is.; 24°4'N 156°32'W; 344-348 m; 22 Nov 1968; 1: 106.1 mm SL. **HUMZ 145587**; Hawaiian Is.; 24°4'N 156°32'W; 344-348 m; 22 Nov 1968; 1: 101.7 mm SL. **HUMZ 145588**; Hawaiian Is.; 24°4'N 156°32'W; 344-348 m; 22 Nov 1968; 1: 111.2 mm SL. **HUMZ 145589**; Hawaiian Is.; 24°4'N 156°32'W; 344-348 m; 22 Nov 1968; 1: 115.6 mm SL. **MNHN 1997-785**; Hawaiian Is.; 20°1,6'N 156°54,2'W, 20°2,7'N 156°53,9'W; 344-356 m; vessel Townsend Cromwell, Cr. 33, Sta. TC 33-34; 8 Nov 1967; 19: 82.4-108.7 mm SL. **RUSI 54422**; Hawaii Is., North of Hilo Bay; 19°54'N 155°3'1"W; 29 March 1968; 5: 88.7-110.9 mm SL. **RUSI 54424**; Hawaii Is., Pailolo Channel; 20°38'1"N 156°41'1"W; 9 Nov 1967; 5: 93.1-121.8 mm SL.

Diagnosis.-A species of *Poecilopsetta* with the following combination of characters: scales on the ocular side maxilla, on the ocular side pectoral fin rays, and on the interorbital space, 52-59 anal fin rays and 75-101 lateral line scales.

Description.-Data are presented for the holotype and values for paratypes and additional material are given in parentheses. A species of *Poecilopsetta* with a rather deep body, large eyes separated by a large space, non-confluent dorsal, caudal and anal fins, subsymmetrical pelvic fin bases and blind side pectoral fin-rays shorter than eyed side. Body depth (BD) 53.6% in SL (44.2-57.6%), head length (HL) 22.5% in SL (22.2-28.7%). Interorbital space, snout, eyes and maxilla with scales. Upper orbit 35.9% in HL (27.0-38.9%), encroaching on dorsal profile of head. Position of lower eye variable: slightly anterior to upper eye, equal to upper eye and occasionally slightly posterior to upper eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On the ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through anterior third of lower eye, 28.5 % in HL (24.7-32.9%). Blind side maxilla almost symmetrical, 29.9% in HL (24.5-34.4%). Lower jaw symmetrical, ocular side 41.2% in HL (34.1-42.2%), blind side 39.4% in HL (35.0-42.7%). Conical teeth present on premaxillae and dentaries. Teeth in three (usually three to four) distinct bands on blind side dentary and premaxilla. Two (one to three) rows of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 6 (6-9) on upper limb and 12 (10-14) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 11.6% in SL (15.8-22.9%), height of arch 34.8% in BD (18.6-26.4%), 84 (75-101) ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 10 (8-12) rays, 0-4 branched rays, length 62.0% in HL (17.7-77.2%). Blind side pectoral fin with 8 (5-10) unbranched rays, length 44.4% in HL

(15.3-54.5%). Pelvic fins with 6 rays. Ocular side pelvic fin 48.6% in HL (29.5-58.2%), blind side 50.0% in HL (27.2-52.8%). No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior half of upper eye. Dorsal fin with 65 (59-70) rays, first ray 42.9% in HL (22.7-42.4%). Longest dorsal fin-ray 47.5% in HL (32.2-50.9%). Anal fin with 54 (52-59) rays, longest ray 48.9% in HL (35.0-51.5%). Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third ray of ocular side pelvic fin. Dorsal, anal, blind side pectoral and pelvic fins scaleless. Ocular side pectoral fin rays with scales. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 29 (28-30) caudal vertebrae. Ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

Fig. 28: *Poecilopsetta hawaiiensis*; CAS 30154; 98.9 mm SL.

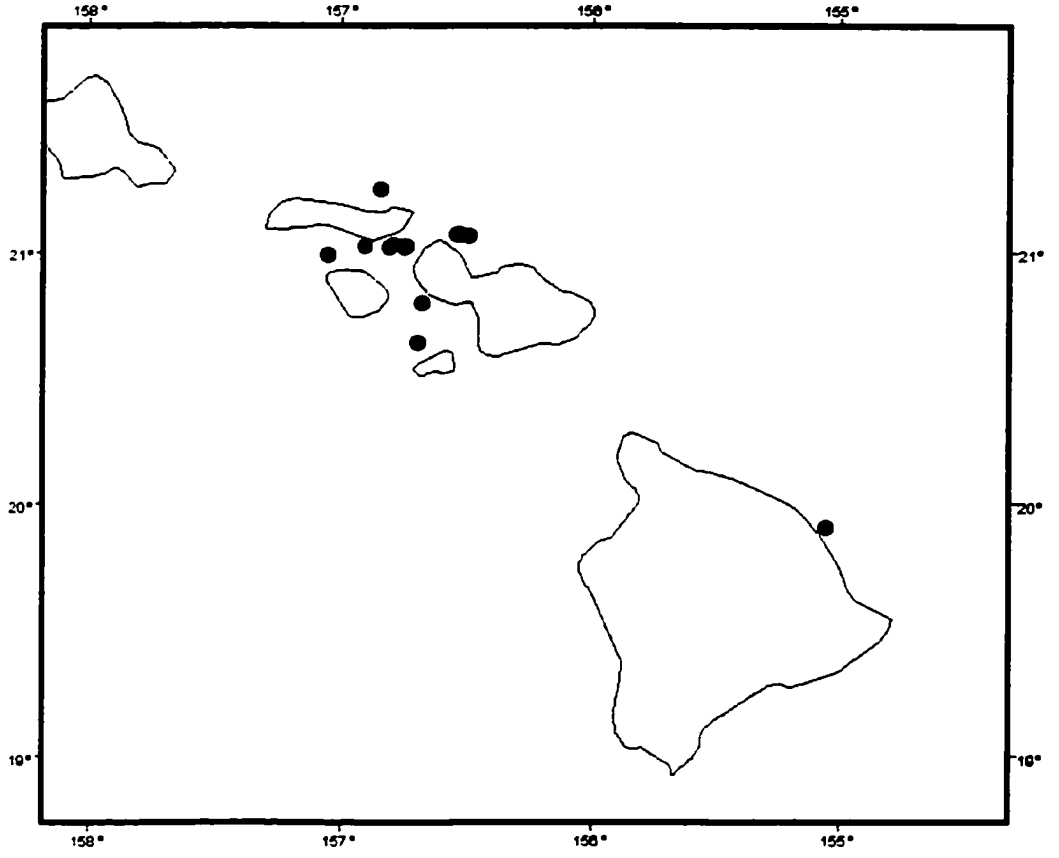


Fig. 29: Collection sites of *Poecilopsetta hawaiiensis*.

Coloration in ethanol.-Ocular side uniformly brown, sometimes with 1 faint broad transverse band at 2/3 the body length. Dorsal and anal fins light brown. Ocular side pectoral fin with black spot on distal tip of rays. Ocular side pelvic fin light brown. Caudal fin with two dark spots on upper and lower margins. Blind side creamy white.

Etymology.-From the latin *hawaiiensis*. The specific name refers to the type locality, Hawaii.

Distribution.-*Poecilopsetta hawaiiensis* is distributed in the Hawaiian islands (Fig. 29). This species is known to occur at depths between 180-195 m.

Remarks.-*P. hawaiiensis* is very similar to *P. colorata*. *P. hawaiiensis* has 55-70 (usually 64-67) dorsal fin rays and 52-59 (usually 54-57) anal fin rays while *P. colorata* has 55-62 dorsal fin rays and 48-53 anal fin rays. Also, these two species are not sympatric, *P. hawaiiensis* is only found in Hawai.

Type series.-Upon examination of the type series of *P. hawaiiensis*, it was found that the lot USNM 231811 contained only one specimen of *P. hawaiiensis* out of five originally in the lot. Four specimens had eyes on the left side of the body and did not correspond to the description of *P. hawaiiensis*. Since then, the left-eyed specimens were removed from the original lot and placed in separate lots. Lot USNM 231811 appears in the list of paratypes (above) but was not measured.

Differential growth.-Differential growth has not been reported for species within the family Poecilopsettidae. Clearly, the ocular side pectoral fin of *P. hawaiiensis* does not grow linearly with the growth in length of the fish (Fig. 30). Since it is difficult to determine the end of the juvenile stage and the beginning of adulthood, the data for juveniles was incorporated in the overall data. This would explain the wide range in the ratio of the length of the ocular side pectoral fin in relation to head length (Table 13).

Looking at figure 30 we can see that the ocular side pectoral fin of smaller individuals grows faster than the one of adult individuals of the species *P. hawaiiensis*.

Larvae.-Larvae of *P. hawaiiensis* have been described in Ahlstrom *et al.* (1984) and Bray and Leis (2000). In this study, two specimens were examined. As for the other species for

which larvae are known, the only differences between larvae, juveniles and adults are coloration and position of the pelvic fins in the larvae (Table 15). Once again, the pelvic fins are only slightly asymmetrical compared to the condition found in adults. See the general description of larvae in the section about *P. beanii* for the location of the different lines on the ocular and blind sides.

Coloration of the larvae of *P. hawaiiensis*.-On the ocular side (Fig. 31), line 1 has six spots, line 2 has seven spots, line 3 has five spots and line 4 also has five spots. In *P. hawaiiensis*, the spots on line 1 and 4 do not have corresponding spots on the fins themselves. Instead, paler, larger circular spots are found on the fins and are more numerous than the number of spots along the edges of the body (lines 1 and 4). Also, darker blotches are found immediately below line 1 and immediately above line 4. These blotches are associated to a spot on the line next to it. In *P. hawaiiensis*, the pterygiophore zone is wide. In larvae, we can see faint circles along the body muscles in that area. We can clearly see four darker circles over line 2 and four darker blotches under line 3. The spot on the caudal peduncle is found but not the two at the base of the caudal skeleton. This spot is also found on the blind side.

Two spots are found on the caudal fin, as in the adults.

On the head, only two spots can be seen, one at the distal tip of the lower jaw and one on the branchiostegal membrane.

No spots are found in the abdominal region of these larvae. They may have faded since the other spots are much lighter than in the other species. Also, spots in the abdominal region were observed by Ahlstrom *et al.* (1984) Bray and Leis (2000) for that species.

On the blind side (Fig. 32), line A has six spots, line B has seven spots, line C, D E and line F have five spots.

On the head, only one spot can be seen, it is on the branchiostegal membranes. No spots can be seen on the abdominal region of the two larvae examined. Once again, this is probably due to a faded coloration.

Several differences are seen between larvae of *P. hawaiiensis* and *P. beanii*, the main ones being the narrow body height and higher caudal vertebrae count for *P. beanii*. In comparing larvae of *P. colorata* and *P. hawaiiensis*, the differences are more subtle which is not surprising since adults of these species are very similar. The most obvious difference is the absence of two spots at the base of the caudal skeleton in *P. hawaiiensis*. Also, larvae of *P. hawaiiensis* have a larger interorbital space than larvae of *P. colorata*. Furthermore, *P. hawaiiensis* has larger circular blotches over the spots on lines 1 and 4. These blotches are absent in *P. colorata*. Other minor differences are seen in the number of spots found in rows along the body and in the absence of a second row of larger circular blotches between lines 2 and 3 in *P. hawaiiensis*.

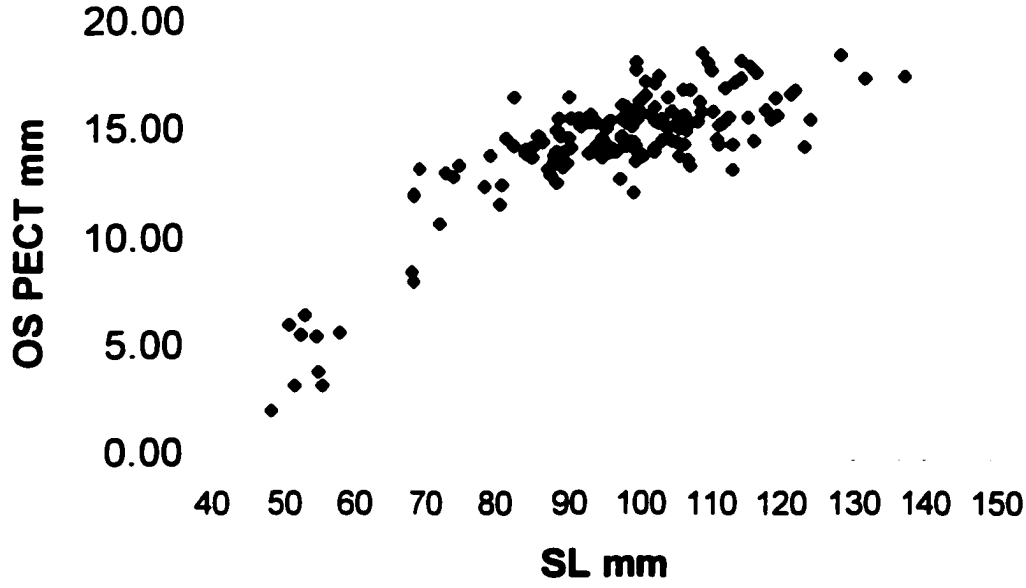


Fig. 30: Length of ocular side pectoral fin (OS PECT) in standard length (mm) in *Poecilopsetta hawaiiensis*.

Table 15: Morphometrics for larvae, juveniles and adults of *Poecilopsetta hawaiiensis*. For abbreviations see Tables 3 and 11.

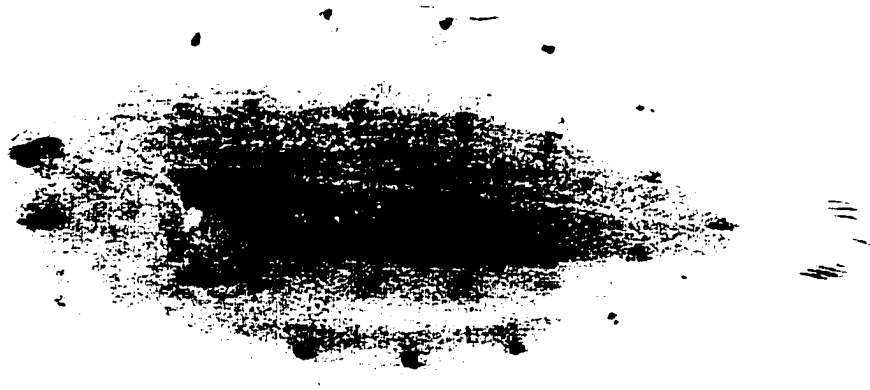
Measurements	Larvae n=2	Juveniles and adults n=157
SL	48.1-52.8 mm	50.7-136.9 mm
ln SL		
BD	2.06-2.09	1.74-2.26
HL	3.71-3.83	3.49-4.51
ln HL		
UO	3.33-3.71	2.57-3.36
UJO	3.40-3.41	3.04-4.06
UJB	3.72	2.91-4.08
LJO	2.68-2.72	2.37-2.93
LJB	2.56-2.62	2.34-2.86
PectOS		1.30-5.66
PectBS		1.83-6.52
PelOS	2.58-3.00	1.88-3.40
PelBS	2.47-2.68	1.89-3.68
HDR	2.08-2.24	1.97-3.10
FDR	3.04-3.35	2.36-4.41
HAR	2.38-2.48	1.94-2.86

A)

B)

Fig. 31: Ocular side of larvae of *Poecilopsetta hawaiiensis*, A) BPBM 10011; 48.1 mm SL, B) BPBM 10011; 52.8 mm SL.

A)



B)

Fig. 32: Blind side of larvae of *Poecilopsetta hawaiiensis*, A) BPBM 10011; 48.1 mm SL, B) BPBM 10011; 52.8 mm SL.

***Poecilopsetta inermis* (Breder, 1927)**

Figures 19, 33-36; Tables 9, 10, 16

Paralimanda inermis Breder, 1927, Bull. Bingham Ocean. Coll., 1 p. 87.

Poecilopsetta inermis: Norman 1931, Treubia, 13: 425. Norman 1934, A systematic monograph of the flatfishes (Heterosomata). Vol I: 389.

Poecilopsetta albomarginata Reid 1934: Hoshino 2000, Ichthyol. Res., 47: 95-100.

Common name: Unarmed mottled flounder

Holotype.-*P. inermis*: **YPM 516**; not seen.

Holotype.-*P. albomarginata*: **USNM 93303**; Caribbean, Virgin Is., N of Tobago Is.; 18°38'45"N 64°52'45"W to 18°40'15"N 64°50'15"W; 183-549 m (100-300 fm); vessel Caroline, sta. 100, Johnson-Smithsonian Expd.; 4 Mar 1933; 1: 96.7 mm SL.

Paratypes.-*P. albomarginata*: **BMNH 1935.1.26:1**; 18°34'N 64°52'W, 1:103.9 mm SL. **USNM 93304**; Caribbean, Virgin Is.; 18°40'15"N 64°50'15"W; 274 m (150 fm); vessel Caroline, sta. 100, Johnson-Smithsonian Expd.; 4 Mar 1933; 2: 107.7-115.7 mm SL.

Additional material: **ANSP 101312**; Atlantic Ocean, off Trinidad; 11°34'N 62°49'W; 293-366 m (160-200 fm); vessel Oregon, sta. 2781; 20 Apr 1960; 2: 102.9-107.3 mm SL. **CAS 56861**; Atlantic, off St. Kitts and Nevis; 17°9'N 62°44'48"W; 512-768 m (280-420 fm); 4 Aug 1978; 1: 100.7 mm SL. **CAS 61150**; Atlantic, Puerto Rico, W of Mayaguez; 18°13'30"N 67°18'42"W; 357-384 m (195-210 fm); 21 Aug 1987; 2: 77.1-105.6 mm SL. **CAS 61151**; Atlantic, Puerto Rico, off NE coast; 18°30'N 65°42'12"W; 441-512 m (241-280 fm); 15 Aug 1987; 1: 106.2 mm SL. **CAS 61152**; Atlantic, Rise W of St. Croix; 17°39'12"N 64°57'24"W; 595-659 m (325-360 fm); 10 Aug 1987; 1: 109.7 mm SL. **UF 119201**; Atlantic Ocean, Florida Keys; 24°20'33"N 83°6'31"W; 308-306 m; 14 May 1996; 1: 94.7 mm SL. **UF 119202**; Atlantic Ocean, Florida Keys; 24°18'34.2"N 82°37'3"W; 188-183 m (103-100 fm); 1 May 1998; 1: 85.1 mm SL. **UF 119203**; Atlantic Ocean, Florida Keys; 24°19'10"N

82°58'10"W to 24°18.90'N 82°55.61W; 282-295 m; 25 Apr 1995; 3: 76.6-87.0 mm SL. **UF 210726**; Atlantic, Suriname; 7°34'N 54°50'W; 366 m (200 fm); vessel Oregon, sta. 2005; 6 Nov 1957; 10: 73.6-105.4 mm SL. **UF 211143**; Atlantic, Trinidad; 10°3'N 60°1'W; 366 m (200 fm); vessel Oregon, sta. 1981; 3 Nov 1957; 4: 76.5-98.5 mm SL. **UF 211145**; Atlantic, Venezuela; 9°45'N 59°45'W; 366 m (200 fm); vessel Oregon, sta. 1984; 3 Nov 1957; 4: 56.1-90.6 mm SL. **UF 211184**; Atlantic, Brazil; 2°4'N 47°0'W; 229 m (125 fm); vessel Oregon, sta. 2080; 17 Nov 1957; 6: 51.2-64.7 mm SL. **UF 229258**; Caribbean sea, Nicaragua; 14°53'54"N 81°23'12"W; 296-375 m; vessel Pillsbury, sta. 1356; 31 Jan 1971; 8: 76.0-87.0 mm SL. **USNM 159440**; Atlantic, Suriname; 7°34'N 54°50'W; 366 m (200 fm); vessel Oregon, sta. 2005; 6 Nov 1957; 1: 54.5 mm SL. **USNM 159443**; Atlantic, Brazil; 2°4'N 47°00'W; 229 m (125 fm); vessel Oregon, sta. 2080; 17 Nov 1957; 2: 64.2-65.0 mm SL. **USNM 159489**; Atlantic. Brazil; 2°04'N 47°00'W; 229 m (125 fm); vessel Oregon, sta. 2080; 17 Nov 1957; 1: 55.5 mm SL. **USNM 159524**; Atlantic, off French Guyana; 7°15'N 53°25'W; 210 m (115 fm); vessel Oregon, sta. 2022; 9 Nov 1957; 4: 50.9-74.2 mm SL. **USNM 159527**; Atlantic, off Suriname; 7°34'N 54°19'W; 274 m (150 fm); vessel Oregon, sta. 2012; 8 Nov 1957; 6: 76.9-87.9 mm SL. **USNM 217981**; Caribbean, Panama; 9°43'N 79°20'W; 95 m (52 fm); vessel Oregon, sta. 5739, cr. 104; 19 Oct 1965; 4: 48.6-55.5 mm SL. **USNM 217987**; Caribbean, Nicaragua; 12°52'N 82°09'W; 443 m (242 fm); vessel Oregon II, sta. 10205; 21 Nov 1968; 7: 68.5-88.5 mm SL. **USNM 217990**; Caribbean, Trinidad; 11°30'N 62°29'W; 329 m (180 fm); vessel Oregon, sta. 2772; 18 Apr 1960; 71.4-104.4 mm SL. **USNM 217992**; Caribbean, Nicaragua; 14°10'N 81°55'W; 439-457 m (240-250 fm); vessel Oregon, sta. 3565, cr. 78; 21 May 1962; 14: 51.6-71.3 mm SL. **USNM 217993**; Caribbean, off British Honduras; 17°28'30"N 87°57'30"W; 274-329 m (150-180 fm); vessel Oregon, sta. 6404, cr. 115; 13 Jan 1967; 4: 90.0-108.9 mm SL. **USNM**

217995; Caribbean, Colombia; 10°24'N 75°50'W; 348-357 m (190-195 fm); vessel Oregon, sta. 4880; 24 May 1964; 4: 80.0-92.5 mm SL. **ZMUC 853468**; Western Atlantic Ocean; 08°19'N 44°35'W; Dana st. 1171-4; 13 Nov 1921; 3: 23.4-32.4 mm SL. **ZMUC 853469**; Western Atlantic Ocean; 07°22'N 46°51'W; Dana st. 1172-3; 14 Nov 1921; 3: 9.5-16.8 mm SL. **ZMUC 853470**; Western Atlantic Ocean; 10°24'N 54°38'W; Dana st. 1178-2; 19 Nov 1921; 1: 37.3 mm SL. **ZMUC 853471**; Gulf of Mexico; 23°58'N 83°22'W; Dana st. 1225-1; 2 Feb 1921; 1: 30.9 mm SL. **ZMUC 853472**; Western Atlantic Ocean; 26°13'N 78°48'W; Dana st. 1238-2; 11 Feb 1921; 1: 11.7 mm SL.

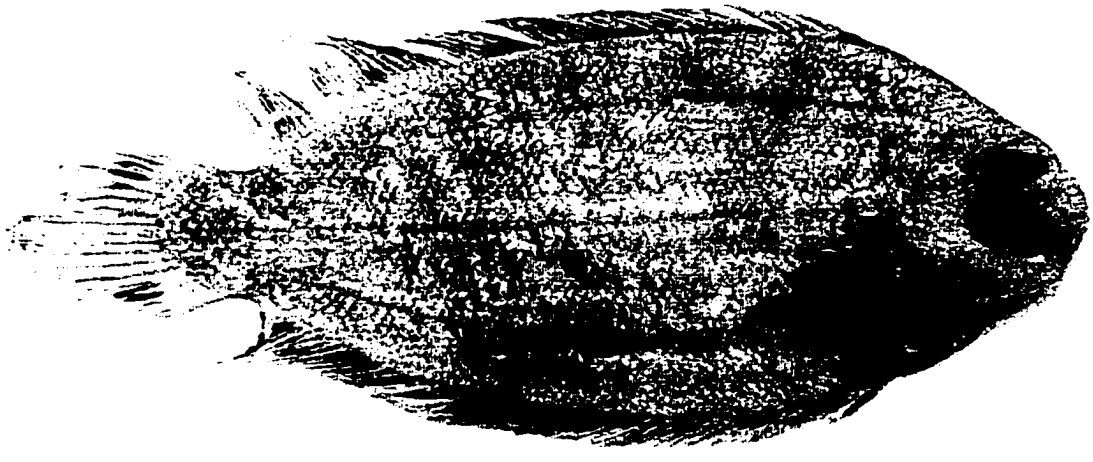


Fig. 33: *Poecilopsetta inermis*; USNM 217993; 108.9 mm SL.

Diagnosis.-A species of *Poecilopsetta* with the following combination of characters: 28-32 (usually 30-31) caudal vertebrae, 64-80 lateral line scales, body depth 2.15-3.01 in SL.

Description.-Data are presented for the additional material. A species of *Poecilopsetta* with a somewhat deep body, large eyes separated by a very narrow space, non-confluent

dorsal, caudal and anal fins and subsymmetrical pelvic fin bases. Body depth (BD) 33.3-46.9% in SL, head length (HL) 21.1-28.0% in SL. Interorbital space, snout, eyes and maxilla scaleless. Upper orbit 33.4-45.8% in HL, encroaching on dorsal profile of head. Position of lower eye variable: equal to upper eye, slightly anterior to upper eye or slightly posterior to lower eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through anterior third of lower eye, 22.4-33.8% in HL. Blind side maxilla almost symmetrical, 22.3-30.5% in HL. Lower jaw symmetrical, ocular side 33.3-44.3% in HL, blind side 35.1-43.8% in HL. Conical teeth present on premaxillae and dentaries. Teeth in one to three distinct bands on blind side dentary and premaxilla. One or two rows of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 5-8 on upper limb and 9-12 on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 12.8-20.4% in SL, height of arch 18.3-27.2% in BD, 64-80 ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 7-11 rays, 0-7 branched rays, length 28.4-51.0% in HL. Blind side pectoral fin usually with 7-11 unbranched rays, one specimen with only 4 rays, length 29.5-53.6% in HL. Pelvic fins with 6 rays. Ocular side pelvic fin (33.9-55.9%) in HL, blind side 34.8-53.4% in HL. No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over half to posterior third of upper eye. Dorsal fin with 56-67 rays, first ray 25.4-46.8% in HL. Longest dorsal fin-ray 37.0-61.1% in HL. Anal fin with 49-56 rays, longest ray 41.6-63.7% in HL. Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third ray of ocular side pelvic fin. Dorsal, anal, pectoral and pelvic fins scaleless. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 28-32 caudal vertebrae. Large ctenoid scales on

ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

Coloration in ethanol.-Ocular side evenly brown. Dorsal and anal fins light brown with tip of rays creamy white. Ocular side pectoral fin with brown on the distal portion of rays. Ocular side pelvic fin light brown. Caudal fin with two dark spots on upper and lower margins. Blind side creamy white.

Etymology.-From the Latin *inermis* meaning unarmed probably referring to the cycloid scales on the body as described by Breder (1927) but Hoshino (2000), in his synonymy of *P. albomarginata* with this species, examined the holotype of *P. inermis* and noticed that mainly ctenoid scales were found on the ocular side of this species.

Distribution.-*Poecilopsetta inermis* is distributed along the eastern coast of South America and into the Caribbean sea with a few found in the Gulf of Mexico (Fig. 34). This species is known to occur at depths between 95-768 m.

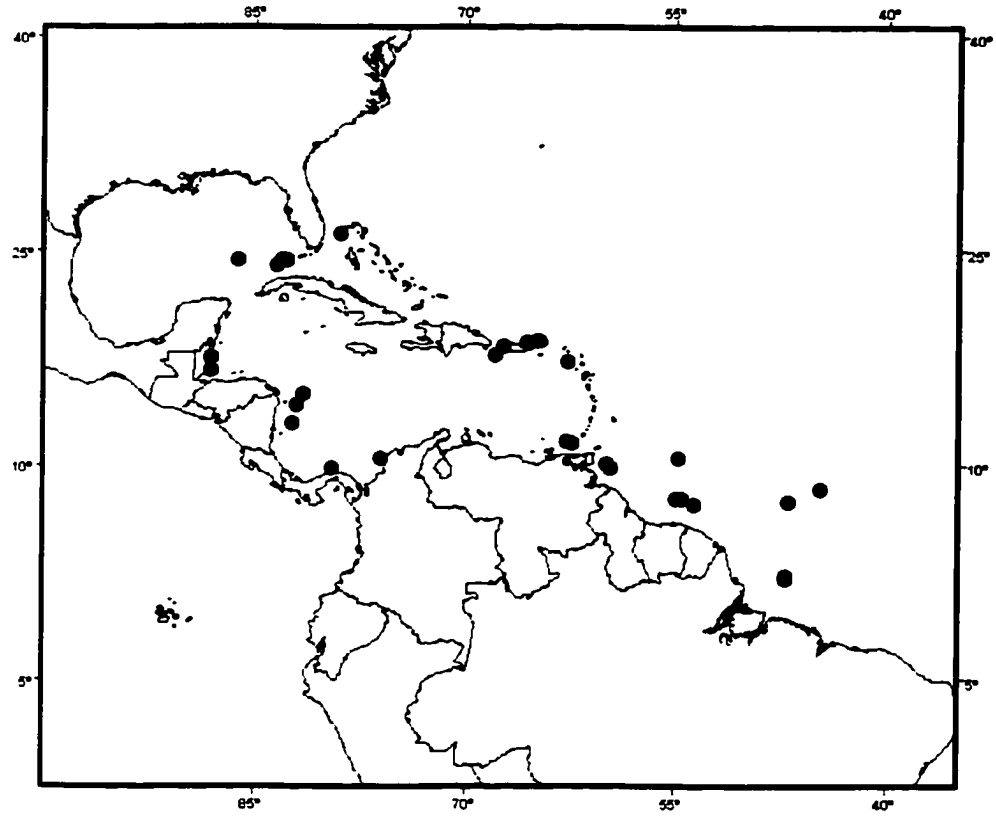


Fig. 34: Collection sites of *Poecilopsetta inermis*.

Remarks.-*Poecilopsetta inermis* is similar to *P. beanii*. *P. beanii* and *P. inermis* are the only species known from the Atlantic Ocean. They can be distinguished by their number of caudal vertebrae. Seventy-eight percent of all *P. beanii* had 32 caudal vertebrae. For *P. inermis*, 96% have 30 and 31 caudal vertebrae. *P. beanii* also has a slightly narrower body than *P. inermis* (Fig. 18). When the three diagnostic characters are used (caudal vertebrae, BD and LL scales), 89% of all fishes from the Atlantic Ocean can be identified. Another five percent can be added to the 89% identified when the geographical information is incorporated. The two species do not completely overlap geographically.

Larvae.-Nine larvae of *P. inermis* were examined for this study. They are similar to the juveniles and adults for all the measurements (Table 16). The main differences are in the coloration and in the symmetry of the pelvic fins in larvae. In larvae the pelvic fins are slightly more symmetrical than in adults. For the larva ZMUC P.853472 of 11.7 mm SL the upper eye has not completely migrated. See the general description of larvae in the section about *P. beanii* for the location of the different lines on the ocular and blind sides.

Coloration of the larvae of *P. inermis*.-Only three of the nine larvae examined have distinct pigmentation patterns, ZMUC P853470 and ZMUC P853471 -not shown- and USNM 159440. On the ocular side (Fig. 35), line 1 and 2 have six spots, and line 3 and 4 have five spots. On the wide pterygiophore zone circular blotches are present. There are six blotches on the pterygiophore zone above line 2. On the pterygiophore zone below line 3, four or five spots can be seen. These blotches are seen only in the largest larva. One spot is found at the base of the caudal peduncle and it is followed by two faint spots (only in the largest specimen) at the tip of the caudal skeleton. These spots are also seen on the blind side.

Two large black spots are found on the caudal fin. On the dorsal and anal fins, irregular brown spots can be seen. These brown spots are not found in association with the lines 1 and 4.

On the abdomen and head, once again only the largest larva had coloration. Three spots are found in the abdominal region, one in the middle, two at the base: one near the opening of the anus and the other near the base of the pelvic fins.

On the head three spots are found: one spot at the tip of the snout, another over the upper jaw at the level of the posterior opening of the nasal organ. The third one is found on the branchiostegal membranes at the proximal tip of the rays.

On the blind side (Fig. 36), line A and B have six spots, line C has four or five spots, line D, E and F have five spots.

Three spots are found on the abdomen. In the middle, near the opening of the anus and near the base of the pelvic fins.

On the head, two spots are found: one spot on the branchiostegal membranes corresponding to the one of the ocular side and a second over the upper jaw at the level of the nasal organ.

Evseenko and Suntsov (1993) described larvae of the genus *Poecilopsetta* collected by the Danish ship Dana between the years 1920-1922. Most of the material comes from the Atlantic Ocean (see also *P. plinthus* and *P. colorata*). The authors assigned all larvae longer than 14 mm SL to the species *P. beanii* based on the number of rows of teeth on the ocular side. Although not mentioned, it is thought that they assumed that the shorter larvae are not old enough to have a second row of teeth. The number of rows of teeth has been used in the original descriptions of *P. beanii* (Goode, 1881; "teeth are inconspicuous, apparently in two rows, stronger and more numerous on the blind side, barely discernable in upper jaw, absent elsewhere in the mouth.") *P. inermis* (Breder, 1927; "Teeth practically uniserial, on blind side (...)") and *P. albomarginata* Reid, 1934 ("Teeth irregularly uniserial on the jaws, (...)"). According to Hoshino (2000) the holotype of *P. inermis* has two or three rows of teeth close to the symphysis of the lower jaw on the ocular side. This observation makes it difficult to use rows of teeth as a discriminating feature for species in the Atlantic. Furthermore, all above-mentioned researchers have indicated that counting the rows of teeth in these species is very difficult. I concur with their opinion. Evseenko and Suntsov (1993) were misled in thinking they could identify the larvae according to dentition and have misidentified the larvae from the Atlantic Ocean. Furthermore, they used an estimated number of scales on the lateral line to confirm their identification. They found about 60 scales in the straight section of the lateral line of the

two longest larvae (32, 36 mm SL: Evseenko and Suntsov, 1993). Unfortunately, no scales remain on the specimens today. Nonetheless, with about 60 scales in the straight section of the lateral line, the authors estimate the total number of lateral line scales to be close to 80. They indicated that only *P. beanii* has lateral line scales counts within that range. They used the original descriptions of the three nominal species of the Atlantic Ocean to eliminate *P. inermis* as a possibility. Often the counts in original descriptions are based on only a few specimens (Goode, 1880; Breder, 1927; Reid, 1934). When we compare the counts of the two valid species in the Atlantic (Table 10) with the estimate for the two larvae, we see that this estimate is within the range of both species.

Based on the number of caudal vertebrae (30-31), the body depth of most of these larvae and the collection data (most were collected in the Western Atlantic), these larvae can be identified as *P. inermis*. Apart from these characteristics, the black spots at the tip of the caudal skeleton are very faint when present on the larvae of *P. inermis*. These spots are present and easily seen in *P. beanii* (Fig. 20, 21).

Table 16: Morphometrics and vertebral counts for larvae, juveniles and adults of *Poecilopsetta inermis*. For abbreviations see Tables 3 and 11.

Measurements	ZMUC larvae P853468-72 n=8	Other larva USNM 159440 n=1	Juveniles and adults n=100
SL	11.7-37.3 mm	54.5	51.2-115.7
In SL			
HL		3.82	3.57-4.73
BD	2.04-2.81	2.26	2.13-3.01
In HL			
UO		2.87	2.18-2.99
UJO		3.37	2.96-4.47
UJB		3.89	3.27-4.48
LJO		2.55	2.26-3.00
LJB		2.62	2.28-2.85
LPelES		2.42	1.79-2.95
LPelBS		2.52	1.87-3.42
HDR		1.93	1.64-2.71
FDR		3.08	2.13-3.94
HAR		1.92	1.57-2.41
Count			
Caudal vertebrae	30-31*	30	28-32

* counts taken from Evseenko and Suntsov, 1993.

Fig. 35: Ocular side of larva of *Poecilopsetta inermis*, USNM 159440; 54.5 mm SL.

Fig. 36: Blind side of larva of *Poecilopsetta inermis*, USNM 159440; 54.5 mm SL.

***Poecilopsetta macrocephala* Hoshino, Amaoka and Last, 2001**

Figures 37-39, Tables 13,14

Poecilopsetta macrocephala: Hoshino, Amaoka and Last, 2001, Species Diversity 6:73-81.

Common name: Large head mottled flounder

Holotype.-**CSIRO H5213-01**; N of Dampier Archipelago, WA.; 18°46'S 116°19'E; 555 m; demersal trawl, R/V 'Surefire'; 12 Feb. 1992; 1: 95.3 mm SL.

Paratypes.-**CSIRO H5213-02**; same as holotype; 2: 97.4-102.6 mm SL.

Additional material: **AMS I.22817-009**; Northwest Shelf, 240 km N of Port Hedland; 18°6'S 117°45'E; 492-520 m; 4: 78.7-103.5mm SL. **NTM S.12593-005**; Off Rowley Shoals, Northwest Shelf, W.A.; 17°24'S 118°52'E; 445 m, 4 Nov. 1985; 5: 70.1-94.9 mm SL.

Diagnosis.-A species of *Poecilopsetta* with the following combination of characters: large head (3.52-3.96 in HL), short ocular side pectoral fin (2.34-3.31 in HL) and few (75-80) lateral line scales.

Description.-Data are presented for the holotype and values for additional material are given in parentheses. A species of *Poecilopsetta* with a rather elongated body, very large eyes separated by a very narrow space, non-confluent dorsal, caudal and anal fins, subsymmetrical pelvic fin bases and blind side pectoral fin-rays longer than eyed side. Body depth (BD) 40.1% in SL (35.1-40.5%), head length (HL) 28.4% in SL (25.3-28.0%). Interorbital space, snout, eyes and maxilla scaleless. Upper orbit 45.3% in HL (44.5-51.1%), encroaching on dorsal profile of head. Position of lower eye equal to upper eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side

maxilla not reaching to vertical through anterior third of lower eye, 33.5% in HL (33.4-38.4%). Blind side maxilla almost symmetrical, 31.0% in HL (29.1-35.7%). Lower jaw symmetrical, ocular side 43.3% in HL (42.4-48.3%), blind side 43.4% in HL (42.2-46.7%). Conical teeth present on premaxillae and dentaries. Teeth in three (two to four) distinct bands on blind side dentary and premaxilla. Two (one to two) rows of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 6 (6-8) on upper limb and 11 (10-12) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 18.1% in SL (19.0-20.2%), height of arch 25.2% in BD (22.8-28.8%), 75 (75-80) ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 7 (7-9) rays, 4 (0-5) branched rays, length 32.1% in HL (30.2-42.8%). Blind side pectoral fin with 7 (7-8) unbranched rays, length 44.9% in HL (40.5-53.4%). Ocular side pectoral fin 72% (68-87%) the length of the blind side pectoral fin. Pelvic fins with 6 rays. Ocular side pelvic fin (36.1-43.2%) in HL, blind side 34.7% in HL (35.9-39.5%). No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior 1/3 of upper eye. Dorsal fin with 66 (62-67) rays, first ray 30.2% in HL (28.8-37.0%). Longest dorsal fin-ray 45.0% in HL (39.8-50.3%). Anal fin with 55 (53-57) rays, longest ray 33.8% in HL (38.1-50.8%). Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third ray of ocular side pelvic fin. Dorsal, anal, pectoral and pelvic fins scaleless. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 29 (28-30) caudal vertebrae. Large ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

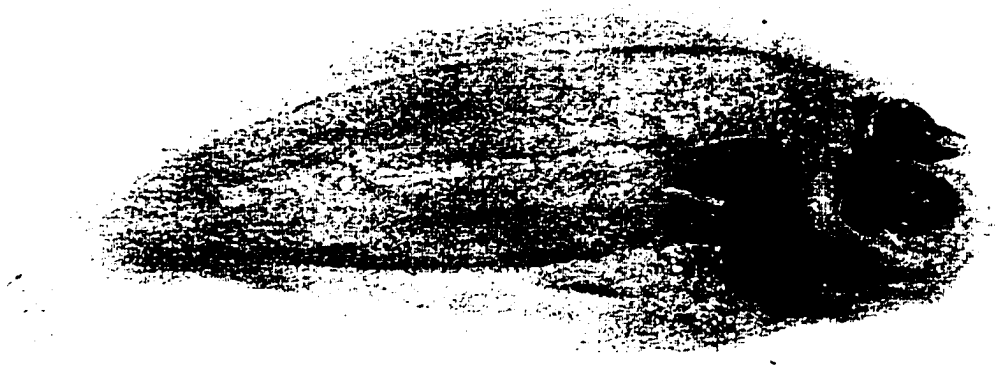


Fig. 37. *Poecilopsetta macrocephala*, holotype: CSIRO H5213-01; 95.3 mm SL.

Coloration in ethanol.-Ocular side sometimes with one faint broad transverse band 2/3 the body length. Dorsal and anal fins light brown. Ocular side pectoral and pelvic fin without pigment. Caudal fin sometimes with two dark spots on upper and lower margins, or with a triangular spot or completely brown with three dark spots. Blind side creamy white with small dark spots.

Etymology.-From the Greek *macrocephala* (*macro* meaning long and *cephala* meaning head). The specific name refers to the long head of this species.

Distribution.-*Poecilopsetta macrocephala* is distributed along the coast of Northwestern Australia, on the Northwest shelf and north of Port Hedland (Fig. 38). This species is known to occur at depths between 445-555 m.

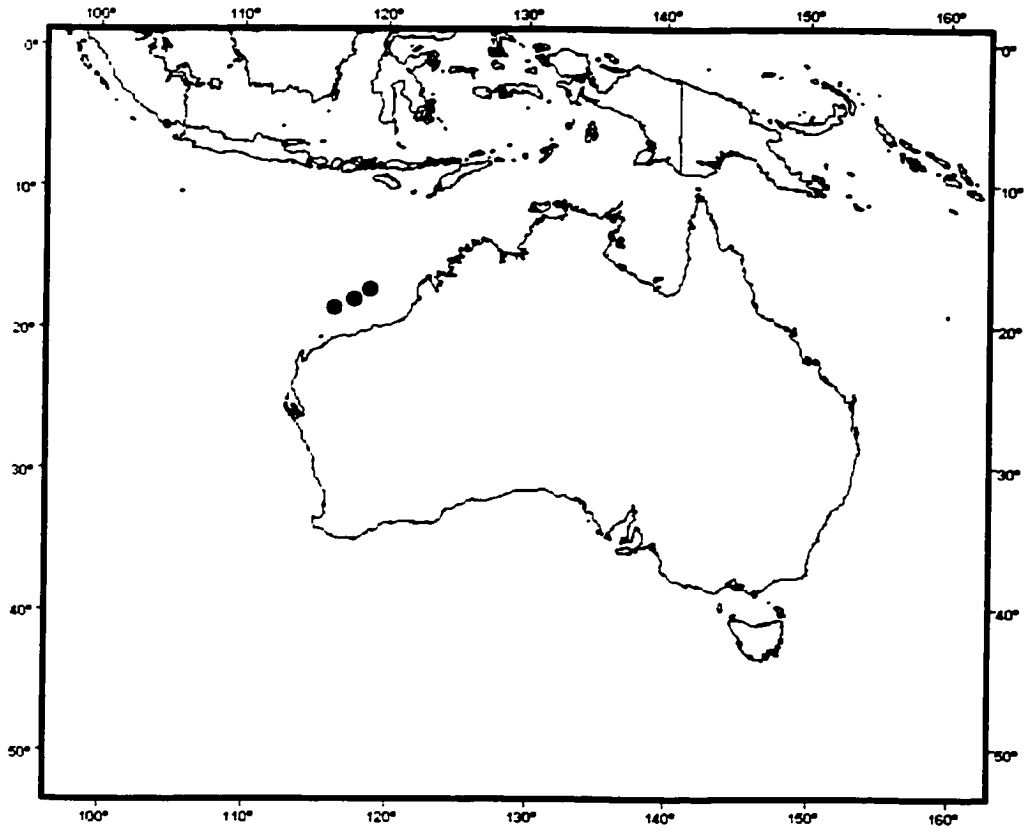


Fig. 38: Collection sites of *Poecilopsetta macrocephala*.

Remarks.-*Poecilopsetta macrocephala* is very similar to *P. vaynei* and *P. dorsialta*. They are different from other *Poecilopsetta* by the short ocular side pectoral fin (shorter than blind side) and the low number of lateral line scales. *P. macrocephala* and *P. vaynei* differ from *P. dorsialta* by the length of the first dorsal fin ray and the height of the dorsal fin (Tables 7,8; 13,14). *P. macrocephala* as a longer head than *P. vaynei* (Tables 7,8). *P. macrocephala*, *P. vaynei* and *P. dorsialta* all share an incomplete ossification of the upper orbit. In *P. macrocephala* the blind side frontal and blind side lateral ethmoid do not touch in their upper portion to complete the bony arch protecting the upper eye (Fig. 39).

Fig. 39: X-ray of cranium of *Poecilopsetta macrocephala* showing the incomplete formation of the bony structure behind upper eye.

***Poecilopsetta natalensis* Norman, 1931**

Figures 40, 41; Tables 7, 8, 13, 14

Poecilopsetta natalensis: Norman, 1931, Treubia, 13: 426. Norman 1934, A systematic monograph of the flatfishes (Heterosomata). Vol I: 393. Shen 1982, Quart. Journ. Taiwan Museum 35: 203-204. Heemstra 1986, Smith's sea fishes: 864. Quéro *et al.* 1988, Cybium 12(4): 322. Adam *et al.* 1998, J.L.B. Smith Ichthyological Bulletin 67: 15. Fricke 1999, Fishes of the Mascarene Islands (Réunion, Mauritius, Rodriguez): an annotated checklist. With records of new species: 572.

Common name: African righteye flounder (According to Fishbase, this common name should have appeared in Smith's sea Fishes but there is no mention of a common name for *P. natalensis* in this book. Author unknown).

Holotype.-**BMNH 1922.3.27:7**; off Natal; 342 m (188 fm); 116.7 mm SL.

Additional material: **ANSP 145376**; Indian Ocean, off Mozambique; 25°12'S 34°04'E; vessel Anton Bruun, Cr. 8, Sta. 397A; 230-295 m; 29 Sept. 1964; 1: 128.9 mm SL. **ANSP 145607**; Indian Ocean; 26°07'S 34°11'E; vessel Anton Bruun, Cr. 8, Sta. 397C; 600-665 m; 29 Sept. 1964; 1: 77.9 mm SL. **CAS 66552**; Indian Ocean, Madagascar, off Cap St. Vincent; 4: 94.6-121.5 mm SL. **RUSI 28478**; Mozambique, Bay of Maputo; Dec. 1987; 2: 122.2-125.9 mm SL. **USNM 307295**; Indian Ocean, Madagascar, north of Tulear; 22°19'06"S 43°06'06"E to 22°20'36"S 43°06'06"E; vessel Vityaz, Cr. 17, Sta. 2644; 330-335 m; 2 Dec. 1988; 8: 95.3-122.6 mm SL.

Diagnosis.-A species of *Poecilopsetta* with the following combination of characters: lateral line with fewer than 94 scales, all fins darker than body, dark lines around postero-lateral edges of the eyes, ocular side pectoral fin long (about 2 in HL).

Description.-Data are presented for the holotype and values for additional material are given in parentheses. A species of *Poecilopsetta* with a rather elongated body, large eyes separated by a very narrow space, non-confluent dorsal, caudal and anal fins and subsymmetrical pelvic fin bases. Body depth (BD) 41.7% in SL (35.8-41.4%), head length (HL) 22.4% in SL (19.6-23.9%). Interorbital space, snout, eyes and maxilla scaleless. Upper orbit 42.0% in HL (40.3-46.3%), encroaching on dorsal profile of head. Position of lower eye slightly anterior or equal to upper eye. Nostrils asymmetrical; those of blind side

higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through anterior third of lower eye, 26.1% in HL (25.0-31.9%). Blind side maxilla almost symmetrical, 23.3% in HL (23.7-31.6%). Lower jaw symmetrical, ocular side 37.1% in HL (38.5-42.4%), blind side 37.7% in HL (37.3-41.0%). Conical teeth present on premaxillae and dentaries. Teeth in (two to four) distinct bands on blind side dentary and premaxilla. (Two to three) rows of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 8 (5-8) on upper limb and 10 (9-11) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 18.2% in SL (16.9-18.8%), height of arch (21.3-24.9%) in BD, 77 (79-83) ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 10 (7-10) rays, 5 (3-7) branched rays, length 51.2% in HL (42.4-62.7%). Blind side pectoral fin with 9 (8-10) unbranched rays, length 45.0% in HL (37.1-52.6%). Pelvic fins with 6 rays. Ocular side pelvic fin 46.9% in HL (35.1-54.9%), blind side 38.3% in HL (38.6-52.5%). No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior half of upper eye. Dorsal fin with 62 (57-64) rays, first ray 36.0% in HL (28.2-45.3%). Longest dorsal fin-ray 49.9% in HL (45.2-62.8%). Anal fin with 54 (49-54) rays, longest ray 45.5% in HL (44.1-59.1%). Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of second or third ray of ocular side pelvic fin. Dorsal, anal, pectoral and pelvic fins scaleless. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 31 (27-33) caudal vertebrae. Large ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

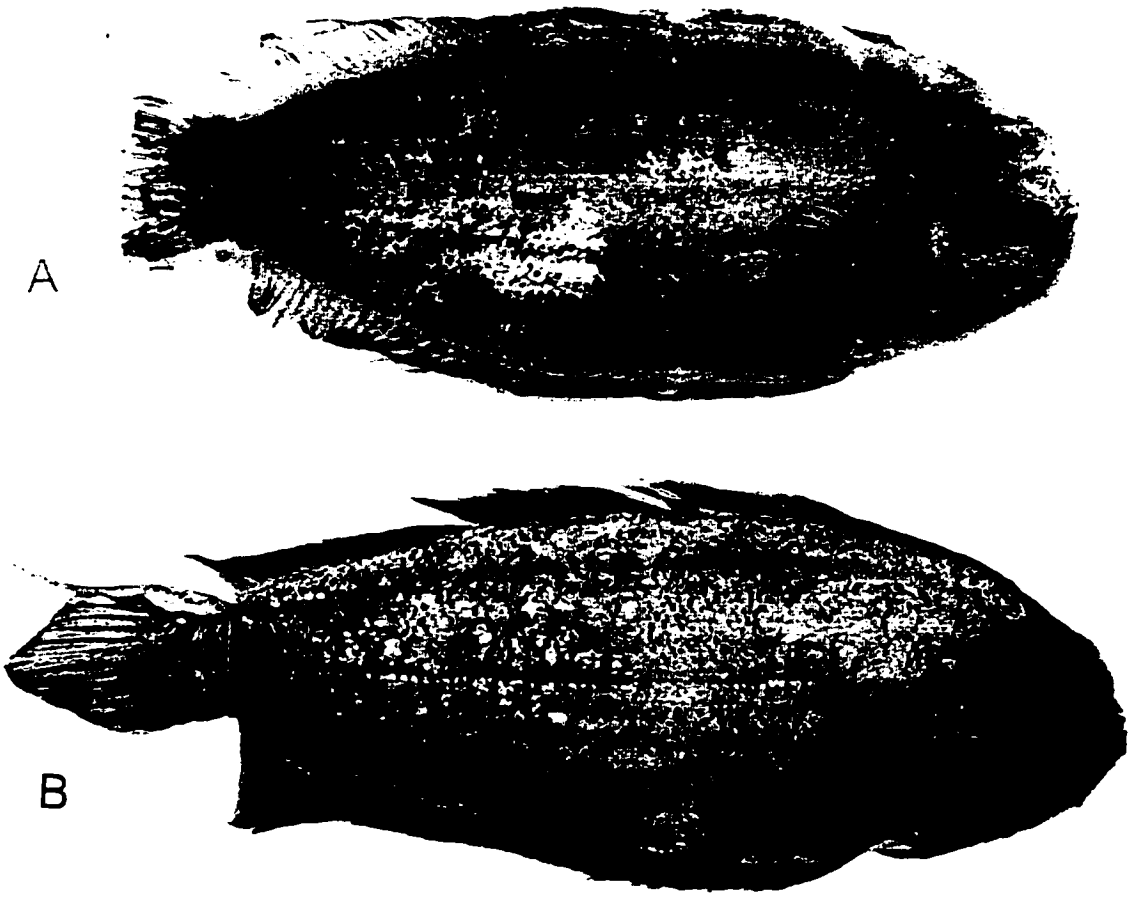


Fig. 40: *Poecilopsetta natalensis* A) holotype: BMNH 1922.3.27:7; 116.7 mm SL, B) CAS 66552; 121.5 mm SL.

Coloration in ethanol.-Ocular side brown. Eyes dark black around the posterior edges. Dorsal and anal fins dark brown. Ocular side pectoral fin black. Ocular side pelvic fin brown. Caudal fin with two dark spots on upper and lower margins. Blind side creamy white with small dark spots.

Etymology.-From the Latin *natalensis*. The specific name refers to the type locality, Natal.

Distribution.-*Poecilopsetta natalensis* is distributed along the eastern coast of Africa, from Natal to Mozambique. It is also found near Madagascar. In the Pacific, *P. natalensis* has been reported from off Taiwan (Shen, 1982) (Fig. 41). This species is known to occur at depths between 230-295 m.

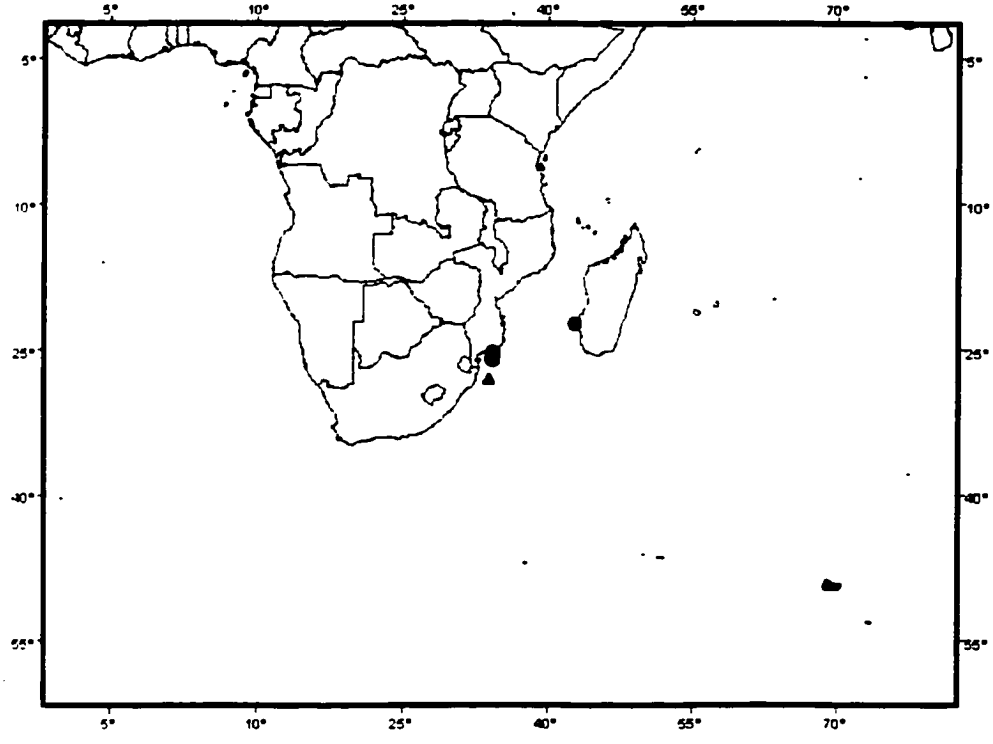


Fig. 41: Collection sites of *Poecilopsetta natalensis*. The triangle represents approximate collection site of holotype off Natal.

Remarks.-*Poecilopsetta natalensis* is similar to *P. zanzibarensis*. *P. natalensis* has fewer lateral line scales than *P. zanzibarensis* and more branched pectoral fin rays on the ocular side. *P. natalensis* is also close to *P. vaynei* and *P. macrocephala*. *P. natalensis* has a longer ocular side pectoral fin than *P. vaynei* and *P. macrocephala*.

***Poecilopsetta normani* Foroshchuck and Fedorov, 1992**

Figures 42, 43; Tables 7, 8

Poecilopsetta normani: Foroshchuck and Fedorov, 1992, Journal of Ichthyology 32(7): 37-44.

Common name: Norman's mottled flounder

Holotype.-**ZISP 49132**; Saya de Malha Bank; 11°12'S 62°14'4"E; R/V El'sk; 24 Oct. 1977; 270-255 m; male: 95.0 mm SL. Radiograph only.

Paratypes.-**ZISP 49133**; same as holotype; 3: 119.0-137.0 mm TL. Radiograph only. **ZISP 49134**; Saya de Malha Bank; 11°00'S 61°40'E to 11°50'S 62°20'E; R/V El'sk; 230-270 m; Oct-Nov. 1977; 77.2 mm SL. Radiograph only.

Additional material: **ANSP 145324**; Indian Ocean; 6°48'S 39°51'E; vessel Anton Bruun, Cr. 9, St. 425; 400-300 m; 20 nov 1964; 3: 94.2-96.3 mm SL. **ANSP 145374**; Indian Ocean; 2°56'S 40°28'E; vessel Anton Bruun, Cr. 8, St. 421G; 240 m; 8 Nov. 1964; 4: 84.9-100.6 mm SL. **USNM 307298**; Indian Ocean, Madagascar, Tulear to Mauritius; 10°19'30"N 59°08'48'E'; vessel 'Vityaz', cr. 17, Sta. 2825; 395-420 m; 14 Jan. 1989; 1: 121.7 mm SL.

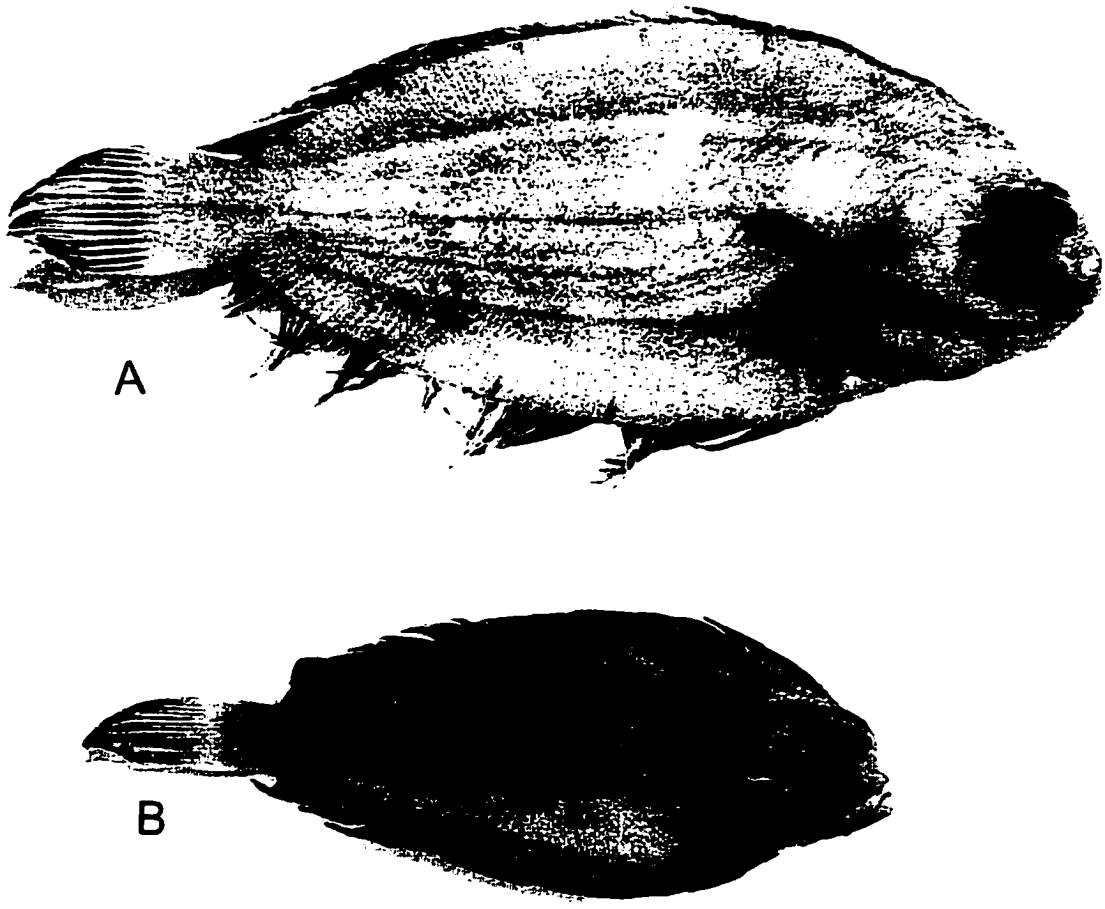


Fig. 42: *Poecilopsetta normani*; A) USNM 307298; 121.7 mm SL, B) ANSP 145374; 85.0 mm SL.

Diagnosis.-A species of *Poecilopsetta* with the following combination of characters: high number of ocular side pectoral fin rays (13-17), lateral line scales (110-133) and ctenoid scales on ocular side.

Description.-Data are presented for the holotype and values for the additional material are given in parentheses. A species of *Poecilopsetta* with a rather deep body, large eyes separated by a scaled interorbital space, non-confluent dorsal, caudal and anal fins and

subsymmetrical pelvic fin bases. Body depth (BD) (39.8-45.0%) in SL, head length (HL) (22.8-25.2%) in SL. Snout and maxilla with scales. Upper orbit (36.8-39.8%) in HL, encroaching on dorsal profile of head. Position of lower eye slightly anterior or equal to upper eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through anterior third of lower eye, (23.7-29.2%) in HL. Blind side maxilla almost symmetrical, (21.6-27.2%) in HL. Lower jaw symmetrical, ocular side (31.6-37.9%) in HL, blind side (31.2-38.8%) in HL. Conical teeth present on premaxillae and dentaries. Teeth in (two to three) distinct bands on blind side dentary and premaxilla. (One or two) rows of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, (7-9) on upper limb and (11-13) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch (16.6-19.3%) in SL, height of arch (18.4-24.9%) in BD, (110-133) ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with (13-17) rays, (8-11) branched rays, length (57.1-70.2%) in HL. Blind side pectoral fin with (11-15) unbranched rays, length (34.7-44.6%) in HL. Pelvic fins with 6 rays. Ocular side pelvic fin (38.8-44.4%) in HL, blind side (37.2-44.9%) in HL. No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior 1/2 of upper eye. Dorsal fin with 64 (59-66) rays, first ray (25.5-35.4%) in HL. Longest dorsal fin-ray (40.1-48.4%) in HL. Anal fin with 55 (51-56) rays, longest ray (38.4-50.7%) in HL. Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of second or third ray of ocular side pelvic fin. Dorsal, anal and pelvic fins scaleless. Ocular side pectoral fin with scales. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 30 (30-32) caudal vertebrae.

Small ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

Coloration in ethanol.-Ocular side light to dark brown. Eyes brown. Dorsal and anal fins light brown with white tips. Ocular side pectoral fin brown with a black spot at the postero-ventral tip. Ocular side and blind side pelvic fins light brown. Caudal fin with two dark spots on upper and lower margins. Blind side creamy white with small dark spots. Juveniles with multiple brown spots on ocular side and multiple black spots on blind side.

Etymology.-From the Latin *normani*. Named in honour of the English ichthyologist J. R. Norman who described five species within the family Poecilopsettidae. He also was the first to publish a revision of the family.

Distribution.-*Poecilopsetta normani* is distributed along the eastern coast of Africa and in the Indian Ocean off Madagascar and Saya de Malha Bank (Fig. 43). This speices is known to occur at depths between 255-420 m.

Remarks.-*Poecilopsetta normani* is similar to *P. albomaculata* and *P. colorata*. *P. normani* has ctenoid scales on the ocular side of the body (cycloid for *P. albomaculata*) and a high number of blind side pectoral fin rays (11-15) compared to 8-10 for *P. albomaculata* and 5-10 for *P. colorata*.

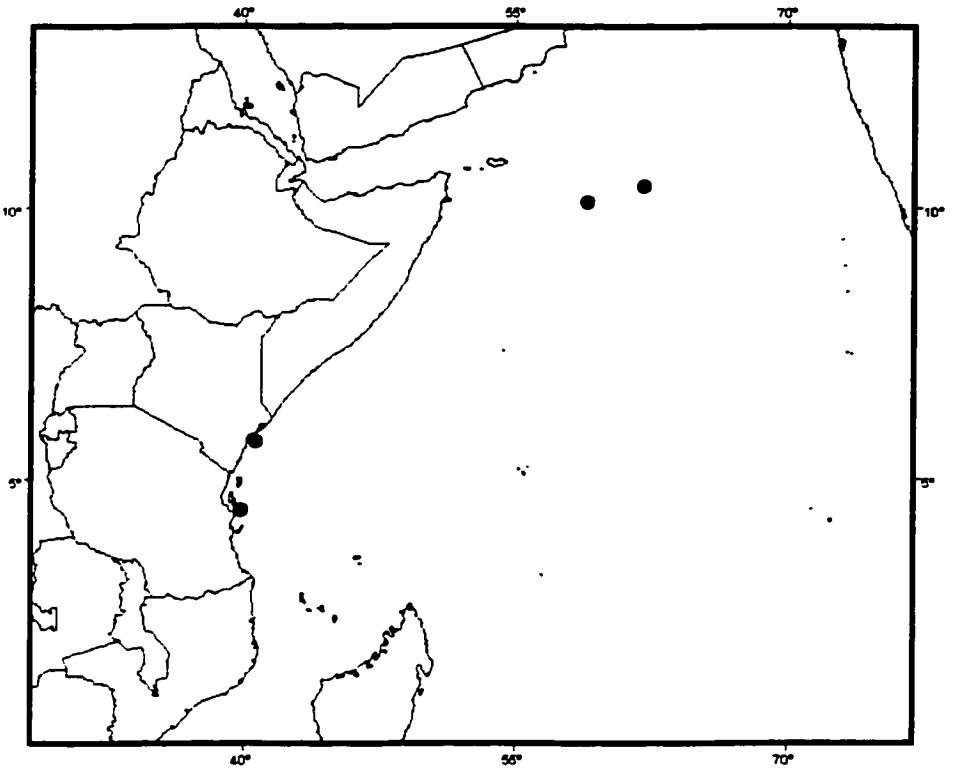


Fig. 43: Collection sites of *Poecilopsetta normani*.

***Poecilopsetta plinthus* (Jordan and Starks, 1904)**

Figures 44, 45; Tables 13, 14

Alaeops plinthus: Jordan and Starks, 1904, Bull. U.S. Comm. Fish. 22: 623.

Poecilopsetta plinthus: Hubbs 1915, Proc. U.S. Nat. Mus., 48, p. 474. Norman 1931, Treubia 13: 426. Norman 1934, A systematic monograph of the flatfishes (Heterosomata). Vol I: 393. Amaoka 1964, Bull. Misaki Mar. Biol. Inst., Kyoto Univ. 7: 9-17. Amaoka 1982, Fishes of the Kyushu-Palau ridge and Tosa Bay: 300-301; 408. Shen 1982, Quart. Journ.

Taiwan Museum 35: 201. Matsuura 1985, Fishes of the Okinawa trough and the adjacent waters Vol 2: 620-621; 740.

Poecilopsetta megalepis Fowler, 1934: Guibord and Chapleau 2002, Cybium 26:135-139.

Common name: Tile-colored righteye flounder (Hensley, 1997)

Holotype.-**USNM 51406**; Japan, Suruga Bay, Honshu Is., Ose Zaki; 110-128 m (60-70 fm); vessel Albatross, Sta. 3708; 8 May 1900; 1: 126.2 mm SL.

Paratypes.-**USNM 51408**; Japan, off Honshu Is., Owari Bay; 24-29 m (13-16 fm); vessel Albatross, Sta. 3723; 15 May 1900; 1: 70.1 mm SL. **USNM 51413**; same as holotype; 6: 36.1-102.9 mm SL.

Holotype.-*P. megalepis*: **USNM 93094**; Pacific Philippines, Balayan Bay and Verde Is. passage, Sombrero Is.; 13°52'22"N 120°46'22"E; 216 m (118 fm); vessel Albatross, Sta.5117; 21 Jan 1908; 1: 98.8 mm SL.

Paratype.-*P. megalepis*: **USNM 93572**; Pacific Philippines, vicinity Marinduque Is, 8.8 miles off Tayabas Lt.; 13°48'N 121°43'E; 194 m (106 fm); vessel Albatross, Sta. 5369; 24 Feb 1909; 1: 85.4 mm SL.

Additional material: **AMS I.15976-017**; 55 miles east of Newcastle, New South Wales (NSW); 32°50'S 152°43'E; 585 m; 7 May 1971; 1: 103.7 mm SL. **AMS I.20918-016**; 1-2 miles North northeast Raine Is., Queensland (QLD); 11°35S 144°2E; 270-275 m; 12 Feb 1979; 10: 77.2-99.0 mm SL. **AMS I.23896-002**; Sydney, Jerwis Bay, NSW; 34°21'S 151°21'E; 270-281 m; 13 Dec 1978; 1: 105.5 mm SL. **AMS I.24039-003**; East of Sydney, NSW; 33°43'S 151°50'E; 275-280 m; 5 Dec 1978; 2: 82.4-85.6 mm SL. **AMS I.25800-017**; Just north of Townsville, QLD; 18°00'S 142°2'E; 220 m; 8 Jan 1986; 6: 92.6-103.6 mm SL. **AMS I.26821-001**; Ballina, Tweed Heads, NSW; 28°5'S 153°57'E; 225 m; 6 Nov 1978; 1:

101.7 m SL. **BMNH 1931.11.16:3**; Yokohama, 1: 73.8 mm SL. **BMNH 1931.8.19:8**; Suruga Bay, Japan; vessel Albatross; 1: 103.0 mm SL. **BMNH 1931.8.19:9**; Omai Saki, Japan; 1: 74.2 mm SL. **BMNH 1933.6.12:11**; Tanabe, Kii, Japan; 1: 69.5 mm SL. **CAS 122546**; Northwestern and central Pacific, Japan, Kochi Pref., Honshu Is., Bingo Suido; 20 Aug 1906; 1: 69.0 mm SL. **CAS 122547**; Northwestern and central Pacific, Japan, Honshu Is., Suruga Wan; 15 Oct 1906; 1: 92.6 mm SL. **CAS 123524**; Northwestern and central Pacific, Japan, Misaki; 2: 74.3-75.8 mm SL. **HUMZ 51722**; off Omaezaki, Shizuoka; 34°36'N 138°14'E; 200-350 m; 10 Mar 1976; 1: 88.1 mm SL. **HUMZ 51875**; near Enshu-Nada; 34°27'N 137°38'E; 250 m; 13 Mar 1976; 1: 109.5 mm SL. **HUMZ 51876**; near Enshu-Nada; 34°27'N 137°38'E; 250 m; 13 Mar 1976; 1: 104.6 mm SL. **HUMZ 51877**; near Enshu-Nada; 34°27'N 137°38'E; 250 m; 13 Mar 1976; 1: 87.5 mm SL. **HUMZ 51878**; near Enshu-Nada; 34°27'N 137°38'E; 250 m; 13 Mar 1976; 1: 100.1 mm SL. **NMV A4575**; QLD., 95 km East of Dunk Is.; 18°00'S 147°2'E; 220 m; vessel Soela; 8 Jan 1986; 3: 95.3-107.9 mm SL. **NMV A4576**; QLD., 90 km east of Dunk Is.; 18°0,10'S 147°1,30'E, 17°57,60'S 146°58,60'E; 224-228 m; vessel Soela; 9 Jan 1986; 4: 88.5-98.9 mm SL. **NTM S.11747-025**; East of Dunk Is.; 17°58'S 146°59'E; 224-228 m; 9 Jan 1986; 4: 94.0-109.0 mm SL. **NTUM 5330**; Tung-Kang, Pingtung; 11 Mar 1975; 2: 85.7-100.6 mm SL. **NTUM 5343**; Tung-Kang, Pingtung, Taiwan; 6 Dec 1981; 4: 84.8-93.9 mm SL. **USNM 77186**; Suruga Gulf, Ose Saki, Japan; 35°3'10"N 138°49'50"E; 104.3 m (57 fm); vessel Albatross, Sta. 5071; 15 Oct 1906; 2: 76.0-87.3 mm SL. **USNM 150688**; East coast Mondoro, Malabrigo It.; 13°27'20"N 121°17'45"E; 198 m (108 fm); vessel Albatross, Sta. 5121; 2 Feb 1908; 1: 89.7 mm SL. **USNM 150697**; Pacific Philippines, Pt. Tagalo It.; 8°41'15"N 123°18'30"E; 187 m (102 fm); vessel Albatross, Sta. 5520; 10 Aug 1909; 1: 102.0 mm SL. **USNM 286354**; Pacific, South China sea, Macclesfield bank; 16°20'N 114°39'E, 16°20'N 114°39'30"E; 392-395 m (214-216 fm); vessel Cape St. Mary, Cr. 3/64, Sta. 57; 20 Jun 1964; 1: 87.0 mm SL.

Diagnosis.-A species of *Poecilopsetta* with the following character: few lateral line scales (57-68).

Description.-Data are presented for the holotype and values for additional material are given in parentheses. A species of *Poecilopsetta* with a slightly deep body, large eyes separated by a moderate space, non-confluent dorsal, caudal and anal fins, subsymmetrical pelvic fin bases and blind side pectoral fin-rays longer than eyed side. Body depth (BD) 42.6% in SL (33.9-48.5%), head length (HL) 23.3% in SL (20.0-26.9%). Interorbital space, snout, eyes and maxilla scaleless. Upper orbit 36.7% in HL (32.3-44.5%), encroaching on dorsal profile of head. Position of lower eye usually equal to upper eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through anterior third of lower eye, 25.7% in HL (25.4-34.5%). Blind side maxilla almost symmetrical, (22.5-32.2%) in HL. Lower jaw symmetrical, ocular side 37.5% in HL (34.8-44.3%), blind side 35.0% in HL (35.2-42.7%). Conical teeth present on premaxillae and dentaries. Teeth in two (two to four) distinct bands on blind side dentary and premaxilla. Two (one to three) rows of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 6 (5-8) on upper limb and 10 (9-12) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 15.7% in SL (16.6-20.5%), height of arch 23.7% in BD (19.8-29.0%), 60 (57-68) ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 8 (6-10) rays, (4-7) branched rays, length 44.2% in HL (34.8-57.2%). Blind side pectoral fin with 7 (6-8) unbranched rays, length (37.8-53.6%) in HL. Pelvic fins with 6 rays. Ocular side pelvic fin 43.8% in HL (33.7-50.6%), blind side 41.9%

in HL (31.3-56.1%). No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior half of upper eye. Dorsal fin with 65 (59-69) rays, first ray 25.9% in HL (21.9-41.2%). Longest dorsal fin-ray 41.3% in HL (32.6-53.4%). Anal fin with 56 (52-59) rays, longest ray 41.1% in HL (36.7-57.9%). Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third or fourth ray of ocular side pelvic fin. Dorsal, anal, pectoral and pelvic fins scaleless. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 31 (30-32) caudal vertebrae. Large ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

Coloration in ethanol.-Ocular side brown with darker spots all over the body and onto head and jaws. Dorsal and anal fins with brown marks and smaller spots. Ocular side pectoral fin with distal tip darker. Ocular side pelvic fin with some small brown spots. Caudal fin with black spots, two or four on upper and lower margins. Blind side creamy white. Some lighter coloured specimens don't have to spots on the body but still have the spots on the head and particularly the jaws. These specimens also have a dark peritoneum on the ocular side.

Etymology.-*plinthus* from the Latin form of the Greek word meaning brick. The specific name refers to brick-like coloration of this species.

Distribution.-*Poecilopsetta plinthus* is distributed from Japan to south-eastern Australia (Sydney) (Fig 45). This species is known to occur at depths between 24-585 m.

Fig. 44: *Poecilopsetta plinthus*, holotype: USNM 51406; 126.2 mm SL.

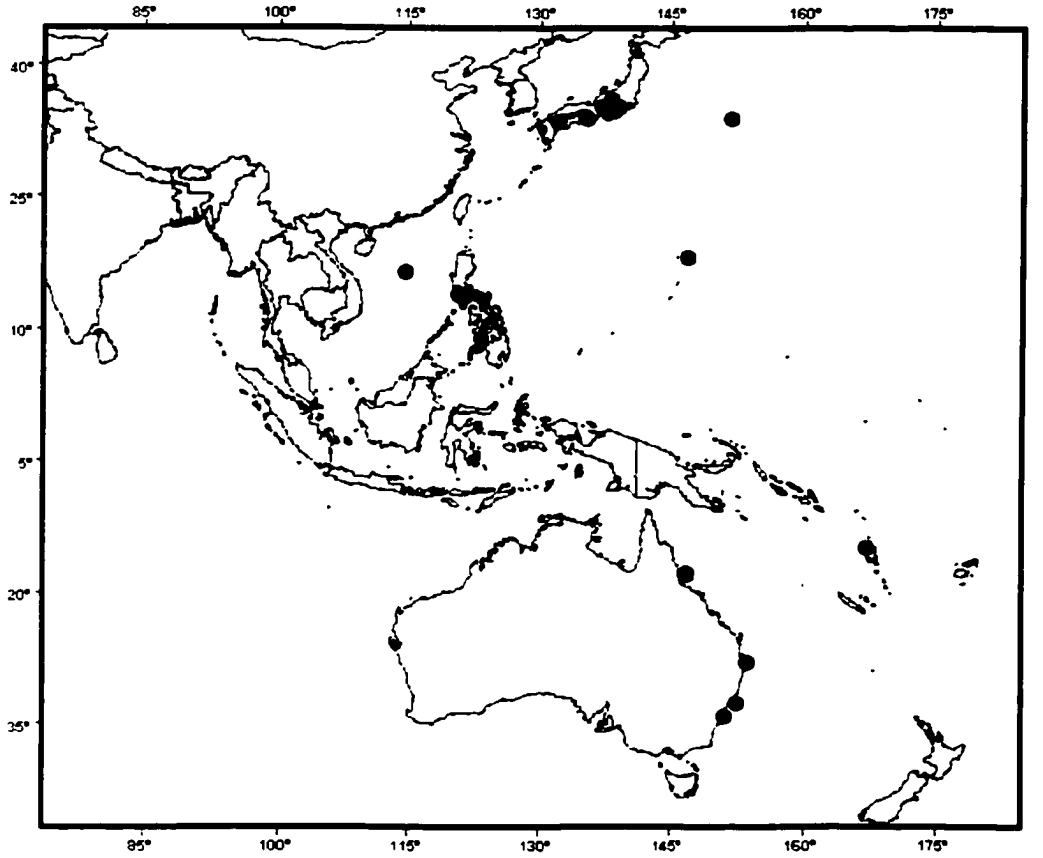


Fig. 45: Collection sites of *Poecilopsetta plinthus*.

Remarks.-Fowler (1934) described a species from the Philippines, *Poecilopsetta megalepis*. In his original description, Fowler (1934) only mentions one type specimen (=holotype – USNM 93094) from Balayan Bay, Philippines. He does not mention the existence of any other paratypes but for some other species described in the same article, Fowler is more explicit. For example, in the description of *Pseudorhombus megalops* he writes: " Also 2 paratypes." (p. 329). Certain sections of his description of *P. megalepis* lead the reader to believe that Fowler examined more than one specimen. He wrote:" Arch of lateral line 2 ½ to 2 ¾ in straight section to caudal base. (...) Dorsal with 8 or 9 obscure dark blotches and anal with 5 or 6, sometimes little evident". This introduces some intraspecific variability. This was interpreted as evidence that he looked at more than one specimen when he described *P. megalepis*.

According to Eschmeyer *et al.* (1998), the Smithsonian Institution (USNM) is holding a type series for *P. megalepis*. This type series is made of (other than the holotype) 13 paratypes: USNM 93571 (1 spm), USNM 93572 (1 spm), USNM 93573 (3 spms), USNM 93574 (2 spms), USNM 93575 (3 spms), USNM 93576 (1 spm), USNM 93577 (1 spm) and 93578 (1 spm). According to article 72.4.1.1 of the International Code of Zoological Nomenclature (ICZN, 1999) a type series can be considered if, in the original description, some clues point towards the existence of other specimens seen by the author but not mentioned in the description. Based on evidence shown previously, the type series held at the USNM is now valid for *P. megalepis*.

After carefully examining the type series mentioned in Eschmeyer *et al.* (1998), it was found that 12 of the 13 paratypes are in fact members of the genus *Nematops* (*N. grandisquamus*, USNM 93577; *N. macrochirus*, 6 males and 5 females). These specimens show characteristics typical for *Nematops*: tentacles on one or both eyes (but they can be absent), two nasal bones and three proximal pterygiophores of the anal fin inserted between the first hemal spine and the first pterygiophore of the anal fin (see Fig.

between the first hemal spine and the first pterygiophore of the anal fin (see Fig. 6). The holotype and the paratype USNM 93572 agree with the description of *P. megalepis*.

It seems likely that the description of *P. megalepis* was based mainly on the holotype and possibly on the single paratype similar to the holotype. This could help explain the intraspecific variability in the description. No other information contained in the description would allow me to think that Fowler used the other paratypes in his description.

Although probably not used in the description, Fowler clearly used the "*Nematops*" paratypes for the comparison of *P. megalepis* with other species of the genus *Poecilopsetta*. He wrote:"Related to *Poecilopsetta praelonga* Alcock in its elongate body, though with greatly longer scales, (...) greatly longer pectoral of colored side, even exceeding head." (Fowler 1934: p. 341). No species of the genus *Poecilopsetta*, including the holotype and paratype of *P. megalepis*, have an ocular side pectoral fin longer than the head (Tables 7,9,13). This characteristic is typical for *N. macrochirus* (Table 5) (Sakamoto, 1993). This confirms the use of the type series by Fowler and validates it according to the International Code of Zoological nomenclature (ICZN, 1999).

A comparative study of the holotype and paratype of *P. megalepis* with other Poecilopsettidae leaves not doubt on the positioning of *P. megalepis* into the genus *Poecilopsetta*. These specimens do not have rostral spines nor elongated dorsal and ocular pelvic fin rays (characters of the genus *Marleyella*) and they also do not have two nasal bones (character of the genus *Nematops*). Moreover, these specimens have measurements and counts that are within the intraspecific variation found for *P. plinthus* (Tables 13,14). Only three measurements (HL, LJB and LL scales; Table 13) are slightly outside the range for *P.* plinthus but are too close to *P. plinthus'* range to justify keeping this species separate from *P. plinthus*. Furthermore, Fowler (1934) did not compare *P. megalepis* with *P. plinthus*. If he had done so, he would probably have seen the great similarity between the holotypes of both *P. megalepis* and *P. plinthus*.

Only one other *P. megalepis* is known, although it was not examined during this study, it was identified by Shen (1982) from a single specimen caught off of Taiwan. He used the number of scales on the lateral line (approximately 56) as a defining character. This is within the range for *P. plinthus*. Also, the other characters observed on the specimen are within the range for *P. plinthus*.

Larvae.-Three publications have described larvae of *P. plinthus* (Minami, 1988; Evseenko and Suntsov, 1993; Uyeda and Sasaki, 2001) although there is some doubt on the identification of one *P. plinthus* larva by Minami (1988) (see Uyeda and Sasaki, 2001).

***Poecilopsetta praelonga* Alcock, 1894**

Figures 46-49; Tables 7, 8, 13, 14, 17

Poecilopsetta praelonga: Alcock, 1894, J. Asiat. Soc. Bengal, 63 (2) p. 139. Norman 1931, Treubia 13: 425. Norman 1934, A systematic monograph of the flatfishes (Heterosomata). Vol I: 391. Shen 1982, Quart. Journ. Taiwan Museum 35: 201. Quéro *et al.* 1988, Cybium 12(4): 329.

Poecilopsetta maculosa Alcock, 1894: Weber & de Beaufort 1929, The fishes of the Indo-Australian Archipelago, E.J. Brill Ltd., Leiden. Vol. 5, p. 137.

Boopsetta umbrarum Alcock, 1896: Norman 1934, A systematic monograph of the flatfishes (Heterosomata). Vol I: 391.

Common name: Alcock's narrow-body flounder (Gloerfelt-Tarp and Kailola, 1984)

Syntype: ZSI F61/1; not seen.

Additional material: **AMS I.22808-055**; Northwest shelf, 220 km north of Port Hedland, Indian Ocean; 17°59'S 118°17'W; 404-420 m; 3 Apr 1982; 1: 129.8 mm SL. **AMS I.22808-056**; Northwest shelf, 220 km north of Port Hedland, Indian Ocean; 17°59'S 118°17'W; 404-420 m; 3 Apr 1982; 1: 66.0 mm SL. **AMS I.22821-041**; Northwest Shelf, 190 km NW of Port Hedland; 18°16'S 118°12'E; 298-320 m; 10 Apr. 1982; 1: 122.5 mm SL. **AMS I.22822-021**; Northwest shelf, 200 km northwest of Port Hedland, Indian Ocean; 18°23'S 117°41'E; 396-418 m; 11 Apr 1982; 1: 127.4 mm SL. **AMS I.22825-006**; Northwest shelf, 200km northwest of Port Hedland, Indian Ocean; 18°59'S 117°10'E; 300-326 m; 13 Apr 1982; 3: 117.9-144.2 mm SL. **AMS I.22826-020**; Northwest shelf, 210 km northwest of Port Hedland, Indian Ocean; 18°44'S 117°2'E; 396-406 m; 13 Apr 1982; 1: 114.3 mm SL. **ANSP 145375**; Indian Ocean; 10°39'N 97°06'E; 290 m; vessel Anton Bruun, Cr. 1, Sta. 22A; 24 Mar 1963; 8: 79.6-106.2 mm SL. **BMNH 1898.7.13:17**; Bay of Bengal; 1: 117.8 mm SL. **BMNH 1927.1.6:61**; Andaman sea; 338 m (185 fm); 1: 73.0 mm SL. **BMNH 1984.11.14:5**; Off south coast of Sumatra, Java; vessel Jetindofish; 1979-1983; 1: 119.8 mm SL. **NTM S.12288-003**; East of Evan shoal, Arafura sea, NT; 9°46'S 130°14'E, 270-300 m; 15 Sept 1987; 7: 75.3-123.0 mm SL. **NTM S.12594-011**; Off Rowley shoals, Northwest Shelf, WA; 17°28'S 118°53'E; 400 m; 4 Nov 1985; 2: 137.0-152.6 mm SL. **NTM S.12605-006**; Off Rowley shoals, Northwest Shelf, WA; 17°52'S 118°27'E, 420 m; 6 Nov 1985; 2: 74.4-79.0 mm SL. **NTM S.12607-005**; Off Rowley shoals, Northwest Shelf, WA; 17°51'S 118°30'E; 410 m; 6 Nov 1985; 6: 69.1-97.2 mm SL. **NTM S.12614-014**; Off Rowley shoals, Northwest Shelf, WA; 17°39'S 118°38'E; 410 m; 7 Nov 1985; 2: 135.8-144.2 mm SL. **NTM S.12631-010**; Off Rowley shoals, Northwest Shelf, WA; 400 m; 4 Nov 1985; 1: 131.9 mm SL. **NTM S.12641-016**; Northwest of Lynber bank, Northwest Shelf; 14°50'S 121°35'E; 275-280 m; 15 Jul 1989; 1: 123.9 mm SL. **NTM S.12727-001**; South-

west of Rowley shoals, WA; 17°52'S 118°28'E; 410 m; 9 Feb 1990; 1: 116.2 mm SL. **NTM S.12728-009**; South west of Rowley shoals, WA; 18°1'S 118°23'E; 420 m; 6 Feb 1990; 2: 90.5-92.8 mm SL. **NTM S.13114-010**; North of Cape Leveque, WA; 13°38'S 122°42'E; 423 m; 24 Jan 1990; 1: 146.3 mm SL. **NTM S.13146-013**; East of Evan shoal, Arafura sea, NT; 9°45'S 130°14'E; 265 m; 6 Feb 1991; 4: 75.8-111.8 mm SL. **NTM S.13147-009**; Northwest of Lynedoch bank, Arafura sea, NT; 9°47'S 130°26'E; 255 m; 9 Dec 1990; 2: 109.0-128.2 mm SL. **NTM S.13995-006**; East of Evan shoal, Arafura sea, NT; 9°40'S 130°15'E; 16 Sept 1987; 1: 134.0 mm SL. **NTM S.14950-001**; North of Lynedoch bank, Arafura sea, Indonesia; 9°18'S 131°6'E; 296-297 m; 2 Jun 1999; 1: 116.3 mm SL. **NTM S.14951-002**; North of Lynedoch bank, Arafura sea, Indonesia; 9°18'S 131°3'E; 304 m; 3 Jun 1999; 1: 127.1 mm SL. **USNM 138004**; Pacific Philippines, vicinity north of Mindanao; 8°45'30"N 123°33'45"E; 309 m (169 fm); vessel Albatross, Sta. D5517; 9 Aug 1909; 2: 124.9-156.9 mm SL. **USNM 138005**; Pacific Philippines, Pt. Tagolo lt.; 8°46'N 123°32'30"E; 320 m (175 fm); vessel Albatross, Sta. 5516; 9 Aug 1909; 1: 138.1 mm SL. **USNM 138006**; Pacific Philippines, Pt. Tagolo lt.; 8°48'N 123°31'E; 366 m (200 fm); vessel Albatross, Sta. 5518; 9 Aug 1909; 1: 99.7 mm SL. **USNM 138007**; Pacific Philippines, Pt. Tagolo lt.; 8°47'N 123°31'15"S; 333 m (182 fm); vessel Albatross, Sta. 5519; 9 Aug 1909; 1: 124.5 mm SL. **USNM 138009**; Pacific Philippines, between Negros and Siquijor; 9°15'45"N 123°22'E; 511 m (279 fm); vessel Albatross, Sta. 5536; 19 Aug 1909; 3: 87.5-115.7 mm SL. **USNM 138010**; Pacific Philippines, north of Mindanao and vicinity Pt. Tagolo lt.; 8°48'44"N 123°27'35"E; vessel Albatross, Sta. 5523; 10 Aug 1909; 1: 97.3 mm SL. **USNM 138011**; Pacific Philippines, north of Mindanao, Macabalan Pt. lt.; 8°37'37"N 124°35'E; 392 m (214 fm); vessel Albatross, Sta. 5501; 4 Aug 1909; 1: 109.7 mm SL. **USNM 138012**; Pacific Philippines, off southeastern Mindanao, Balanja Pt.; 12°25'35"N 121°31'35"E; 428 m (234 fm); vessel Albatross, Sta. 5260; 3 Jun 1908; 1: 73.1 mm SL.

USNM 150694; Pacific Philippines, off southeastern Mindanao, Balanja Pt.; 12°25'35"N 121°31'35"E; 428 m (234 fm); vessel Albatross, Sta. 5260; 3 Jun 1908; 1: 137.9 mm SL.

Diagnosis.-A species of *Poecilopsetta* with the following combination of characters: no scales on the ocular side pectoral fin and maxilla, 91-111 scales in the lateral line, 29-32 caudal vertebrae and two darks spots at the distal tip of the hypural plates near the body midline.

Description.-Data are presented for the additional material. A species of *Poecilopsetta* with a rather elongated body, eyes separated by a very narrow space, non-confluent dorsal, caudal and anal fins and subsymmetrical pelvic fin bases. Body depth (BD) 33.8-45.2% in SL, head length (HL) 22.3-27.4% in SL. Interorbital space, snout, eyes and maxilla scaleless. Upper orbit 33.1-45.4% in HL, encroaching on dorsal profile of head. Position of lower eye equal to or slightly anterior to upper eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through first third of lower eye, 25.0-33.5 % in HL. Blind side maxilla almost symmetrical, 24.6-33.6% in HL. Lower jaw symmetrical, ocular side 32.8-42.2% in HL, blind side 32.6-44.3% in HL. Conical teeth present on premaxillae and dentaries. Teeth in two to four distinct bands on blind side dentary and premaxilla. Two to four rows of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 5-9 on upper limb and 8-12 on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 16.2-20.7% in SL, height of arch 18.4-39.2% in BD, 91-111 ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 6-11 rays, 1-2 branched rays, length 25.8-61.9% in HL. Blind side pectoral fin with 6-9

unbranched rays, length 29.1-64.5% in HL. Pelvic fins with 6 rays. Ocular side pelvic fin 35.8-51.5% in HL, blind side 34.6-50.3% in HL. No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior 1/3 of upper eye. Dorsal fin with 57-65 rays, first ray 22.5-44.8% in HL. Longest dorsal fin-ray 39.8-61.3% in HL. Anal fin with 48-55 rays, longest ray 39.4-57.9% in HL. Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third or fourth ray of ocular side pelvic fin. Dorsal, anal, pectoral and pelvic fins scaleless. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 29-32 caudal vertebrae. Large ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

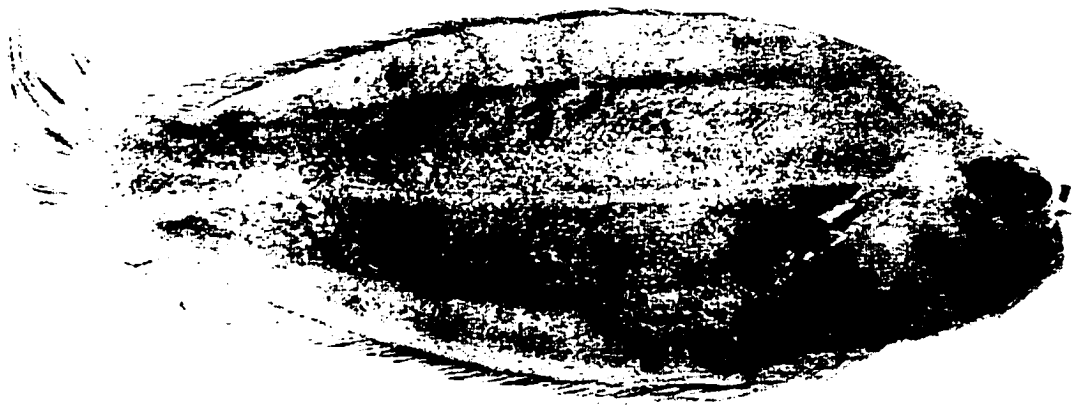


Fig. 46: *Poecilopsetta praelonga*; USNM 138004; 127.2 mm SL.

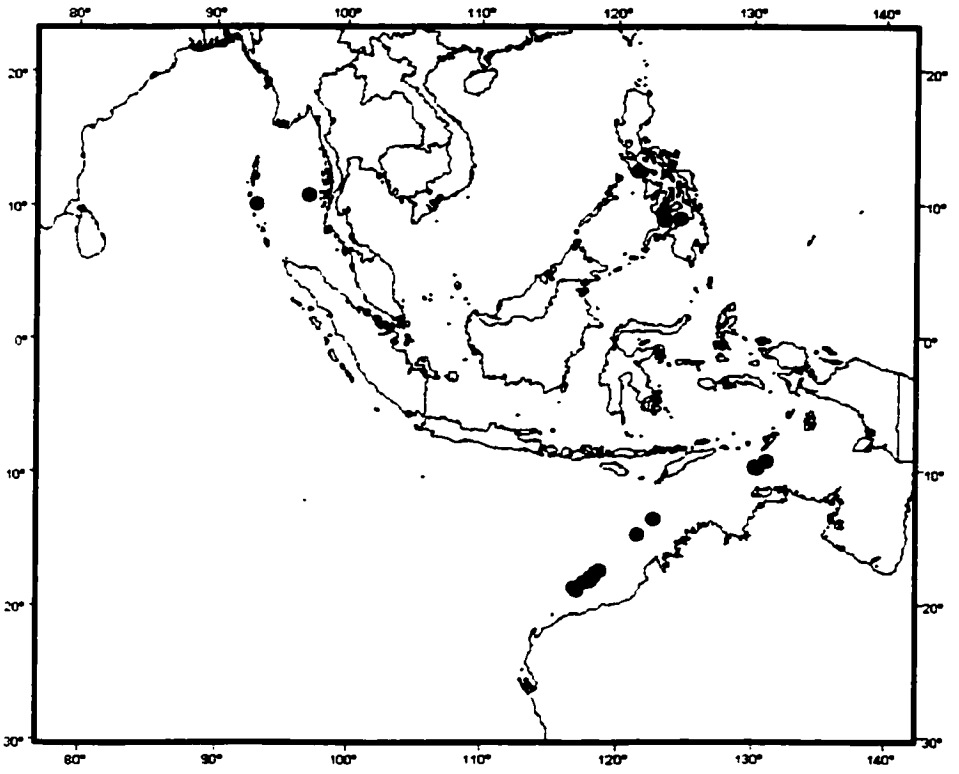


Fig. 47: Collection sites of *Poecilopsetta praelonga*.

Coloration in ethanol.-Ocular side brown sometimes with some dark spots characteristics of larvae and juveniles still present. Dorsal and anal fins darker. Ocular side pectoral fin brown on all its length. Ocular side pelvic fin brown. Caudal fin brown with two dark spots on upper and lower margins. Blind side creamy white sometimes with brown head. Darker spots, also found in larvae and juveniles, still present but faint even in larger adults.

Etymology.-From the Latin *praelonga* (*prae* meaning before and *longa* meaning long). The specific name refers to the syntype, a juvenile. The name *praelonga* refers to the stage before the adult.

Distribution.-*Poecilopsetta praelonga* is found from the Indian Ocean near Indonesia to the north-western coast of Australia (Fig. 47). This species is known to occur at depths between 255-511 m.

Remarks.-*Poecilopsetta praelonga* is similar to *P. colorata* but is different in having no scales on the pectoral or ocular side maxilla and in having a slightly narrower body. *P. praelonga* is also very close to *P. zanzibarensis*. *P. zanzibarensis* differs from *P. praelonga* by the number of caudal vertebrae (32-33 for *P. zanzibarensis* and 30-32-usually 30-31- for *P. praelonga*), by the position of black spots at the base of hypural plates (near edges in *P. zanzibarensis*, near the mid-line for *P. praelonga*), and by the larger band of muscles in *P. zanzibarensis* (in *P. praelonga* the pterygiophore zone without muscles is larger).

Larvae.- Larvae of *P. praelonga* have been previously described by Hoshino *et al.* (2000). In this article, three specimens are described. The specimens are transformation larvae (Kendall *et al.*, 1984) from the Indian Ocean off Western Australia. The specimens examined in this study are also transformation larvae and were also collected in the Indian Ocean off Western Australia. The larvae are similar to juveniles and adults (Table 17; Hoshino *et al.*, 2000). Major differences are coloration and asymmetry of pelvic fins. In the larvae, the pelvic fins are almost symmetrical, they are subsymmetrical in adults.

Coloration of the larvae of *P. praelonga*.-On the ocular side (Fig. 48), line 1 has eight spots, the first spot of this row is located in the muscles associated with the dorsal fin, immediately over the upper eye, line 2 has seven spots, line 3 has five spots and line 4 has six spots. We can see six faint circles above line 2 and five below line 3. Five darker blotches are also found below line1 and four are found above line 4. There is a spot at the

base of the caudal peduncle followed by two spots at the tip of the caudal skeleton. These two spots are not at the edges of the caudal skeleton (like in other larvae described) but they are more towards the body mid-line. These three spots are also found on the blind side.

On the dorsal and anal fins there are darker lines on two or three consecutive rays. These dark lines are in association with the spots on lines 1 and 4. In two larvae examined the caudal fin is damaged but in the third one (Fig. 48 B) the distal tips of the caudal fin rays are dark almost forming a triangular mark on the fin.

In the abdominal region, there are four spots, one approximately in the middle of this section of the body and the others near the base of the body, one near the opening of the anus, one almost at the base of pelvic fins and a third one in between the last two spots.

The head of the larvae have more spots than any other larvae described in this study. One is found over of the upper eye, two other are found at the base of the neurocranium at one end of the hyomandibular and at one end of the preopercular bones. Two are found on the snout, one at the tip of the snout and another just over the upper jaw, at the level of the nasal organ, these two spots are close together and almost look contiguous. There is one spot at the tip of the lower jaw and one at the corner of the lower jaw. Another spot is found at the curve in the preopercular bone. The last spot on the head is found on the branchiostegal membranes.

On the blind side (Fig. 49), line A has eight spots, line B has seven spots, line C has seven spots, line D has six or seven spots, line E has four or five spots and line F has six spots.

In the abdominal region on the blind side, the distribution of spots is slightly variable between the specimens examined. There are six or seven spots all distributed on the intestines (which are easily seen through the transparent body wall). No apparent

pattern can be seen in the distribution of these spots except for those located near the opening of the anus and near the base of the pelvic fins.

Numerous spots are found on the head. One is found over the upper eye (corresponding to the one on the ocular side), one is found at the tip of the snout (same as ocular side), one is on the upper jaw at the level of the nasal organ, one is found at the tip of the mouth and one is found on the retroarticular bone. Two spots are found on the branchiostegal membranes and two last spots are found above these last spots on the opercular series.

The larvae of *P. praelonga* show almost the same coloration pattern as *P. colorata*, *P. hawaiiensis* and *P. inermis*. Nonetheless, larvae of *P. praelonga* are distinct in having numerous spots on the head and abdominal region, especially on the blind side. Also, all larval specimens of *P.praelonga* examined for this study have an extra spot in the third and fourth rows on the ocular side. Although this difference seems subtle, it is easily noticeable because these two spots are found near the single spot at the base of the caudal peduncle and they form two corners of a square formed with the two spots at the tip of the caudal skeleton (Fig. 48). These spots forming a square at the base of the caudal peduncle of the fish do not seem to be present in larvae examined by Hoshino *et al.* (2000). One last difference between larvae of *P. praelonga* and the others is the proximity of the two spots at the base of the caudal peduncle. These two spots are closer to the body mid-line in *P. praelonga* than in other species. This characteristic can also help identify adults of *P. praelonga*.

Table 17: Morphometrics of larvae, juveniles and adults of *Poecilopsetta praelonga*. For abbreviations see Tables 3 and 11.

Measurements	Larvae n=3	Juveniles and adults n=62
SL	66.0-74.7	73.0-152.6
In SL		
HL	4.20-4.33	3.65-4.48
BD	2.21-2.47	2.23-2.96
In HL		
UO	2.89-3.02	2.20-3.00
UJO	2.99-3.31	3.08-4.00
UJB	3.16-3.34	2.97-4.07
LJO	2.47-2.56	2.37-3.05
LJB	2.37-2.48	2.26-3.07
PectOS		1.62-2.77
PectBS		1.55-3.20
PelOS	2.41*	1.94-2.79
PelBS	1.99*	2.02-2.89
HDR	2.11*	1.63-2.51
FDR	2.33-3.01	2.23-4.45
HAR	2.08*	1.73-2.54

*data are missing for two larvae.

A)

B)

Fig. 48: Ocular side of larvae of *Poecilopsetta praelonga*, A) AMS I. 22808-056; 66.0 mm SL, B) NTM S.12607-005; 74.7 mm SL.

A)

B)

Fig. 49: Blind side of larvae of *Poecilopsetta praelonga*, A) AMS I. 22808-056; 66.0 mm SL, B) NTM S.12607-005; 74.7 mm SL.

Poecilopsetta vaynei Quéro, Hensley and Maugé, 1988

Figures 50, 51; Tables 7, 8

Poecilopsetta vaynei: Quéro, Hensley and Maugé, 1988, Cybium 12(4): 321-330.

Common name: Vayne's mottled flounder

Holotype.-**MNHN 1988-653**; 12°41'S 48°14'5"S; 290-295 m; vessel Vauban, Ch. 18; 18 Jan. 1972; 1: 103.1 mm SL.

Paratype.-**MNHN 1988-652**; 12°53'3" 43°10'4"E; 480-520 m; vessel Vauban, Ch. 2; 4 Mar. 1971; 1: 99.7 mm SL.

Additional material: **AMS I.22808-054**; Northwest Shelf, 220 km N of Port Hedland; 17°59'S 118°17'E; 404-420 m; 3: 93.6-99.1 mm SL. **AMS I.2226-019**; Northwest Shelf, 210 km NW of Port Hedland; 18°44'S 117°02'E; 396-406 m, 13 Apr. 1982; 6: 87.9-100.3 mm SL. **NTM S. 12594-012**; off Rowley Shoals, Northwest Shelf, W.A.; 17°28'S 118°53'E; 400 m; 4 Nov. 1985; 4: 90.2-107.7 mm SL. **NTM S.12614-046**; off Rowley Shoals, Northwest Shelf, W.A.; 17°39'S 118°38'E; 410 m; 7 Nov. 1985; 1: 81.4 mm SL. **NTM S.13146-025**; E of Evan Shoal, Arafura Sea N.T.; 09°45'S 130°14'E; 265 m; 6 Feb. 1991; 1: 75.8 mm SL. **USNM 138014**; Pacific Philippines, W coast of Luzon; 16°38'N 119°57'18"E; 340 m (186 fm); 10 May 1909; 1: 68,6 mm SL. **WAM P.25401-014**; Browse Is., W.A.; 13 47 S 123 18 E; 242 m; vessel Umitaka Maru; 23 Dec. 1969; 2: 79.7-91.5 mm SL.

Diagnosis.-A species of *Poecilopsetta* with the following combination of characters: small head (3.97-4.33 in SL), few lateral line scales (70-81) and short ocular side pectoral fin (2.77-3.66 in HL).

Description.-Data are presented for the holotype and values for additional material are given in parentheses. A species of *Poecilopsetta* with a rather elongated body, large eyes separated by a very narrow space, non-confluent dorsal, caudal and anal fins, subsymmetrical pelvic fin bases and blind side pectoral fin-rays longer than eyed side. Body depth (BD) 38.9% in SL (33.4-42.0%), head length (HL) 25.2% in SL (23.1-24.9%). Interorbital space, snout, eyes and maxilla scaleless. Upper orbit 40.0% in HL (39.8-51.4%), encroaching on dorsal profile of head. Position of lower eye equal to upper eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through anterior third of lower eye, 30.3% in HL (27.4-42.0%). Blind side maxilla almost symmetrical, 27.0% in HL (28.9-38.7%). Lower jaw symmetrical, ocular side 41.9% in HL (39.6-48.7%), blind side 42.7% in HL (39.7-47.8%). Conical teeth present on premaxillae and dentaries. Teeth in two (two to four) distinct bands on blind side dentary and premaxilla. Two rows (one to three) of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 6 (6-7) on upper limb and 12 (9-13) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch (16.0-18.9%) in SL, height of arch 27.6% in BD (24.4-29.0%), 79 (70-81) ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 8 (8-12) rays, 6 (0-9) branched rays, length 33.9% in HL (27.3-36.1%). Blind side pectoral fin with 6 (6-9) unbranched rays, length 37.5% in HL (39.0-48.4%). Ocular side pectoral fin 9% (7-43%) shorter than blind side pectoral fin. Pelvic fins with 6

rays. Ocular side pelvic fin 41.2% in HL (41.2-54.6%), blind side 36.9% in HL (37.4-43.6%). No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior 1/2 of upper eye. Dorsal fin with 67 (63-69) rays, first ray 29.7% in HL (31.4-44.9%). Longest dorsal fin-ray 43.4% in HL (40.3-54.9%). Anal fin with 56 (51-58) rays, longest ray 44.0% in HL (40.3-52.2%). Dorsal and anal fin rays unbranched. Pelvic fins almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of third ray of ocular side pelvic fin. Dorsal, anal, pectoral and pelvic fins scaleless. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 30 (29-31) caudal vertebrae. Large ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

Fig. 50: *Poecilopsetta vaynei*; NTM S.12594-012; 99.5 mm SL.

Coloration in ethanol.-Ocular side light brown. Dorsal and anal fins light brown. Ocular side pectoral fin with pigment at the tip. Ocular side pelvic fin without pigment. Caudal fin

with two or more dark spots on upper and lower margins. Sometimes a spot can be found on the posterior end of dorsal and anal fins. Blind side creamy white with small dark spots.

Etymology.-Named for Jean-Jacques Vayne (Quéro *et al.*, 1988) an illustrator and colleague of the authors.

Distribution.-*Poecilopsetta vaynei* is distributed from Reunion Island to the north-western coast of Australia in the Indian Ocean, from Arafura sea and off Luzon (Philippines) in the Pacific Ocean (Fig. 51). This species is known to occur at depths between 242-520 m.

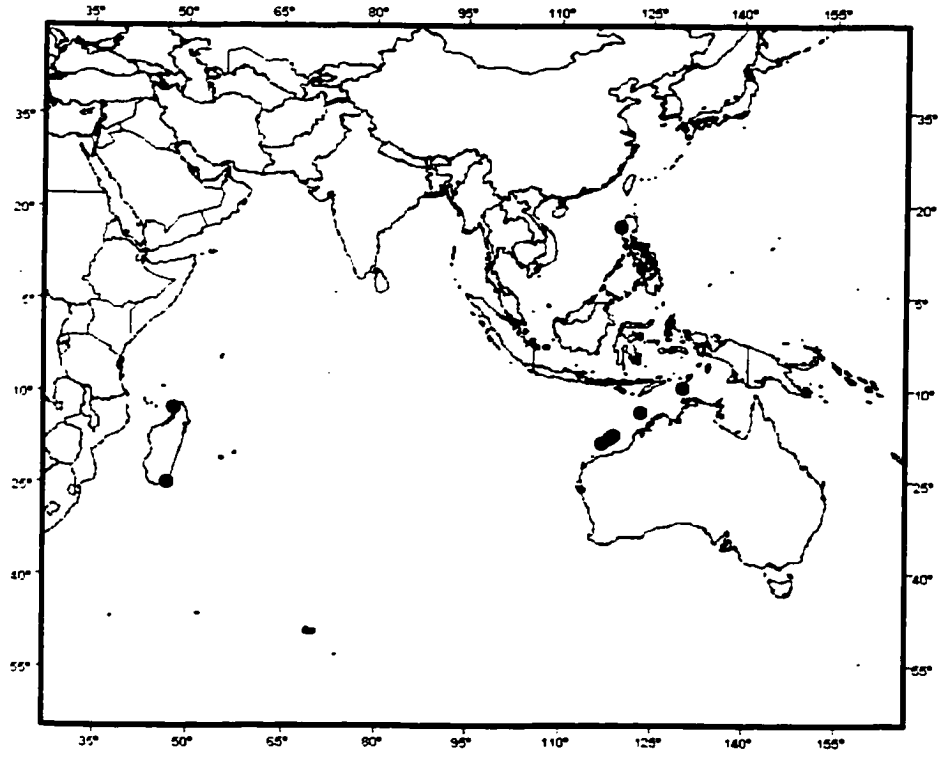


Fig. 51: Collection sites of *Poecilopsetta vaynei*.

Remarks.-*Poecilopsetta vaynei* is similar to *P. dorsialta* and *P. macrocephala*. *P. vaynei* shares a short ocular side pectoral fin and incomplete ossification of the upper orbit with these two species (Fig. 39). *P. vaynei* differs from *P. macrocephala* by the length of the head (3.97-4.33 in SL) compared to (3.57-3.96) (Table 7). *P. macrocephala* also has a lower number of ocular side pectoral fin rays (7-9; average 7.8) compared to 8-12; average 9.9. *P. vaynei* is different from *P. dorsialta* on the basis of a shorter first dorsal fin ray and shorter dorsal fin length. *P. vaynei* differs from *P. praelonga* by the number of lateral line scales (70-81 for the former and 91-111 for the latter).

***Poecilopsetta zanzibarensis* Norman, 1939**

Figures 52, 53; Tables 7, 8

Poecilopsetta zanzibarensis: Norman, 1939, The John Murray expedition 1933-1934 Scientific reports, p. 102-103. Quéro *et al.* 1988, Cybium 12(4): 329.

Common name: Zanzibar mottled flounder

Holotype.-**BMNH 1939.5.24:1785-1792**; Zanzibar area, St. 106; 183-194 m; 101.7 mm SL.
Paratypes.- **BMNH 1939.5.24:1785-1792**; same as holotype; 8: 71.4-97.8 mm SL. **BMNH 1939.5.24:1777-1784**; Zanzibar area, St. 105; 238-293 m; 9: 70.9-99.6 mm SL. **BMNH 1939.5.24:1793**; Zanzibar area, St. 107; 421-457 m; 1: 87.0 mm SL. **MNHN 1976-404**; Tanzania, John Murray Expedition; 1: poor condition. **USNM 109506**; Indian Ocean, Tanzania, Zanzibar area, sta. 106; 1: 71.8 mm SL.

Additional material: **ANSP 145374**; Indian Ocean; 2°56'S 40°28'E; vessel Anton Bruun, Cr. 8, St. 421G; 240 m; 8 Nov. 1964; 1: 69.6 mm SL. **ANSP 145608**; Indian Ocean; 2°50'S 40°31'E; 290 m, vessel Anton Bruun, cr. 8 St 421H; 8 Nov. 1964; 1: 70.2 mm SL. **RUSI 13781**; Kenya off Shimoni; 04°38'S 39°46'E, 9 Dec. 1980, 1: 69.0 mm SL. **RUSI 14045**, Kenya off Mombasa, 03°49'S 40°00'E, 11 Dec. 1980, 1: 84.2 mm SL. **RUSI 14113**; Kenya off Malindi; 03°11'S 40°38'E; 12 Dec. 1980; 3: 68.9-78.0 mm SL. **RUSI 43023**; off Kenya; 02°59'S 40°34'E; 12 Dec. 1980; 3: 86.0-97.0 mm SL.

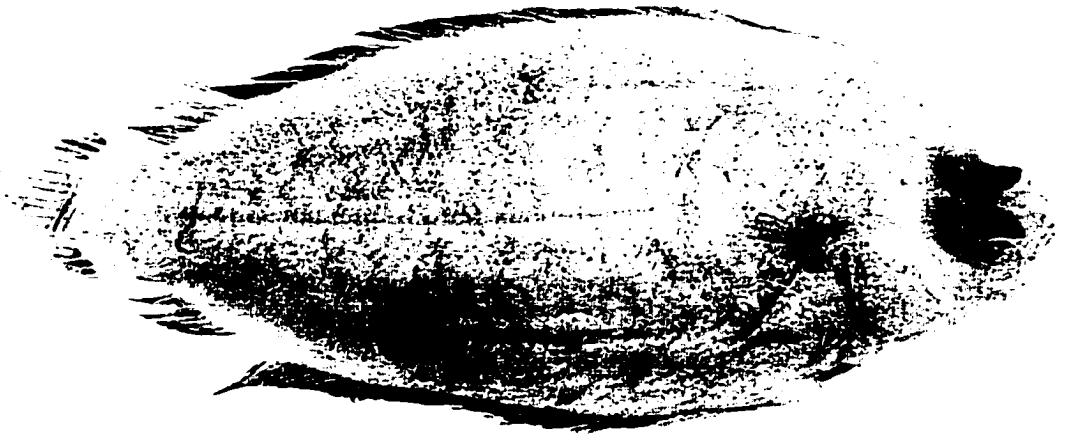


Fig. 52: *Poecilopsetta zanzibarensis*, paratype: BMNH 1939.5.24:1785-1792; 96.8 mm SL.

Diagnosis.-A species of *Poecilopsetta* with the following combination of characters: more than 83 lateral line scales, 32-33 caudal vertebrae, large band of muscles along the body and two spots at the base of hypural plates found toward the edges of the caudal peduncle.

Description.-Data are presented for the holotype and values for additional material are given in parentheses. A species of *Poecilopsetta* with a rather elongated body, large eyes separated by a narrow space, non-confluent dorsal, caudal and anal fins and subsymmetrical pelvic fin bases. Body depth (BD) 43.8% in SL (31.1-41.3%), head length (HL) 23.3% in SL (21.3-25.4%). Interorbital space scaled halfway. Snout, eyes and maxilla scaleless. Upper orbit 41.3% in HL (36.2-46.8%), encroaching on dorsal profile of head. Position of lower eye slightly anterior or equal to upper eye. Nostrils asymmetrical; those of blind side higher than on ocular side. Both anterior nostrils with skin flap covering the opening. On ocular side, posterior nostril a narrow opening above premaxilla just anterior to lower eye. Mouth oblique, symmetrical. Ocular side maxilla not reaching to vertical through anterior third of lower eye, 23.3% in HL (22.7-31.5%). Blind side maxilla almost symmetrical, 22.9% in HL (19.9-28.6%). Lower jaw symmetrical, ocular side 37.3% in HL (35.7-42.5%), blind side 37.1% in HL (36.1-43.3%). Conical teeth present on premaxillae and dentaries. Teeth in two to three (two to three) distinct bands on blind side dentary and premaxilla. Two (one to two) rows of teeth on ocular side dentary and premaxilla. Gill rakers longer than wide and not serrated, 7 (5-8) on upper limb and 10 (9-12) on lower limb. Branchial septum entire. Lateral line with strong arch over pectoral fin, width of arch 17.3% in SL (15.5-19.2%), height of arch 24.5% in BD (18.8-27.0%), 97 (90-101) ctenoid scales on lateral line. No lateral line on blind side. Ocular side pectoral fin with 11 (8-11) rays, none (1-2) branched rays, length 43.3% in HL (19.9-52.1%). Blind side pectoral fin with 9 (8-11) unbranched rays, length 44.7% in HL (17.1-47.8%). Pelvic fins with 6 rays. Ocular side pelvic fin 40.2% in HL (32.3-45.7%), blind side (36.6-45.6%) in HL. No branched rays in pelvic fins. Origin of dorsal fin over upper eye, first ray over posterior half of upper eye. Dorsal fin with 62 (59-64) rays, first ray 35.4% in HL (18.9-45.0%). Longest dorsal fin-ray 43.9% in HL (37.5-51.2%). Anal fin with 51 (48-55) rays, longest ray 43.8% in HL (33.2-52.6%). Dorsal and anal fin rays unbranched. Pelvic fins

almost symmetrical, origin of ocular side fin slightly anterior to that of blind side. Blind side pelvic fin origin at level of second or third ray of ocular side pelvic fin. Dorsal, anal, pectoral and pelvic fins scaleless. Twenty caudal fin rays, 14 medial rays branched. Ten precaudal vertebrae, 32 (32-33) caudal vertebrae. Small ctenoid scales on ocular side. Cycloid scales on blind side. Anus on midventral line. Cone-shaped urinary papilla on ocular side between anus and anal fin.

Coloration in ethanol.-Ocular side evenly brown. Dorsal and anal fins light brown. Ocular side pectoral fin with dark pigment on the lower rays. Ocular side pelvic fin light brown. Caudal fin with two dark spots on upper and lower margins. Blind side creamy white with small dark spots.

Etymology.-From the latin *zanzibarensis*. The specific name refers to the type locality, Zanzibar.

Distribution.-*Poecilopsetta zanzibarensis* is distributed along the eastern coast of Africa from Tanzania to Somalia (Fig. 53). This species is known to occur at depths between 183-457 m.

Remarks.-*Poecilopsetta zanzibarensis* was found with *P. normani* in some collections. Many characters differentiate *P. normani* from *P. zanzibarensis*: lateral line scales (90-101 for *P. zanzibarensis*, 110-133 for *P. normani*), ocular side pectoral fin rays (8-11 for *P. zanzibarensis* and 13-17 for *P. normani*), blind side pectoral fin rays (8-11 for *P. zanzibarensis* and 11-15 for *P. normani*) and the length of the ocular side pectoral fin (1.92-5.02 for *P. zanzibarensis* and 1.43-1.75 for *P. normani*). *P. zanzibarensis* is different from *P. natalensis* by: the number of caudal vertebrae (32-33 for *P. zanzibarensis*, 27-31

for *P. natalensis*), lateral line scales (90-101 for *P. zanzibarensis*, 77-83 for *P. natalensis*) and coloration around the eyes (absent in *P. zanzibarensis* and present in *P. natalensis*). *P. zanzibarensis* also has fewer branched rays (often none but occasionally one or two) in the ocular side pectoral fin than *P. natalensis* (7-10).

P. zanzibarensis is closer to *P. praelonga* although both species were never seen in the same lots. These two species are not known to be sympatric. *P. zanzibarensis* differs from *P. praelonga* by the number of caudal vertebrae (32-33 for *P. zanzibarensis* and 30-32-usually 30-31- for *P. praelonga*), by the position of black spots at the base of hypural plates (near edges in *P. zanzibarensis*, near the mid-line for *P. praelonga*), and by the larger band of muscles in *P. zanzibarensis* (in *P. praelonga* the pterygiophore zone without muscles is larger).

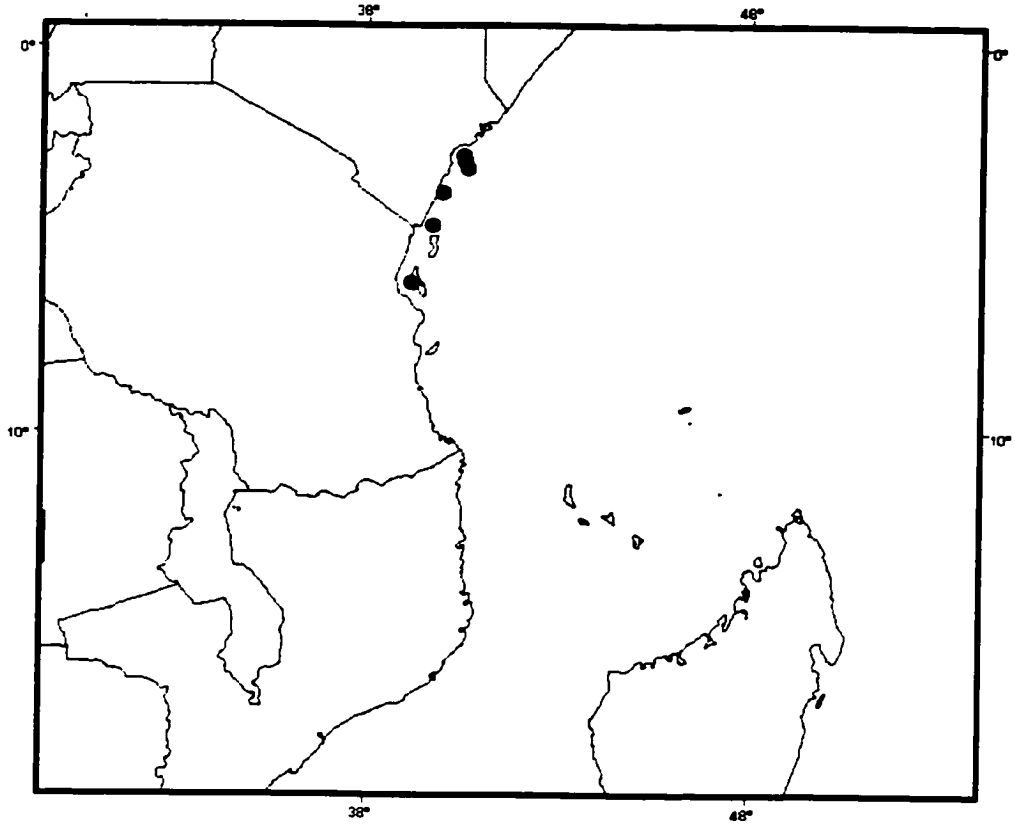


Fig. 53: Collection sites of *Poecilopsetta zanzibarensis*.

Poecilopsetta sp.

Figures 54, 55; Table 18

Material: **AMS I.27228-001**; Southeast of Broken Bay, NSW; 33°39'S 151°55'E; 369-402 m; 23 Dec 1986; 1: 71.1 mm SL.

See the general description of larvae in the section about *P. beanii* for the location of the different lines on the ocular and blind sides.

Coloration of the larva of *P. sp.*- On the ocular side (Fig. 54), line 1 and line 2 have seven spots, line 3 and line 4 have five spots. We can see faint circles along the body, above line 2 there are three dark blotches and below line 3 there are four. There is a spot at the base of the caudal peduncle followed by two at the tip of the caudal peduncle. These spots are also seen on the blind side.

On the dorsal fin, few rays are black distally. These blackened rays are found between two consecutive spots of the first row. On the anal fin, there are also a few rays with black tips and those blackened rays are found over the spots of the last row when the fin is closed or folded against the body. On the caudal fin, most rays have black tips, forming a black V on the fin (Fig. 54). The tips of the pelvic fin rays are black.

In the abdominal region there are five spots, one approximately in the middle of this section of the body and the others near the base of the body. One is near the opening of the anus, one almost at the base of pelvic fins, a third one at the level of the first anal fin ray but slightly higher than the fin and a fourth one at the same level of the third one but on top of the abdominal cavity.

The head of the larva has a slight variation to the basic pattern of spots for the genus: one is found over of the upper eye, two are found on the snout, one at the tip of the snout and another just over the upper jaw, at the level of the nasal organ. One spot is found caudal to the neurocranium on the mid-body line. There is one spot at the tip of the lower jaw and one on the retroarticular. Another spot is found at the curve in the preopercular bone. The last spot on the head is found on the branchiostegal membranes.

On the blind side (Fig. 55), line A and B have seven spots, line C has six spots, line D has eight spots, line E has six spots and line F has five spots.

In the abdominal region on the blind side, there are seven spots all distributed on the intestines (which are easily seen through the transparent body wall). One spot is

found high on the abdominal cavity, two are found in the middle of the cavity with one in the centre and the other to its right at the edge of the abdomen. The other spots are found on the ventral portion of the cavity, two are near the opening of the anus and two are near the base of the pelvic fins.

Few spots are found on the head: one is found at the tip of the snout (same as ocular side), one is on the upper jaw at the level of the nasal organ, one is found at the tip of the mouth and one is found at the corner of the mouth. One spot is found at the curve of the preopercular bone and one faint spot is found to its right. One spot is found on the branchiostegal membranes.

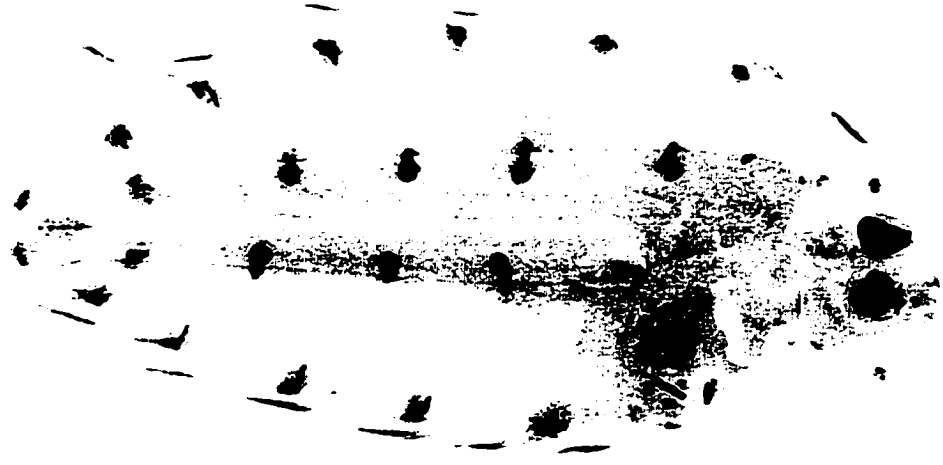


Fig. 54: Ocular side of larvae of *Poecilopsetta sp.*; AMS I.27228-001; 71.1 mm SL.

Fig. 55: Blind side of larva *Poecilopsetta sp.*: AMS I.27228-001; 71.1 mm SL.

Table 18: Morphometric and meristic characters of *Poecilopsetta sp.* AMS I.27228-001.

For abbreviations see Tables 3 and 11.

Measurements	Larva
SL	71.1 mm SL
In SL	
HL	4.58
BD	2.19
In HL	
UO	2.99
UJO	2.98
UJB	3.11
LJO	2.26
LJB	2.25
PelOS	2.01
PelBS	2.26
HDR	1.74
FDR	1.88
HAR	1.73
Meristic characters	
Dorsal fin rays	59
Anal fin rays	52
Gill rakers	11-11
Caudal vertebrae	32

Remarks.-This specimen cannot be identified to a particular species of the genus *Poecilopsetta* but there is no doubt this specimen belongs to this genus. The similarities between this larva and larvae described earlier in this work (see sections on *P. beanii*, *P. colorata*, *P. hawaiiensis*, *P. inermis* and *P. praelonga*) are numerous and seem to indicate that this specimen is in fact from the genus *Poecilopsetta*. Furthermore, in the genus *Nematops*, for which no larvae are known, specimens of the size of this larva (71.1 mm SL) are adults with functional gonads. The fishes of the genus *Nematops* are generally smaller than the fishes of the genus *Poecilopsetta* and this could mean that their larval stage are much shorter than the ones in *Poecilopsetta*. For the genus *Marleyella*, no larvae are known but species in this genus are found only in the Indian Ocean mainly off the coast of Africa.

This larva was collected off New South Wales in the Pacific Ocean, in an area where only *P. plinthus* is known to occur. When we compare the larva of *P. sp.* with *P. plinthus* (Tables 13, 14, 18) we can see they are very similar but two specimens of *P. plinthus* are the size of this larva. These two specimens are no longer larvae, they have their adult coloration this suggests that *P. plinthus* does not have a long larval stage. Also, the number of gill rakers on the first arch is higher for the undetermined larva than for *P. plinthus*. For these reasons, the larva does not belong to the species *P. plinthus*, the only poecilopsettid species found in New South Wales, Australia.

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Chapter 2

Monophyly and interrelationships of the family Rhombosoleidae and new phylogeny for the order Pleuronectiformes.

The family Rhombosoleidae (Pleuronectiformes) (*sensu* Cooper and Chapleau, 1998a) includes 19 species in nine genera (see body outlines in Appendix 2) found mainly in temperate waters around Australia and New Zealand, with one genus (*Oncopterus*) in the Atlantic Ocean near South America and one genus (*Psammodiscus*) found in the warm waters of the Indo-Pacific (Norman, 1934). Norman's classification was:

Genus *Oncopterus* (*O. darwinii* Steindachner, 1874)

Genus *Psammodiscus* (*P. ocellatus* Günther, 1862)

Genus *Azygopus* (*A. pinnifasciatus* Norman, 1926)

Genus *Pelotretis* (*P. flavilatus* Waite, 1911)

Genus *Ammotretis* (*A. rostratus* Günther, 1862; *A. brevipinnis* Norman, 1926; *A. lituratus* (Richardson, 1844); *A. macrolepis* McCulloch, 1914 and *A. elongatus* McCulloch, 1914)

Genus *Colistium* (*C. nudipinnis* (Waite, 1911) and *C. guntheri* (Hutton, 1873))

Genus *Peltorhamphus* (*P. novaezeelandiae* Günther, 1862)

Genus *Rhombosolea* (*R. retiaria* Hutton, 1873; *R. plebeia* (Richardson, 1843); *R. leporina* Günther, 1862 and *R. tapirina* Günther, 1862)

Three species and one subspecies were described after Norman's publication: *Azygopus pinnifasciatus flemingi* Nielsen, 1961; *Peltorhamphus latus* James, 1972; *P. tenuis* James, 1972 and *Taratretis derwentensis* Last, 1978.

In the Rhombosoleidae, the asymmetry of the pelvic fins is spectacular: the ocular side pelvic fin is long and sometimes reaches the space between the dentaries (i.e., *Ammotretis* and *Colistium* particularly). In some species (*Rhombosolea spp*), the asymmetry is highlighted by the absence of the blind side pelvic fin. These fishes, although not very large (maximum length near 400 mm), are of commercial value (Phillipps, 1925; Ayling and Cox, 1982) and their flesh is highly appreciated due to its fine taste (Manikiam, 1969; Scott *et al.*, 1980; Last *et al.*, 1983). According to Manikiam (1969), 7.24 % of all fish landed in New Zealand, in 1967, were rhombosoleids. According to the New Zealand Ministry of Fisheries, in the past ten years, the landings of flatfishes in New Zealand have exceeded 4500 t. In 1998-1999, the landings dropped to 3700 t with a record low of 2963 t reached in 1999-2000. The flatfish fisheries slightly recovered in 2000-2001 with catches of 3100 t.

In addition to the listing of New Zealand species in handbooks and in reports from trawling expeditions (Waite, 1911; Manikiam, 1969; McDowall, 1978), rhombosoleids have been the subject of many studies. These studies dealt mainly with the determination of life history traits and the general ecology of some species. Thus, spawning, fecundity, egg development, size at maturity and growth are well documented for two New Zealand species: *Rhombosolea plebeia* and *R. leporina* (Robertson and Raj, 1971; Colman, 1972b; 1973; 1974b; Smith *et al.*, 1980; Eldon and Smith, 1986; Francis, 1988). Movements of the same two species within the Hauraki Gulf in New Zealand were also studied (Colman, 1974a). Abnormal pigmentation and development (Graham, 1956; Colman, 1972a) and variation in fin ray counts were recorded for *R. plebeia* (Colman, 1976). This very useful information is usually not available for flatfishes, especially deep-sea species or those without economic value. Colman (1975) also described a juvenile specimen of *Colistium nudipinnis*. Graham (1956) studied the feeding behaviour, spawning, habitat and made a

myriad of observations for all New Zealand species (*C. nudipinnis*, *C. guntheri*, the four species of the genus *Rhombosolea*, *Pelotretis* and the only *Peltorhamphus* species known then, *P. novaezeelandiae*). Rapson (1940), Roper and Jillett (1981), Roper (1986) and Crossland (1982) have also published invaluable information on reproduction, growth, feeding, geographical distribution, and abundance of eggs and larvae of *Pelotretis* and on species of *Peltorhamphus* and *Rhombosolea*. Finally, Roper (1981) and Livingston (1987a and 1987b) studied the sensory organs and morphological specialisations associated with feeding. More recently, the literature has focused mainly on aquacultural issues with studies dealing with the impact of parasites on the growth of *Colistium nudipinnis* and *C. guntheri* (Diggles *et al.*, 2000; Diggles, 2000).

The literature on Australian rhombosoleids has mainly focused on their identification in field guides (Scott *et al.*, 1980; Last *et al.*, 1983; Allen and Swainston, 1988). The development and distribution of larvae, especially for *Rhombosolea tapirina* and *Ammotretis rostratus* (Crawford 1984, 1986; Jenkins, 1986, 1988), has also been studied. More recently, research has focused on reproductive biology and endocrinology (Barnett and Pankhurst, 1999; Hobby *et al.*, 2000), feeding (Shaw and Jenkins, 1992; Carter *et al.*, 1996), effects of salinity and temperature on eggs and larvae (Hart and Purser, 1995), and genetic variation and its implication in aquaculture (van den Enden *et al.*, 2000).

In historical publications on fish taxonomy, flatfishes were all grouped under the family Pleuronectidae. Jordan and Goss (1889) divided the family into seven subfamilies: Hippoglossinae, Pleuronectinae, Samarinae, Platessinae, Oncopterinae, Soleinae and Cynoglossinae. Jordan and Evermann (1898) elevated the family Pleuronectidae to the suborder level, Heterosomata, with two families: Pleuronectidae and Soleidae. The

foundation of the classification still in use nowadays originated with the work of Regan (1910) who elevated the suborder Heterosomata to the order level, created a new family within the order (Bothidae) and separated the Pleuronectidae into three subfamilies: Pleuronectinae, Samarinae and Rhombosoleinae. The Rhombosoleinae then consisted of four genera: *Ammotretis*, *Rhombosolea*, *Peltorhamphus* and *Oncopterus*. Norman (1934) added the genera *Psammodiscus*, *Azygopus*, *Colistium* and *Pelotretis* to the Rhombosoleidae and created a fifth subfamily: Poecilopsettinae.

Subsequently, Chabanaud (1946) recommended a familial ranking for Rhombosoleinae on the basis of three "highly important" characters: 1) asymmetry of the pelvic fins, 2) absence of radials in the pectoral fins and 3) absence of paired postcleithra associated with the pectoral fins. Chabanaud mentioned that Norman did recognise two of these characters (asymmetry of the pelvics and no radials) and even if he did not explicitly mention the third character, a drawing on p. 40 of his monograph clearly shows the absence of postcleithrum in *R. plebeia*. According to Chabanaud (1946), the last character (absence of postcleithrum) separated the soleids from the Pleuronectoidei, evidence not supported by Chapleau and Keast (1988). Furthermore, he indicated that the other two characters were shared between the soles and the rhombosoleids, supporting the elevation of the Rhombosoleinae to the familial ranking. Nonetheless, Chabanaud's recommendation has not been widely accepted. Sakamoto (1984), Nelson (1984; 1994) and Schwarzhans (1999), to name only three, have kept using the subfamilial ranking.

Phylogenetic studies dealing with flatfishes have focussed mainly on relationships at the familial and subfamilial levels (Lauder and Liem, 1983; Chapleau, 1993; Cooper and Chapleau, 1998a; Schwarzhans, 1999; Evseenko, 2000; Hoshino, 2001b).

Lauder and Liem (1983) published the first cladogram of flatfish relationships. They presented their cladogram as a tentative hypothesis of relationships based only on a

few, mostly reductive, characters. They concluded that more studies were needed to elaborate a stronger hypothesis of relationships within the Pleuronectiformes.

Hensley and Ahlstrom (1984) published a summary of all known phylogenetically informative characters for flatfishes. This work was the first one to raise doubts on the monophyly of certain groups and to question the historical assemblages. They were the first to question the grouping of the genera *Mancopsetta* and *Achiropsetta* (circumantarctic left-eyed flatfishes) into the Bothidae. These two authors observed some similarities between *Mancopsetta* and *Achiropsetta* and the Rhombosoleidae, especially with the genus *Azygopus*. They hypothesised that *Mancopsetta* and *Achiropsetta* might be closely related to the Rhombosoleidae. It is important to note that they did not perform a formal cladistic analysis, but had set the stage for the analysis of Chapleau (1993).

Chapleau and Keast (1988) in an article on the family Soleidae suggested that the subfamilies within the Pleuronectidae be raised to the familial level. The study of Chapleau (1993) was the first cladistic analysis dealing solely with the Pleuronectiformes. Its goal was to assess the monophyly of the order Pleuronectiformes and to obtain a hypothesis of relationships within the order using all available information. He produced a cladogram describing familial and subfamilial relationships within the order (see appendix 1). In his cladogram, a node at the base of lineage IV showed unresolved relationships between two subfamilies: Rhombosoleinae and Poecilopsettinae.

The taxonomic change proposed by Chapleau and Keast (1988) (i.e., elevation of the subfamilies of the Pleuronectidae to familial rank) was adopted by Cooper and Chapleau (1998a) in their revised hypothesis of relationships within the order (see Appendix 1) and by others since (Hoshino, 2001a and 2001b). Revised versions of Chapleau's (1993) work have been published adding taxa that were not available to Chapleau. Cooper and Chapleau (1998a) included the Paralichthodidae and Evseenko (2000) added the Achiropsettidae.

Later, Schwarzhans (1999) looked at otolith morphology to clarify the relationships between pleuronectiform genera. No formal analyses were performed, his classification was based on otolith morphology and on a combination of previously published phylogenies, some of them built using an eclectic approach (a mix of plesiomorphies and apomorphies). Schwarzhans (1999) split the Rhombosoleidae into five groups, two of which made up the new Rhombosoleidae (*Pelotretis* group and *Rhombosolea* group). The genus *Azygopus* was grouped with the Samarinae, *Peltorhamphus* was placed within the soleids and a fifth group included genera *Ammotretis*, *Colistium*, *Oncopterus*, *Psammodiscus* and *Taratretis* which were removed from their original subfamily and are thought to be primitive within the order. Although the monophyly of the Rhombosoleidae has never been tested using a cladistic approach, this group has always been thought to be an assemblage of closely related genera.

Hoshino's (2001b) analysis provided a cladistic analysis of the family Citharidae with a revised data matrix to determine relationships within the order (Fig. 1). Some characters used in his analysis were from Chapleau (1993) and others, such as myological characters, were new. He corroborated the monophyly of the Citharidae and provided a hypothesis of relationships between the Rombosoleidae and Poecilopsettidae (Hoshino, 2001b).

Finally, Berendzen and Dimmick (2002) presented the first hypothesis of relationships between the members of the Pleuronectiformes based on molecular evidence. However, this article is of little relevance to this study since no rhombosoleid or achiropsettid were included in the analysis. Moreover, no formal changes to flatfish classification were suggested due to the preliminary nature of the analysis.

Few attempts have been made at defining interrelationships within the Rhombosoleidae. Sakamoto (1984) published a phenogram depicting the relationships (based on 78 morphological characters) between the species of the family Pleuronectidae.

In Sakamoto's study, the Rhombosoleidae are represented by 11 species from six genera and some very interesting osteological information on the rhombosoleids is presented. His results, although not cladistic in nature, showed the Rhombosoleidae (without *Psammodiscus*, *Colistium* and *Oncopterus*) to be a group that shared many similarities (see Appendix 1). Since the aim of a phenetic study is to assess relationships based on overall similarities (Wiley, 1981) without any particular attempt at defining genealogical descent, the monophyly and a hypothesis of inter- and intrarelationship for the Rhombosoleidae remains to be formulated.

The Achiropsettidae are a small group of poorly known circumantarctic left-eyed flatfishes from the marine waters of South America, South Africa, and New Zealand (Evseenko, 2000). The taxonomy of this family (*sensu* Evseenko 1984) is still a matter of controversy (see Evseenko, 2000). To date, five genera have been described with most of them being monotypic with the exception of *Achiropsetta* and *Mancopsetta* (Eschmeyer *et al.*, 1998). According to Evseenko (2000) the Achiropsettidae should include only four monotypic genera: *Achiropsetta* (*A. tricholepis* Norman, 1930); *Mancopsetta* (*M. maculata* (Günther, 1880)); *Pseudomancopsetta* (*P. andriashevi* Evseenko, 1984) and *Neoachiropsetta* (*N. milfordi* (Penrith, 1965)). All of these species share one key characteristic: the absence of pectoral fins. *Mancopsetta* should be the type genus of the family because it was described earlier but Evseenko (1984) suggested that the type genus of the family should be *Achiropsetta*, a name reflecting their shared apomorphy.

The phylogenetic relationships of this family within the order have also always been uncertain. Norman (1934) included the two genera known at the time (*Mancopsetta* and *Achiropsetta*) in the subfamily Bothinae (Bothidae), a group of left-eyed flounders. Hensley and Ahlstrom (1984) doubted Norman's inclusion of *Mancopsetta* within the Bothidae. Based on caudal fin morphology, the absence of intramuscular bones, the presence of one

free epural, the position of the anus on the midventral line, the absence of vertebral transverse apophyses and the number of rays in the ocular side pelvic fin, they removed *Mancopsetta* from the bothids. They even considered the possibility that *Mancopsetta* could be closely related to the Rhombosoleidae, the two perhaps forming a monophyletic group. Their hypothesis was based on similarities observed between some species of the Rhombosoleidae and *Mancopsetta*. No cladistic analysis was performed and the highlighted similarities were ignored by subsequent authors (Schwarzhans, 1999) or were considered evidence of parallel evolution between the two taxa (Evseenko, 1996).

Evseenko (1984, 1996) suggested that the Achiropsettidae were a transitional group between the Citharidae (*sensu* Hubbs, 1945) and the Paralichthyidae and Bothidae. This was never confirmed by a formal cladistic analysis. Furthermore, the characteristics used by Evseenko (1984, 1996) to define the phylogenetic status and monophyly of the Achiropsettidae were a mix of plesiomorphic and apomorphic characters.

Schwarzhans (1999) found the general appearance of *Mancopsetta* otoliths to be similar to otoliths of a number of other "aberrant bothids", consequently, he kept *Mancopsetta* as a member of the Bothidae.

In his third attempt (see Evseenko 1984, 1996) to clarify achiropsettid relationships within the Pleuronectiformes, Evseenko (2000) used the data matrix of Chapleau (1993) to reassess the phylogenetic status of the Achiropsettidae. Although he did not perform a formal cladistic analysis, Evseenko's results showed the Achiropsettidae to be the sister-group of Chapleau's lineage V (see Appendix 1). The clade including the Achiropsettidae has either Poecilopsettidae or Rhombosoleidae as a sister-group. This result was closer to Hensley and Ahlstrom's (1984) hypothesis than to previous hypotheses suggested by Evseenko himself (1984, 1996).

Using cladistic methodology, the monophyly of the Rhombosoleidae and a hypothesis of interrelationships of all species within the family will be elaborated using morphological characters. Also, the biogeography of the new monophyletic Rhombosoleidae will be discussed. Finally, a new hypothesis of interrelationships of the higher taxa within the Pleuronectiformes will be elaborated by adding new taxa to the data matrix of Hoshino (2001b) and taxa that had to be excluded from the newly defined Rhombosoleidae.

MATERIALS AND METHODS

Multiple analyses were performed to determine 1) the outgroups to be used in the analysis of interrelationships within the Rhombosoleidae, 2) the monophyly of the Rhombosoleidae, 3) the interrelationships between the species of a newly defined monophyletic Rhombosoleidae, and 4) the phylogenetic status of the genera no longer included in the family Rhombosoleidae. All analyses were performed with data matrices of morphological characters extracted from the literature and from observations made on specimens preserved in ethanol, radiographed or cleared and stained using the method of Goodchild (1981) (see list of materials examined following the conclusion). Analyses of the data matrices were performed with the branch and bound search option and the addition sequence option furthest of PAUP. vers. 4.0b10 (Swofford, 2002). Both ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation) character state optimisation were used for all analyses. The ACCTRAN optimisation places the ambiguous character closer to the root of the tree whereas the DELTRAN optimisation places the ambiguous character further from the root as possible (Kitching *et al.*, 1998). No differences were seen on tree topologies between both optimisations. Character mapping on the trees is from the ACCTRAN optimisation. Primary and secondary

outgroups were used in all analyses. A secondary outgroup (sister-group of a clade formed by the studied taxon and its sister-group) is used to determine character polarity when characters are autapomorphic in the primary outgroup (Winterbottom and Tyler, 1983; Godkin and Winterbottom, 1985). Institutional abbreviations follow Leviton *et al.* (1985) except INIDEP: Instituto National de Investigation y Desarrollo Pesquero, Mar del Plata, Argentina (Diaz de Astarloa, 1996).

Outgroup determination.-The most recent phylogenetic hypothesis of the order Pleuronectiformes was elaborated by Hoshino (2001b). His data matrix was made up of 45 characters (see Appendix 3), 17 of which were new. The other characters had been used by Chapleau (1993) to build the first phylogenetic hypothesis of relationships within the order Pleuronectiformes. Two taxa were added to Hoshino's data matrix, Paralichthodidae (*sensu* Copper and Chapleau, 1998a) and Achiropsettidae. This step was necessary to find the most up to date hypothesis of relationships within the order Pleuronectiformes. This new hypothesis was used to determine the outgroups needed for the determination of the monophyly of the Rhombosoleidae. In the data matrix (Table 19), the taxon Paralichthodidae was coded as 1 for characters: 2, 5, 10-13, 23, 24, 27, 33, 35-37 and 41. Characters 38 and 42-44 were coded "?". The other characters were coded as 0. For the Achiropsettidae (*sensu* Evseenko, 1984) characters 2-4, 6, 7, 9-13, 23, 24, 31, 32, 34-37, 41, 43 and 44 were coded as 1. Character 5 was coded as 0/1 to reflect the states seen in *Achiropsetta* and *Mancopsetta*, characters 14, 33, 38 and 42 were coded as 2 and character 30 was coded as "?". All other characters were coded as 0. Coding for characters 38, 42-44 for the family Achiropsettidae was extracted from Hoshino (2001a). Three character states were modified for the Rhombosoleidae in the original matrix: characters 3, 18 and 30 were coded 0/1 to reflect the variability within the family. Character 18 was coded as in Chapleau (1993), the character state for *Citharus* was

coded 0. Characters 6 and 11 were coded as in Chapleau (1993). The corrected apomorphic state for character 7 (ocular side infraorbitals) is one or two small bones or absent (as defined by Chapleau, 1993). Outgroups used were Psettodidae and a hypothetical plesiomorphic secondary outgroup. The character states for the secondary outgroup are seen in many perciform taxa believed to be the sister-group of the Pleuronectiformes (see Chapleau, 1993). Characters 5, 10, 14 and 27 were treated as ordered because the character states represent an evolutionary sequence.

Monophyletic Rhombosoleidae.-A preliminary analysis was performed using all 19 taxa of the family Rhombosoleidae. Outgroups chosen were Achiropsettidae, the most plesiomorphic taxon within the sister-group of the Rombosoleidae, and Poecilopsettidae (Fig. 56) was chosen as a secondary outgroup. Within the Achiropsettidae, *Mancopsetta* was chosen as the most plesiomorphic taxon (Evseenko, 2000). When both outgroups had different character states for the same character, the state found in the secondary outgroup was coded as 0 because it is the more plesiomorphic outgroup taxon. The analysis consisted of a data matrix of 87 characters. Characters 5, 6, 45 and A5-2 were ordered in the preliminary analysis because the character states represent an evolutionary sequence. For the description of the characters see Appendices 4 and 5.

Interrelationships.-A revised group of species were used in the analysis determining the interspecific relationships within the Rhombosoleidae. *Oncopterus*, *Psammodiscus* and both subspecies of *Azygopus pinnifasciatus* were found not to be within a monophyletic Rhombosoleidae (Fig. 57). They were removed from the final analysis determining the interspecific relationships of the Rhombosoleidae. Outgroups chosen were *Poecilopsettidae* and *Mancopsetta*. Sixty-eight morphological characters were kept from the original data matrix of 87 characters (see description in Appendix 4). The deleted

characters were autapomorphies and characters that did not show any variability once *Oncopterus*, *Psammodiscus* and *Azygopus* were removed. The analysis of the data matrix (Table 20) was performed with these multistate characters treated as ordered: 5,6 and 45. Bootstrap analysis (Felsenstein, 1985) of 1000 replicates was performed using the heuristic search option.

Status of *Psammodiscus*, *Oncopterus* and *Azygopus*.-After removing the genera *Psammodiscus*, *Oncopterus* and *Azygopus* from the Rhombosoleidae, their phylogenetic status within the order was determined. Hoshino's (2001b) modified data matrix (see above) was used to assess the status of the removed genera. The data matrix now consists of 21 taxa and 45 characters (Table 19). For *Psammodiscus*, characters 2,12-13, 23-24, 31-32, 34, 36, 37 and 41 were coded as 1, characters 14 and 33 were coded as 2, characters 25,38, 42-44 were coded as "?". All other characters were coded with 0. For *Oncopterus*, characters 2, 11-13, 23-24, 27, 29, 31-32, 34-37, 43 and 44 were coded as 1, characters 14, 33, 38 and 42 were coded as 2 and character 30 was coded with a "?". All other characters were coded with 0. Character states for 38, 42-44 of *Oncopterus* were taken from Hoshino (2001a). For *Azygopus*, character states for the 45 characters were incorporated with the Achiropsettidae in Hoshino's data matrix. Characters 6, 7 and 9 were coded 0/1 to reflect the variability within the new family. Coding in the data matrix of Hoshino (2001b) followed the coding adopted in the preliminary analysis used to determine the sister-group of the Rhombosoleidae (see above). Characters 5, 10, 14 and 27 were treated as ordered because they represent an evolutionary sequence. Outgroups used were Psettodidae and a hypothetical plesiomorphic ancestor (see Chapleau, 1993).

Table 19: Data matrix of 45 morphological characters and 21 taxa of the order Pleuronectiformes. See Appendix 3 for description of the characters. The ? represents character states that were impossible to determine.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Psettodidae	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Lepidoblepharon	0	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Citharus	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Citharoides	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Paracitharus	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Brachypleura	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1
Tephrinectes	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Scophthalmidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0	0	0	1
Paralichthyidae	0	1	0	0	2	0	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	1
Bothidae	0	1	0	0	2	0	1	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	1
Pleuronectidae	0	1	0	0	2	0	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	1
Poecilopsettidae	0	1	0	0	0	1	1	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	1
Rhombosoleidae	1	1	0/1	1	0	0	1	0	0	0	1	1	1	2	0	0	0	0/1	0	0	0	0	1
Samaridae	0	1	1	1	2	1	1	1	1	1	0	1	1	2	0	0	0	0	0	0	0	0	1
Achiridae	1	1	0	1	0	1	1	1	1	1	1	1	1	2	0	0	0	0	0	0	0	0	0
Soleidae	1	1	1	1	0	1	1	1	1	2	1	1	1	2	0	0	0	1	1	1	1	1	1
Cynoglossidae	1	1	1	0	0	1	1	1	1	2	1	1	1	2	0	0	0	1	1	1	1	1	1
Paralichthodidae	0	1	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1
Achiropsettidae	0	1	1	1	0/1	0/1	0/1	0	0/1	1	1	1	1	2	0	0	0	0	0	0	0	0	1
Oncopterus	0	1	0	0	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	1
Psammodiscus	0	1	0	0	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	1

	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Psettodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidoblepharon	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1
Citharus	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	0	1	0	0	1
Citharoides	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1
Paracitharus	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1
Brachypleura	1	0	0	0	0	1	1	0	1	0	0	1	1	0	1	1	1	0	1	0	0	1
Tephrinectes	1	1	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	0	1	1	0	0
Scophthalmidae	1	0	0	0	0	0	0	0	1	2	0	1	1	0	2	0	0	1	1	1	0	0
Paralichthyidae	1	1	0	0	0	0	0	1	1	2	0	1	1	0	2	0	0	1	2	1	0	0
Bothidae	1	1	0	0	0	0	1	1	1	2	0	1	1	0	2	0	0	1	2	1	0	0
Pleuronectidae	1	1	0	0	0	0	0	1	1	2	0	1	1	0	2	0	0	1	2	1	1	0
Poecilopsettidae	1	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0	0	1	2	1	1	0
Rhombosoleidae	1	1	0	0	0	0	0/1	1	1	2	1	1	1	1	2	0	0	1	2	1	1	0
Samaridae	1	1	0	0	0	0	1	1	1	2	1	1	1	1	2	0	0	1	2	1	1	0
Achiridae	1	1	1	1	1	0	0	0	1	2	1	1	1	1	2	0	0	1	2	1	0	0
Soleidae	1	1	1	2	1	1	0	1	1	2	1	1	1	1	2	0	0	1	2	1	1	0
Cynoglossidae	1	1	1	2	1	0	0	1	1	2	1	1	1	1	2	0	0	1	2	1	0	0
Paralichthodidae	1	0	0	1	0	0	0	0	0	1	0	1	1	1	?	0	0	1	?	?	?	0
Achiropsettidae	1	0	0	0	0	0	?	1	1	2	1	1	1	1	2	0	0	1	2	1	1	0
Oncopterus	1	0	0	1	0	1	?	1	1	2	1	1	1	1	2	0	0	0	2	1	1	0
Psammodiscus	1	?	0	0	0	0	0	1	1	2	1	0	1	1	?	0	0	1	?	?	?	0

Table 20: Data matrix of 68 morphological characters and 16 taxa of the family Rhombosoleidae plus two outgroup taxa. See Appendices 4 and 5 for explanation of the characters. The ? represents character states that were impossible to determine and – represents unapplicable characters.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Ammotretis brevipinnis	0	0	1	1	0	1	1	2	1	1	0	1	1	1	1	0	1	0	1	1	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1
A. elongatus	0	0	1	1	1	2	1	2	1	0	0	1	1	1	2	0	1	0	1	1	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1
A. lituratus	0	0	1	1	0	1	1	2	1	1	0	1	1	1	2	0	1	0	1	1	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1
A. macrolepis	0	0	1	1	0	2	1	2	1	0	0	1	1	1	1	0	1	0	1	1	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1
A. rostratus	0	0	1	1	1	1	1	2	1	0	0	1	1	1	1	0	1	0	1	1	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1
Colistium guntheri	1	0	1	1	1	2	2	2	1	0	?	1	1	0	2	0	?	?	0	1	1	0	0	0	0	0	?	?	1	1	0	?	1	1	1
C. nudipinnis	1	0	1	1	1	1	2	2	1	0	0	1	1	0	2	0	1	0	0	1	1	0	0	0	0	0	2	1	1	1	0	1	1	1	1
Pelotretis flavilatus	1	0	1	1	1	0	2	1	1	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	1	0	1	1
Peltorhamphus latus	1	1	1	1	1	0	2	3	2	0	1	1	1	1	0	0	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1
P. novaezeelandiae	1	1	1	1	1	0	2	3	2	0	1	1	1	1	0	0	1	0	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1
P. tenuis	1	1	1	1	1	0	2	3	2	0	1	1	1	1	0	0	1	0	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1
Rhombosolea leporina	1	1	1	1	2	0	2	1	2	0	0	1	1	1	0	0	1	1	0	0	1	1	1	1	0	0	1	2	1	1	1	1	0	1	1
R. plebeia	1	1	1	1	2	0	2	1	2	0	1	1	1	1	0	0	1	1	0	0	1	1	1	1	0	0	1	2	1	1	1	1	0	1	1
R. retiaria	1	1	1	1	2	0	2	1	2	0	0	1	1	1	0	0	1	1	0	0	1	1	1	1	0	0	1	2	1	1	0	1	0	1	1
R. tapirina	1	1	1	1	2	0	2	1	2	0	1	1	1	1	0	0	1	1	0	0	1	1	1	1	0	0	1	2	1	1	1	1	0	1	1
Taratretis derwentensis	0	0	1	1	0	0	2	1	0	0	0	0	1	1	1	0	1	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1
Outgroups																																			
Mancopsetta maculata	0	0	1	0	0	1	2	1	1	-	-	-	1	1	0	1	0	1	1	1	1	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0
Poecilopsetta	0	0	0	0	0	0	0	0	1	0	-	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
Ammotretis brevipinnis	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	1	0	1	1	1
A. elongatus	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	1	1	0	1	0	0	0	1	0	0	1	1	1	0	1	1	1
A. lituratus	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	1	0	1	1	1
A. macrolepis	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0	1
A. rostratus	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	1	0	1	1	0
Colistium guntheri	?	?	?	?	?	0	?	?	?	?	?	?	0	0	1	?	1	1	0	1	0	0	0	?	?	?	?	1	1	?	1	0	?
C. nudipinnis	1	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0
Pelotretis flavilatus	1	0	0	0	0	1	0	1	0	1	0	1	1	0	1	1	1	1	0	1	0	0	1	0	0	0	1	1	1	1	0	0	0
Peltorhamphus latus	1	1	1	0	0	0	1	1	1	1	1	1	0	0	1	1	1	1	0	1	1	0	1	0	0	1	1	1	1	1	1	1	0
P. novaezeelandiae	1	1	0	0	0	0	1	1	1	1	1	1	0	0	1	1	0	1	0	1	1	0	1	0	0	1	1	1	1	1	1	1	0
P. tenuis	1	1	0	0	0	1	1	1	1	1	0	1	0	0	1	1	0	1	0	1	1	0	1	0	0	1	1	1	1	1	1	1	0
Rhombosolea leporina	1	1	1	1	1	0	1	1	1	2	0	1	1	0	1	0	1	1	0	1	1	0	0	0	1	0	1	1	1	0	0	0	0
R. plebeia	1	1	1	1	1	0	1	1	1	2	0	1	1	0	1	0	1	1	0	1	1	1	0	0	1	0	1	1	1	0	0	0	0
R. retiaria	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	0	1	1	0	1	1	0	0	0	1	0	1	1	1	0	0	0	0
R. tapirina	1	1	1	1	1	0	1	1	1	2	0	1	1	0	1	0	1	1	0	1	1	1	0	0	1	0	1	1	1	0	0	0	0
Taratretis	1	0	0	0	0	0	1	1	0	2	0	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0
Outgroups																																	
Mancopsetta maculata	1	1	0	0	0	2	1	0	0	0	-	0	1	1	1	0	0	0	0	1	-	0	-	1	0	0	1	0	1	0	0	0	0
Poecilopsetta	0	0	0	0	0	0/1	0	0	1	0	-	0	1	1	0	0	0	0	0	0	0	0	0/1	0	0	0	0	1	0	0	0	0	0

RESULTS

Outgroup determination.-A preliminary analysis performed on Hoshino's modified data matrix revealed that the sister-group of the Rhombosoleidae is the clade formed by the families Achiropsettidae, Samaridae, Achiridae, Soleidae and Cynoglossidae (Fig. 56). Within this large clade the family Achiropsettidae is the most plesiomorphic. A representative of the family Achiropsettidae will be used as primary outgroup for the analysis assessing the monophyly of the Rhombosoleidae. The sister-group of the larger clade formed by Rhombosoleidae, Achiropsettidae, Samaridae, Achiridae, Soleidae and Cynoglossidae is the family Poecilopsettidae. A representative of the family Poecilopsettidae will be used as secondary outgroup in the analysis. Differences between this phylogeny and the one presented by Hoshino (2001b) will be discussed later (see phylogenetic status of *Psammodiscus* and *Oncopterus*).

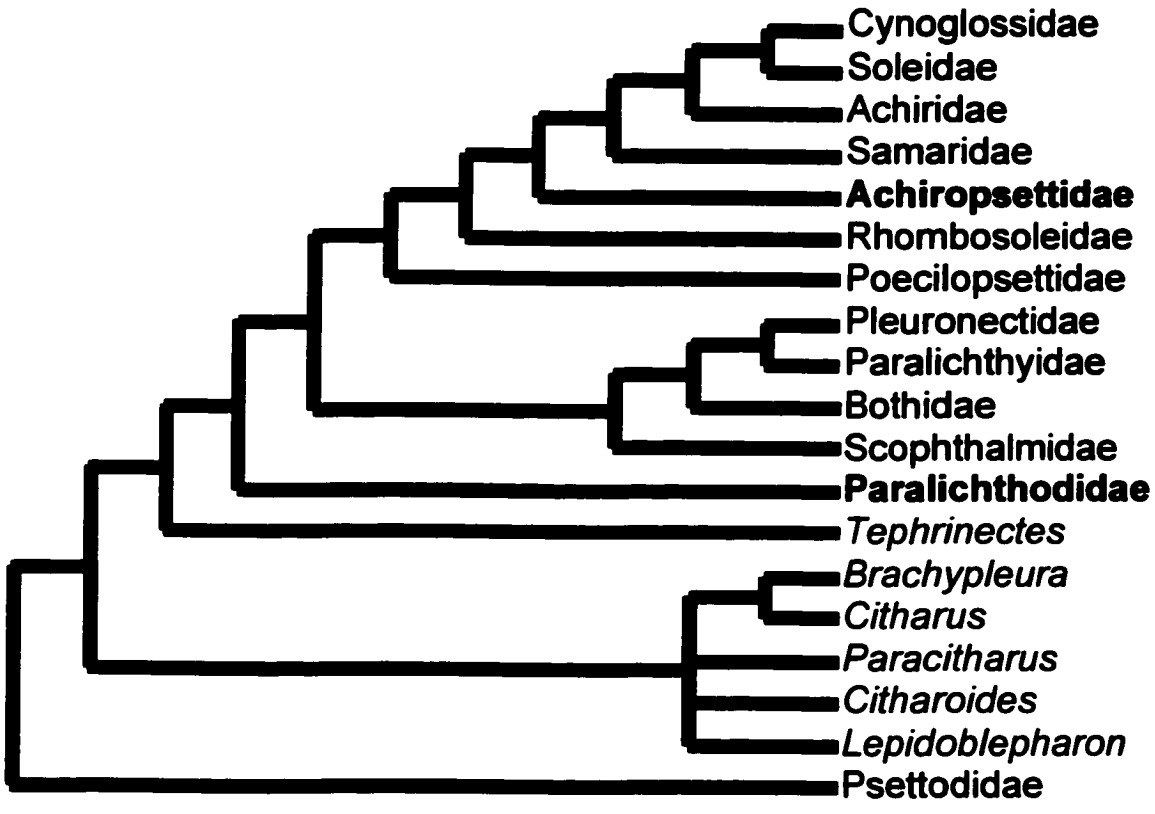

Fig. 56: Strict consensus tree of three most parsimonious cladograms representing the evolutionary relationships within the order Pleuronectiformes. Taxa Paralichthodidae and Achiropsettidae (*sensu* Evseenko, 1984) were added to the original data matrix. Consistency index (CI) =0.505, retention index (RI) =0.777, steps = 103.

Monophyletic Rhombosoleidae.-The result of the heuristic search performed on a data matrix of 87 morphological characters shows that the family Rhombosoleidae as described by Norman (1934) is not monophyletic (Fig. 57). *Oncopterus* and *Psammodiscus* are found within the outgroups and both subspecies of *Azygopus pinnifasciatus* are the sister-group of the primary outgroup *Mancopsetta*. These three former rhombosoleids are

removed from the analysis. Their status will be discussed later (see phylogenetic status of *Psammodiscus* and *Oncopterus*).

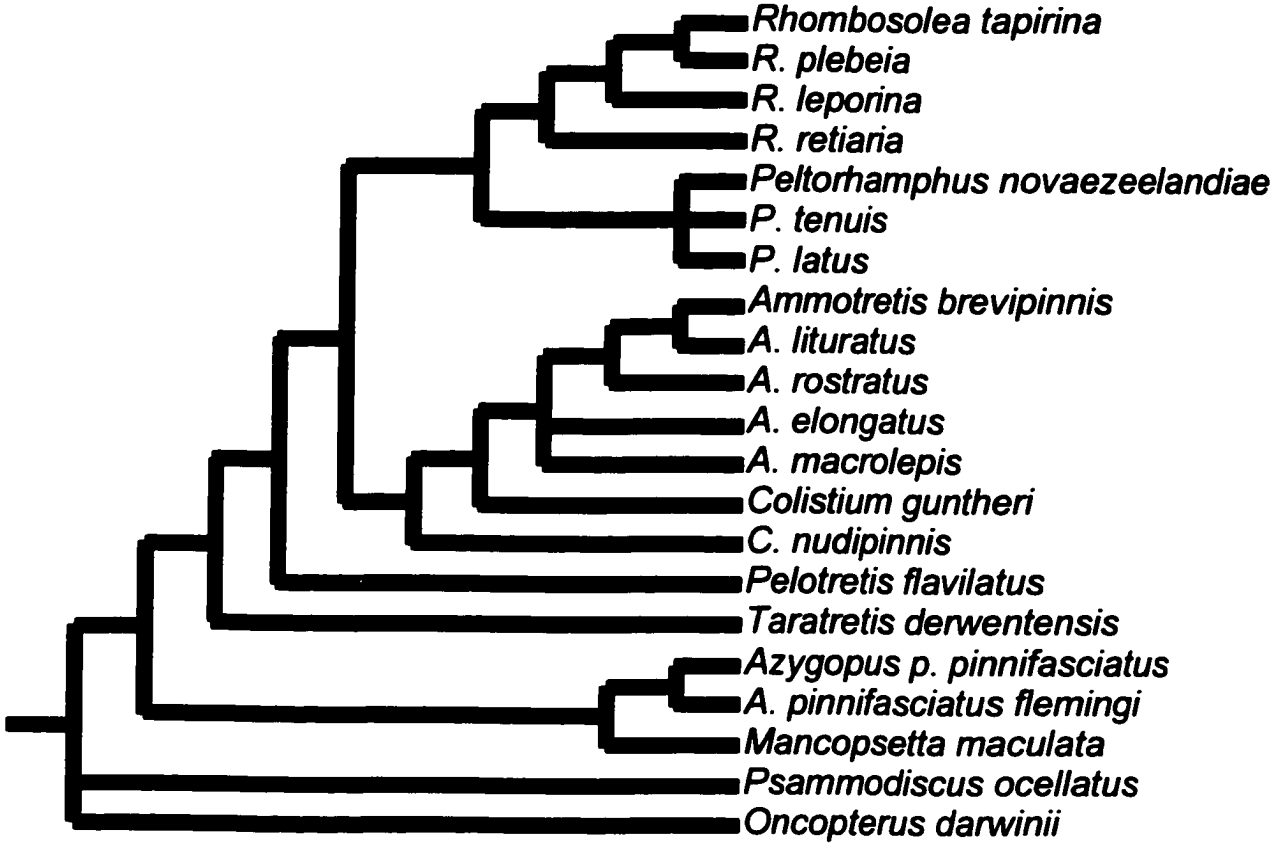

Fig. 57: Strict consensus tree of eight most parsimonious cladograms representing the evolutionary relationships within the family Rhombosoleidae. Consistency index (CI) =0.591, retention index (RI) =0.778, steps = 176.

Interrelationships.-The final analysis of the newly defined family Rhombosoleidae yielded 16 most parsimonious trees of 118 steps, consistency index (CI) = 0.669 and retention index (RI) = 0.813 (Fig. 58). The newly defined Rhombosoleidae (represented by clade A

on the tree), excluding *Psammodiscus*, *Oncopterus* and *Azygopus* are now monophyletic based on eight apomorphies and five homoplastic characters. The apomorphies defining the Rhombosoleidae are: ocular

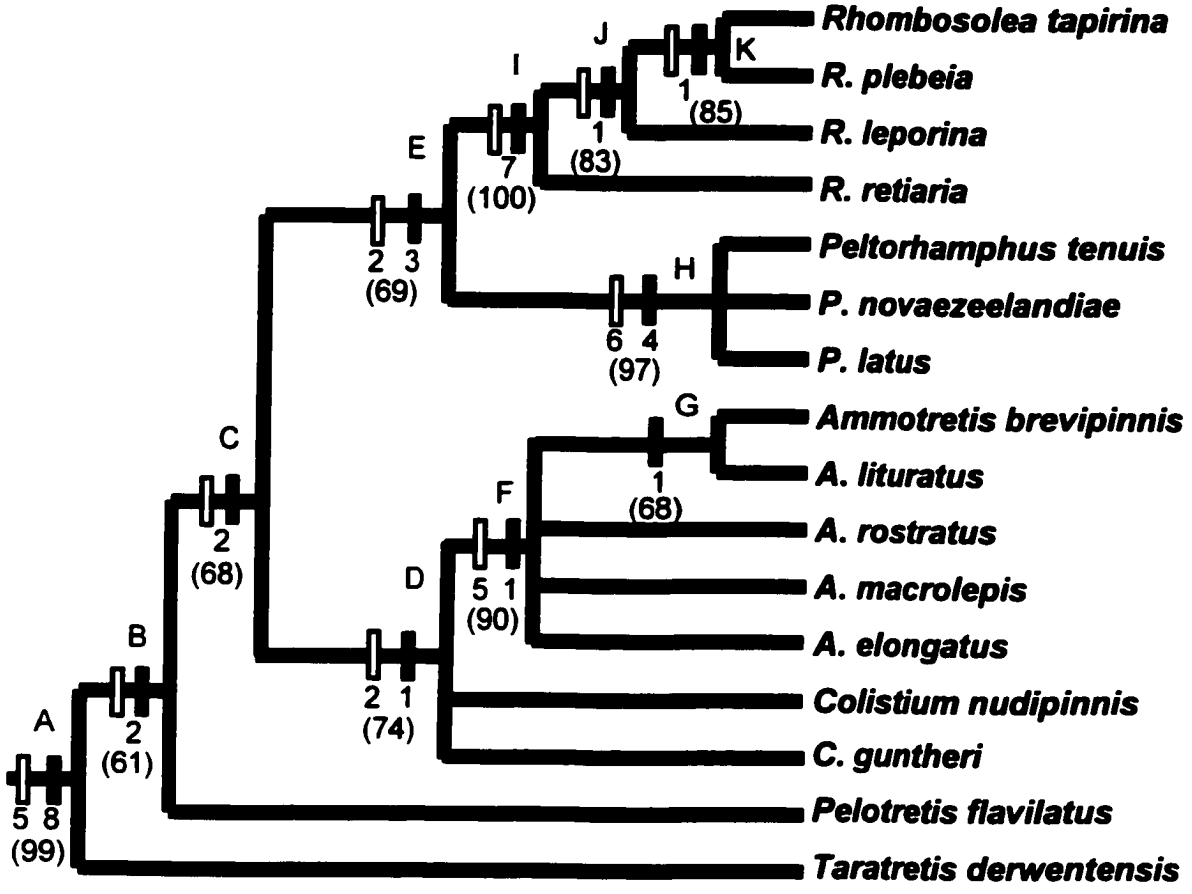

Fig. 58: Strict consensus of 16 equally parsimonious trees representing the relationships between the species of the family Rhombosoleidae. The black bar below the nodes and the number immediately below it represent the apomorphies and their number at each node, the white bar and the number immediately below it represent the homoplasies and their number at each node. The number in parentheses represents the bootstrap value (in %). The letters correspond to the clades in the text. Clade A apomorphies are: 4, 17, 32, 35, 43, 47, 49 and 53,

homoplasies are: 27, 28, 45, 48 and 52. Clade B apomorphies are: 29 and 34, homoplasies are 1 and 5. Clade C apomorphies are 12 and 30, homoplasies are: 33 and 66. Clade D apomorphy is 8, homoplasies are: 8 and 15. Clade E apomorphies are: 2, 9 and 56, homoplasies are: 37 and 44. Clade F apomorphy is: 7, homoplasies are: 1, 19, 46, 67 and 68. Clade G is supported by only one apomorphy: 10. Clade H apomorphies are: 8, 25, 26 and 61, homoplasies are: 11, 51, 52, 58, 65 and 67. Clade I apomorphies are: 20, 22-24, 39, 40 and 60. Clade J apomorphy is: 31 and homoplasy is: 45. Clade K apomorphy is: 57, homoplasy is: 11.

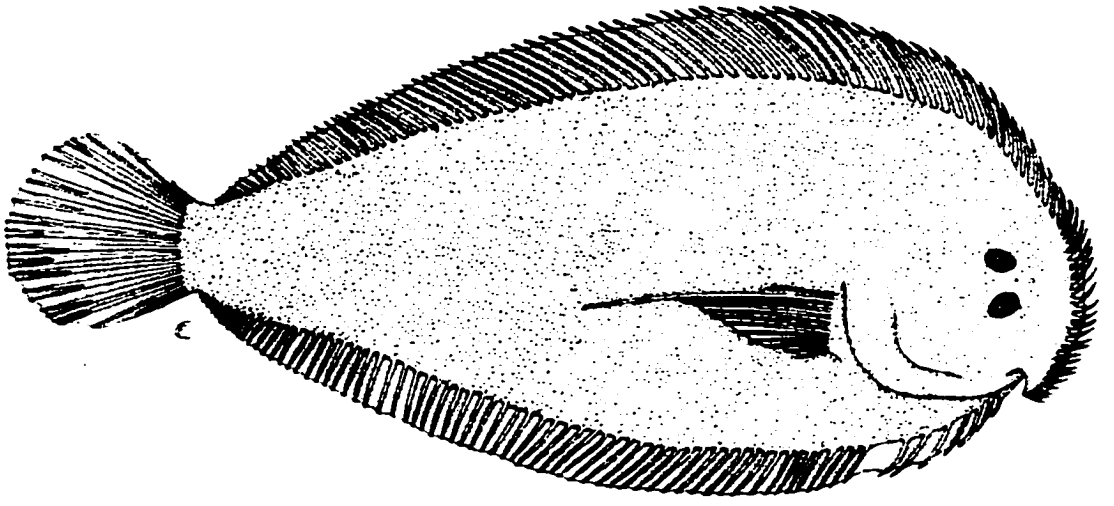

Fig. 59: *Peltorhamphus novaezeelandiae*.

side pelvic fin united to anal fin by a membrane (Character 4) (Fig. 59), absence of gill rakers on the second epibranchial bone (character 17) (Fig. 60), blind side dentary bone not elongated under the articular bone (character 32) (Fig. 61), none or small posterodorsal flange on the blind side articular bone (character 35) (Fig. 61), presence of a bony support on the supraoccipital and frontal bones for the support of dorsal fin

pterygiophores (character 43) (Fig. 62), presence of one or more bones in the sensory canal of the supratemporal branch (character 47) (Fig. 63), presence of orbital bones and lachrymal on the blind side (character 49), and sciatic portion of the urohyal bone is long and extends anteriorly in front of the main part of the bone (character 53) (Fig. 64). The homoplasies at this node are: the blind side nasal bone opening on both sides (character 27), the blind side nasal bone is y-shaped (character 28), one or more bones in the supratemporal section of the lateral line (character 45), one or two bones (excluding lachrymal) in the orbital series on the ocular side (character 48) and a sensory canal on the parietal bone on the blind side (character 52). Clearly, the Rhombosoleidae as defined in this study form a well-defined taxon.

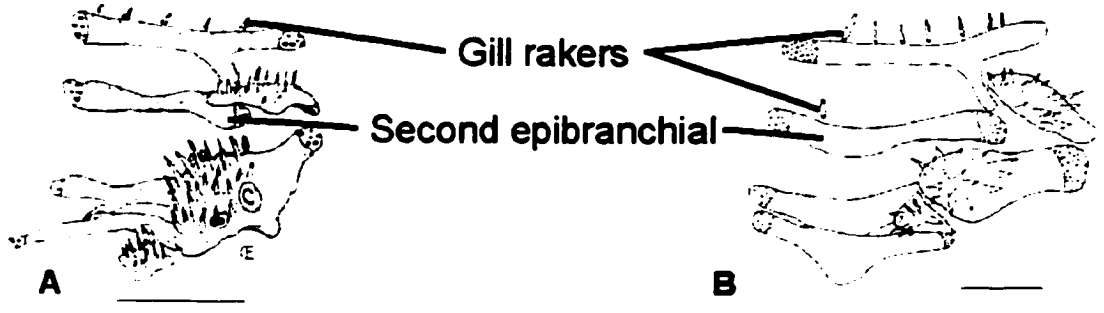

Fig. 60: Branchial bones of A) *Rhombosolea leporina* AMS I.27007-001, scale bar = 1 mm and B) *Mancopsetta maculata* MNHN 1985-968, scale bar = 2 mm.

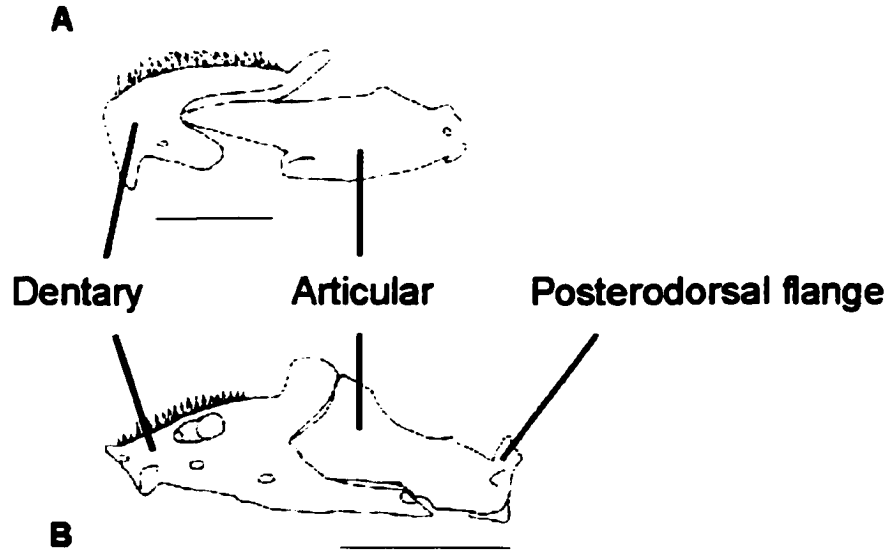

Fig. 61: Blind side jaw of A) *Ammotretis elongatus* AMS I.13207 and B) *Poecilopsetta hawaiiensis* ANSP 176079. Scale bars = 3 mm.

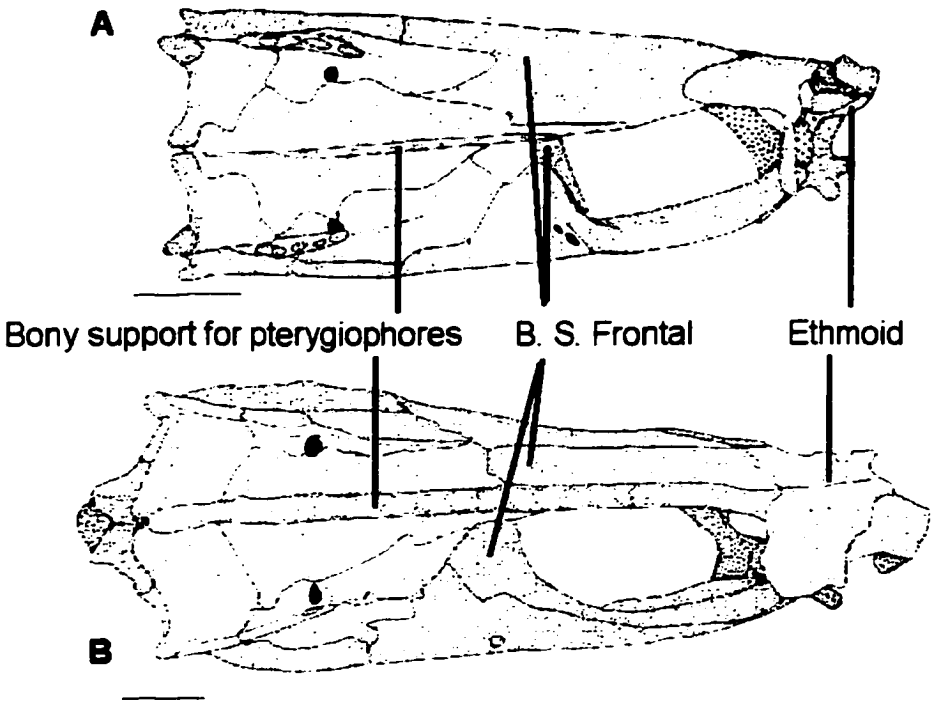

Fig. 62: Dorsal view of the cranium of A) *Rhombosolea leporina* AMS I. 27007-001, scale bar = 2 mm and B) *Peltorhamphus novaezeelandiae* NMNZ P.6118, scale bar = 3 mm.

Clade A is subdivided into *Taratretis* and clade B (Fig. 58). Clade B represents all other genera within the family. It is supported by two apomorphies and two homoplasies. The two apomorphies are: absence of teeth on the dentary on the ocular side (character 29) (Fig. 65) and a small or absent posterodorsal flange on the ocular side articular bone (character 34) (Fig. 65). The homoplasies at this node are: subdivided hypural plates (character 1) (Fig 68) and 3 or 4 blind side pelvic fin rays (character 5).

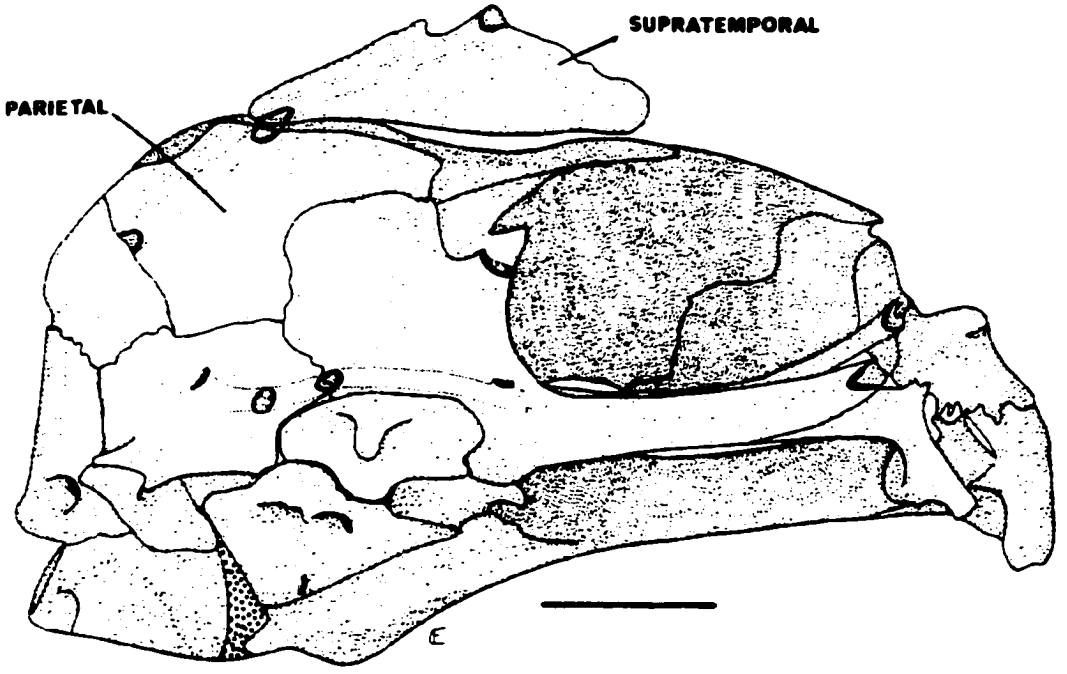

Fig. 63: Ocular side of the cranium of *Ammotretis lituratus* SAMA F.1933, scale bar = 2 mm.

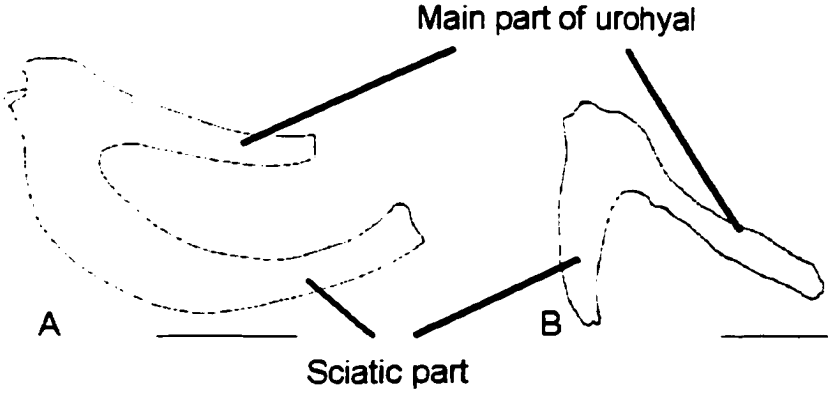

Fig. 64: Urohyal of A) *Rhombosolea leporina* AMS I.27007-001 and B) *Poecilopsetta hawaiiensis* ANSP 176079. Scale bars = 3 mm.

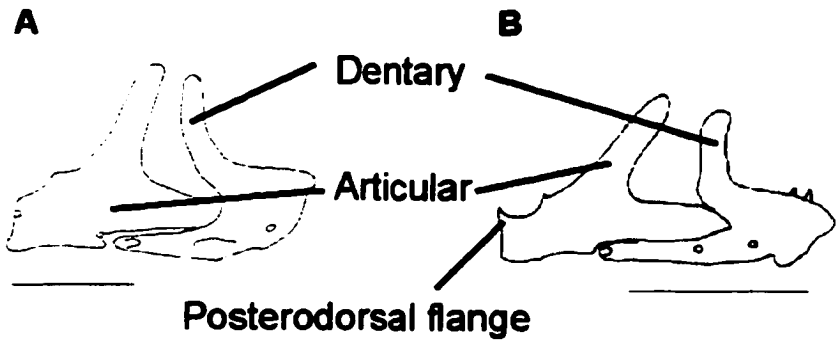

Fig. 65: Ocular side lower jaws of A) *Ammotretis elongatus* AMS I.13207 and B) *Taratretis derwentensis* CSIRO B.1525. Scale bars = 3 mm.

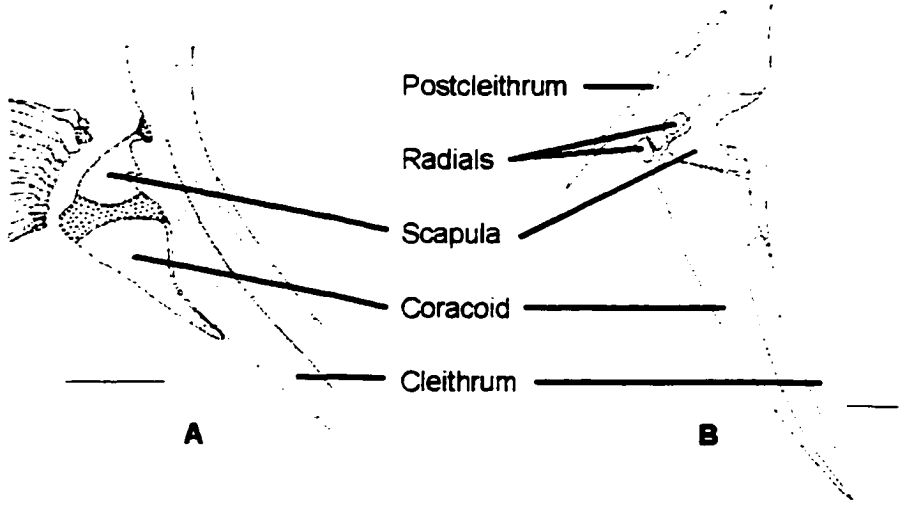

Fig. 66: Ocular side pectoral girdle of A) *Rhombosolea plebeia* ANSP 122857, scale bar = 2 mm and B) *Taratretis derwentensis* SAMA F.94, scale bar = 1 mm. Pectoral fin rays are present but not shown for *Taratretis*.

Clade B is divided into clade C and its sister-group, the monotypic genus *Pelotretis*. Clade C consists of the genera *Ammotretis*, *Colistium*, *Peltorhamphus* and *Rhombosolea*. This clade is defined by two apomorphies and two homoplastic characters. The

apomorphies are: a short coracoid without long ventral projection touching the cleithral bone for most of its length on the ocular side pectoral girdle (character 12) (Fig. 66) and 2) absence of a posterodorsal flange on the articular bone of the blind side (character 30) (Fig. 61). The homoplasies at this node are: asymmetrical lower jaws (character 33) and dorsal fin prolonged in front of the snout (character 66) (Fig. 59).

Clade C consists of two clades, the first clade (D) is made of *Ammotretis* and *Colistium*. Clade D is defined by one apomorphy and two homoplastic characters. The defining apomorphy of this clade is 15 to 23 pterygiophores over the cranium (character 8) (Fig. 67). The homoplasies at this node are: eleven or more ocular side pelvic fin rays (character 6) and long fringes on the ocular side lower lip (character 15). The sister-group of this clade is a clade (E) formed by the genera *Peltorhamphus* and *Rhombosolea*. This clade is supported by three apomorphies and two homoplasies. The apomorphies shared by these two genera are: fusion of hypural plates to the centrum of the last caudal vertebra (character 2) (Fig. 68), absence of postcleithral bone associated with the ocular side pectoral fin (character 9) (Fig. 66), and the absence of radials associated with both pectoral girdles (character 56) (Fig. 66). The homoplasies at this node are: absence of the pterosphenoid bone on the blind side (character 37) and occipital condyle formed by the zygapophyses of both exoccipitals and the basioccipital (character 44).

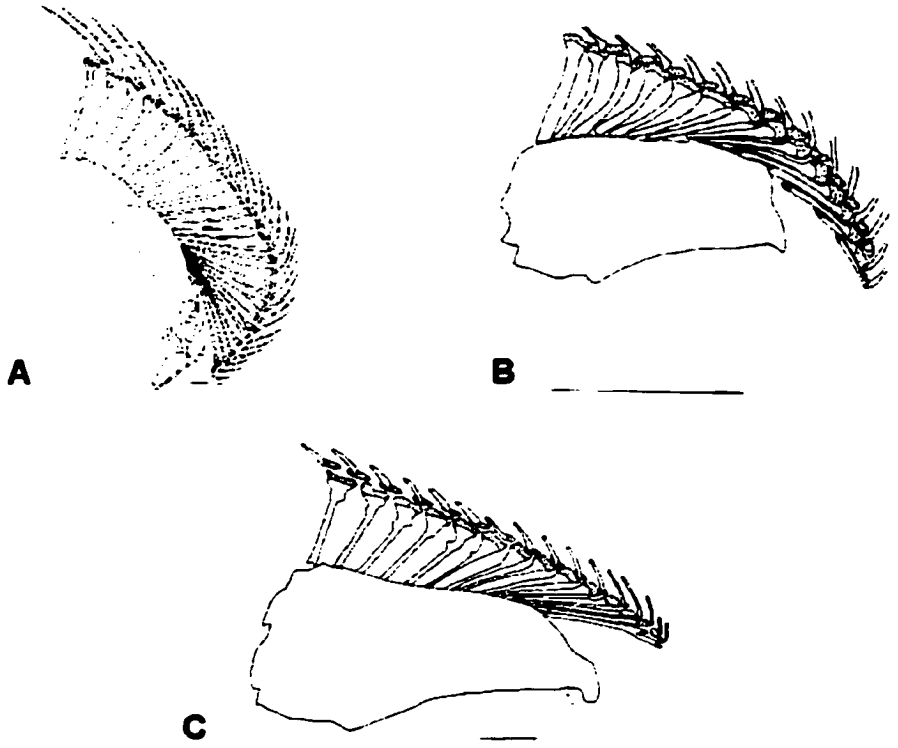

Fig. 67: Outline of the cranium and pterygiophores of the dorsal fin over the cranium. A) *Peltorhamphus novaezeelandiae* AMS I.14666-75 (27 pterygiophores), scale bar = 3 mm, B) *Colistium nudipinnis* NMNZ P.36914 (15 pterygiophores) scale bar = 5 mm and C) *Rhombosolea leporina* AMS I. 27007-001 (14 pterygiophores), scale bar = 2 mm.

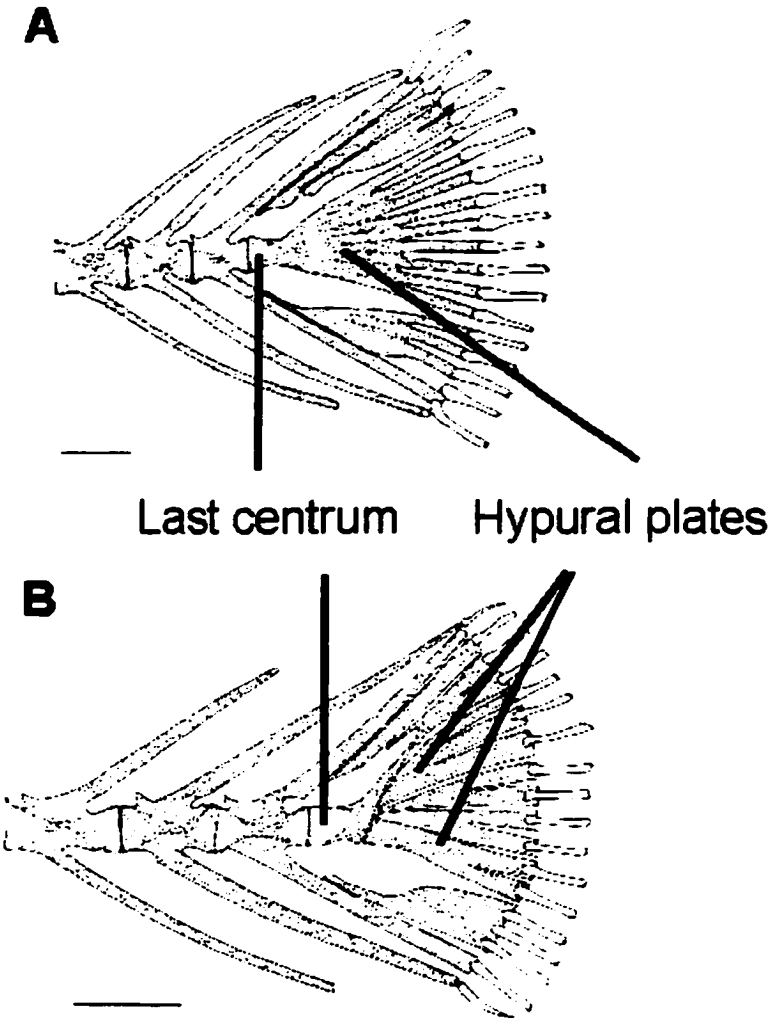

Fig. 68: Caudal skeleton of A) *Peltorhamphus novaezeelandiae* NMNZ P.6118, scale bar = 3 mm and B) *Colistium guntheri* AMS I.14775, scale bar = 1 mm.

Relationships within clade D are mainly unresolved. This clade shows a trichotomous relationship between both species of the genus *Colistium* and the genus *Ammotretis*. The genus *Ammotretis* (clade F) is defined by one apomorphy and five homoplasies. The apomorphy shared by all the members of the genus *Ammotretis* is a reversal. Their ocular side pelvic fin has few cartilaginous blocks, only the radials are

cartilaginous (character 7) (Fig. 69). The homoplasies at this node are: undivided hypural plates (character 1), presence of scales on the dorsal fin rays (character 19), tube-shaped bones in the supratemporal section of the lateral line (character 46), presence of neuromasts on the blind side (character 67) and absence of gill rakers on the first epibranchial bone (character 68).

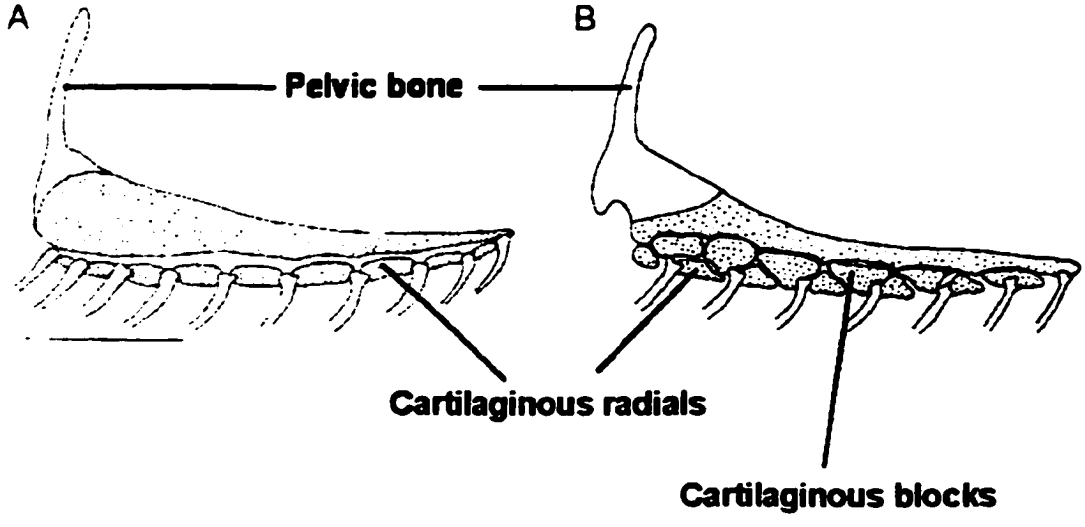

Fig. 69: Ocular side pelvic fin of A) *Ammotretis lituratus* CSIRO T.1587-01, scale bar = 5 mm and B) *Colistium nudipinnis* NMNZ P.36912, scale bar = 3 mm.

Within clade F only one clade is resolved (clade G). The other relationship remains obscure. Clade G, containing the species *Ammotretis brevipinnis* and *A. lituratus*, is defined by a single apomorphy, the presence of a bony tubercle at the tip of the first pectoral ray on the blind side fin (character 10) (Fig. 70).

Clade E (Fig. 58) is formed by the genera *Peltorhamphus* (clade H) and *Rhombosolea* (clade I). The genus *Peltorhamphus* (clade H) is monophyletic and is

defined by four apomorphies and six homoplastic characters. Only the genus *Peltorhamphus* has: 23 or more pterygiophores over the cranium (character 8) (Fig. 67), a flap of skin covering the mouth on the ocular side (character 25) (Fig. 59), the second ocular side pectoral fin ray elongated (character 26) (Fig. 59), and absence of a posterior bony projection of the blind side palatine bone under the ectopterygoid bone (character 61) (Fig. 71). The homoplasies at this node are: absence of a sensory canal in the blind side preorbital bone (character 11), big and round cartilage between the basioccipital and the prootic (character 51), absence of a sensory canal on the blind side parietal (character 52), presence of scales on most of the ocular side pectoral fin (character 58), a labial portion of the ocular side maxilla shorter than the rostral portion (character 65) and neuromasts on the blind side (character 67). The relationships between the species of the genus *Peltorhamphus* are unresolved.

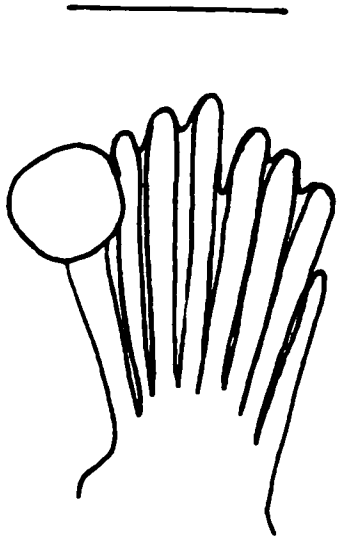

Fig. 70: Blind side pectoral fin of *Ammotretis brevipinnis* SAMA F.5815. Scale bar = 5 mm.

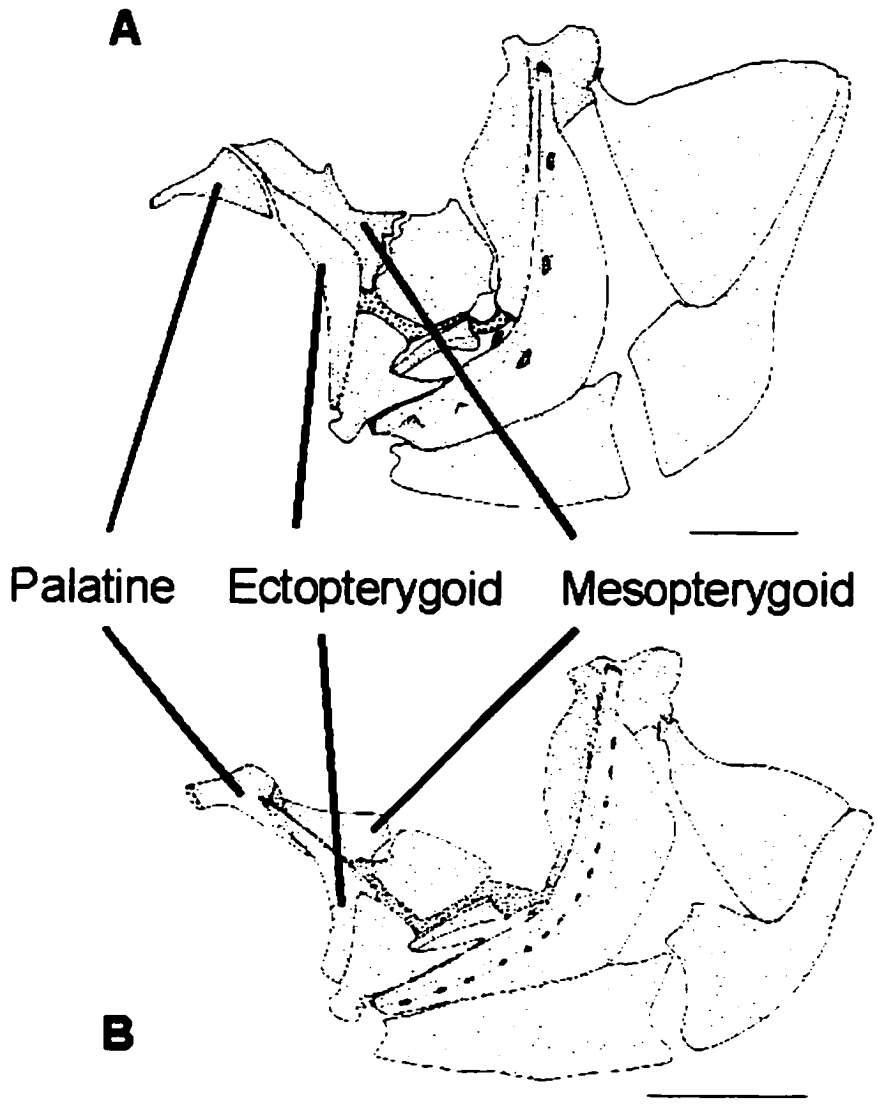

Fig. 71: Blind side suspensorium of A) *Peltorhamphus latus* NMNZ P.6004 and B) *Rhombosolea leporina* AMS I.27007-001. Scale bars = 3 mm.

Clade I on the other hand is fully resolved (Fig. 58). The genus *Rhombosolea* is also monophyletic based on seven apomorphies and seven homoplasies. The apomorphic characters shared by the species of this genus are: cycloid scales on the

ocular side (character 20), a large hyomadibular foramen on the ocular side bone (character 22) (Fig. 72), anteroventral orientation of the hemapophyses of the fourth precaudal vertebra (character 23) (Fig. 73), the presence of a foramen on the labial portion of the head of the ocular side maxilla (character 24) (Fig. 74), absence of a projection of the blind side frontal bone in the interorbital bar (character 39) (Fig. 62), absence of a sensory canal between both frontal bones (character 40) (Fig.75) and a small ethmoid bone (character 60) (Fig. 62). The homoplasies at this node are: absence of blind side pectoral fin rays (character 5), presence of a second row of gill rakers on the 3rd and 4th ceratobranchials (character 18), a U-shaped nasal bone on the blind side (character 28), symmetrical lower jaws (character 33), a sensory canal in the ocular side epioccipital (character 38), the absence of orbital bones (excluding lachrymal) on the ocular side (character 48) and the origin of the dorsal not in front of the snout (character 66).

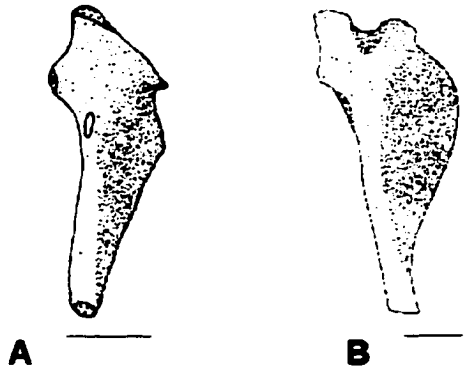

Fig. 72: Ocular side hyomandibular bone of A) *Rhombosolea leporina* AMS I.27007-001 and B) *Peltorhamphus tenuis* NMNZ P.6017. Scale bars = 2 mm.

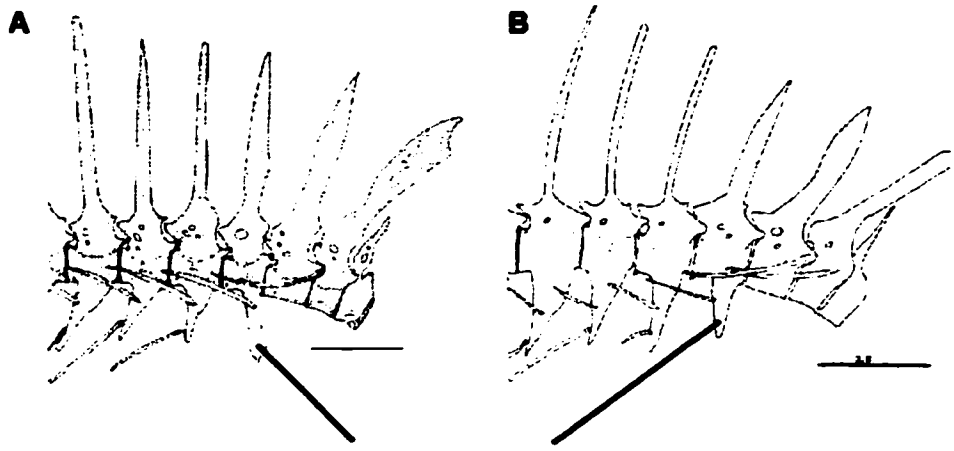

Fig. 73: First seven precaudal vertebrae and their ribs of A) *Rhombosolea leporina* AMS I.27007-001, scale bar = 2 mm and B) *Ammotretis elongatus* AMS I.13207, scale bar = 3 mm.

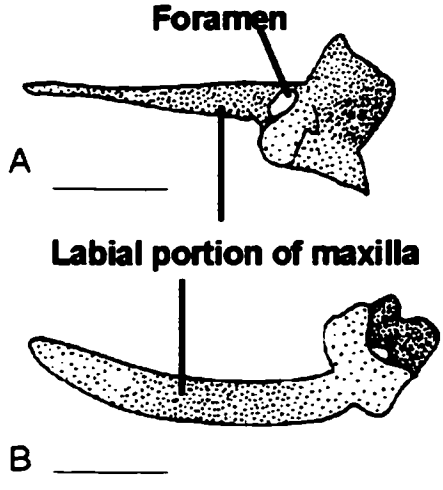

Fig. 74: Ventral view of the ocular side maxilla of A) *Rhombosolea leporina* AMS I. 27007-001, scale bar = 1 mm and B) *Ammotretis elongatus* AMS I.13207, scale bar = 2 mm.

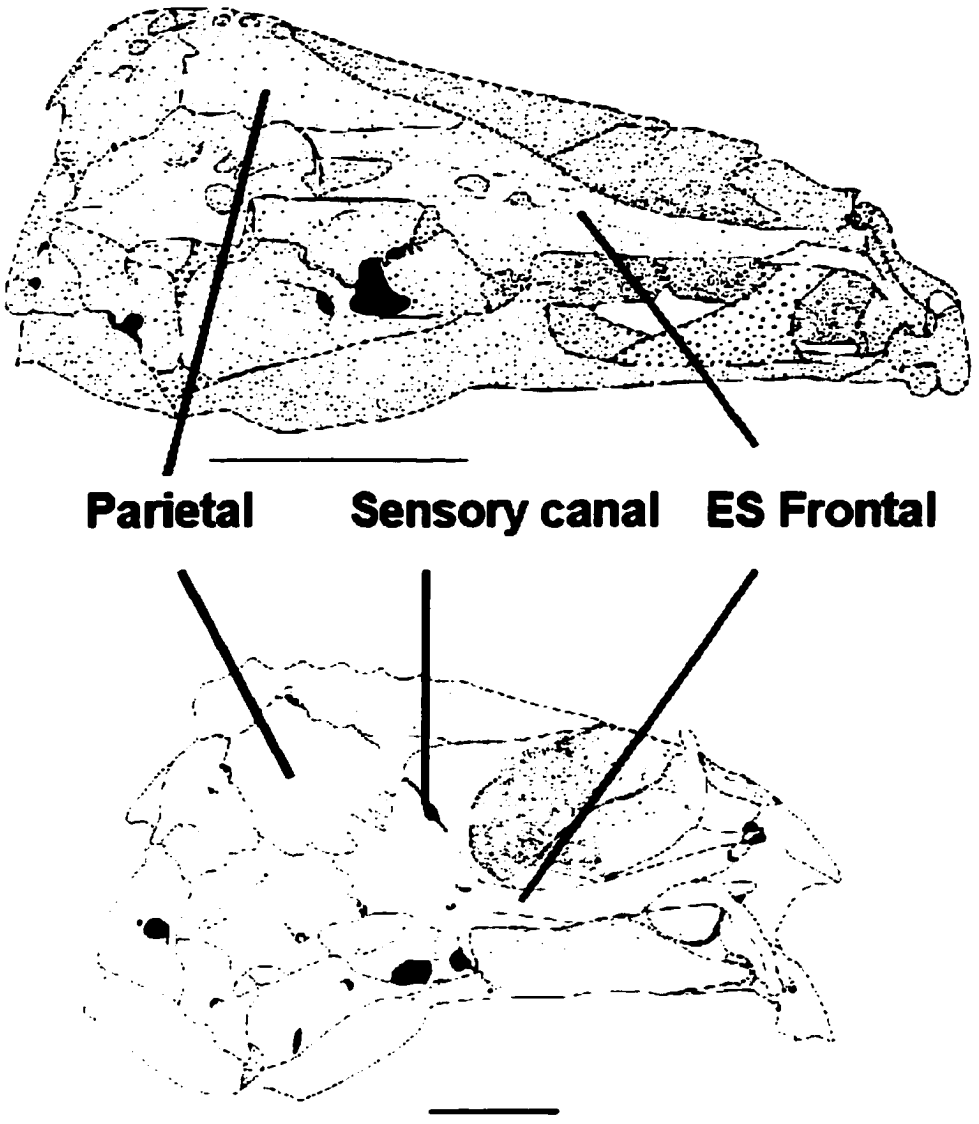

Fig. 75: Ocular side view of the cranium of A) *Rhombosolea leporina* AMS I.27007-001 and B) *Peltorhamphus latus* NMNZ P.6004. Scale bars = 3 mm.

Within the genus *Rhombosolea*, *R. retiaria* is the sister-group of the other species (clade J). Clade J is supported by one apomorphy and one homoplastic character. The apomorphy of this clade is the presence of the urinary papilla on the mid-ventral body line (character 31). The homoplasy is more than one bone in the supratemporal section of the lateral line (character 45). Clade J is divided into clade K and its sister-group the species

R. leporina. Clade K consisting of the species *R. tapirina* and *R. plebeia* is supported by one apomorphy and one homoplasy. The apomorphy shared by both species is the presence of only one dorsal fin ray associated with the first pterygiophore of the dorsal fin (character 57) (Fig.76). The homoplasy at this node is the absence of a sensory canal in the ocular side preorbital bone (character 11).

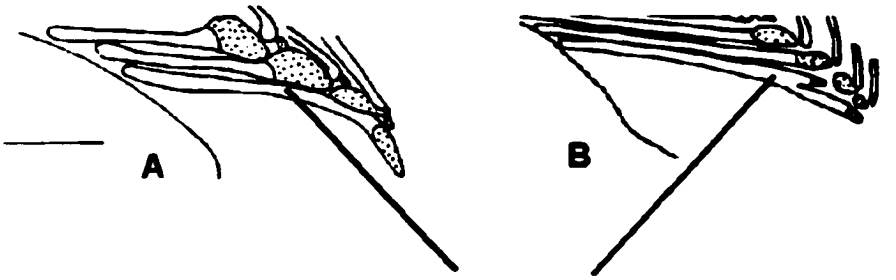

Fig. 76: First few pterygiophores of the dorsal fin of A) *Rhombosolea plebeia* AMS I.27006-001 and B) *R. leporina* AMS I.27007-001. Scale bars = 2 mm. In *R. plebeia* and *R. tapirina* the first dorsal fin pterygiophore supports only one dorsal fin ray compared to two for the other rhombosoleids.

Status of *Psammodiscus*, *Oncopterus* and *Azygopus*.-*Psammodiscus ocellatus* and *Oncopterus darwinii* were removed from the Rhombosoleidae after they were shown to have more affinities with outgroups than with any Rhombosoleidae (Fig. 57). The analysis performed on Hoshino's (2001b) data matrix yielded 6 equally most parsimonious trees of 109 steps (Fig. 77). According to this analysis, *Psammodiscus* and *Oncopterus* are part of a trichotomy with a large clade formed by Rhombosoleidae, Poecilopsettidae and clade V (Fig. 77). *Psammodiscus* and *Oncopterus* and the other members of clade III share: an

incomplete neural arch on the first precaudal vertebra (character 14) (Fig. 78) an inclination of the second neural spine over the cranium (character 34) (Fig 79) and the presence of the pseudo-interradialis muscle (character 44). *Psammodiscus* and *Oncopterus* are excluded from clade IV because: they have ocular side infraorbitals (character 7) and they have separated branchiostegal membranes (character 25). In the two different topologies either one of these characters is also found at this node: their epioccipital bones do not form the foramen magnum (character 4) or they have blind side infraorbital bones (character 6).

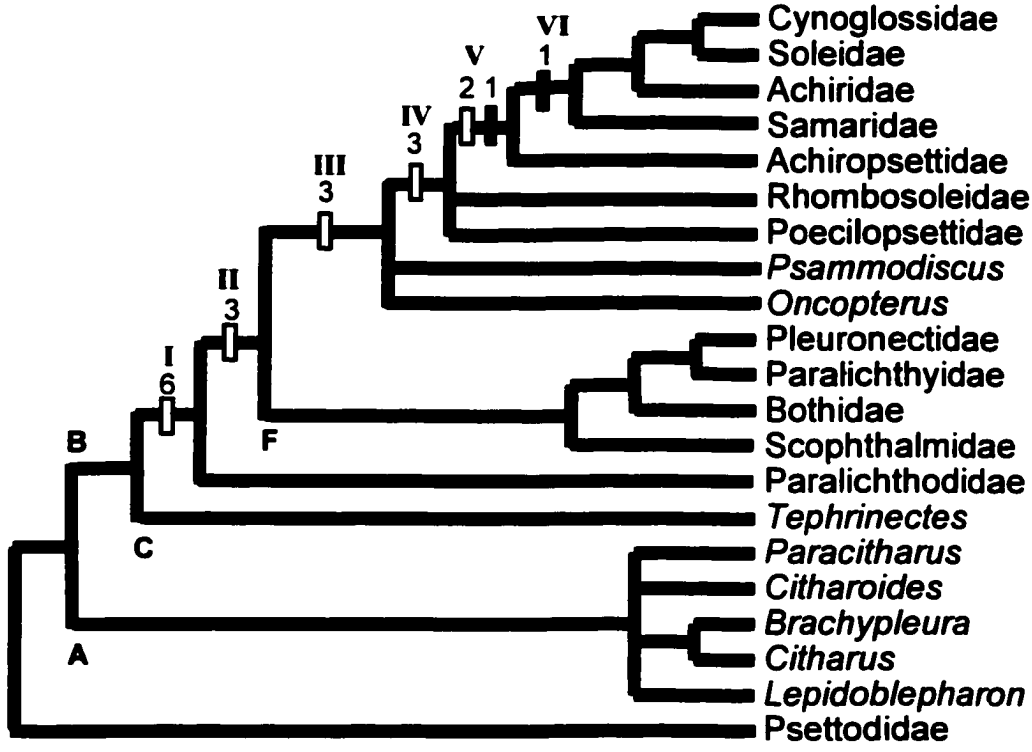

Fig. 77: Strict consensus cladogram of 6 equally parsimonious trees (steps = 109, consistency index (CI) = 0.477, retention index (RI) = 0.771) of the relationships between the families and genera of the order Pleuronectiformes. The black bar below the nodes and the number immediately above represent the apomorphies

and their number at each node, the white bar and the number immediately above represent the homoplasies and their number at each node. The apomorphies and homoplasies are given only for nodes of newly added taxa. The letters correspond to the clades in Hoshino (2001b). The roman numerals represent newly formed clades. Clade I is supported by six homoplasies: 23, 29, 35, 38, 41 and 42. Clade II is supported by three homoplasies: 31, 32 and 33. Clade III is supported by three homoplasies: 14, 34 and 44. Clade IV is supported by three homoplasies: 4 or 6 depending on the topology (see discussion), 7 and 25. Clade V is supported by one apomorphy: 9 and by two homoplasies: 3 and 10. Clade VI is supported by one apomorphy: 8.

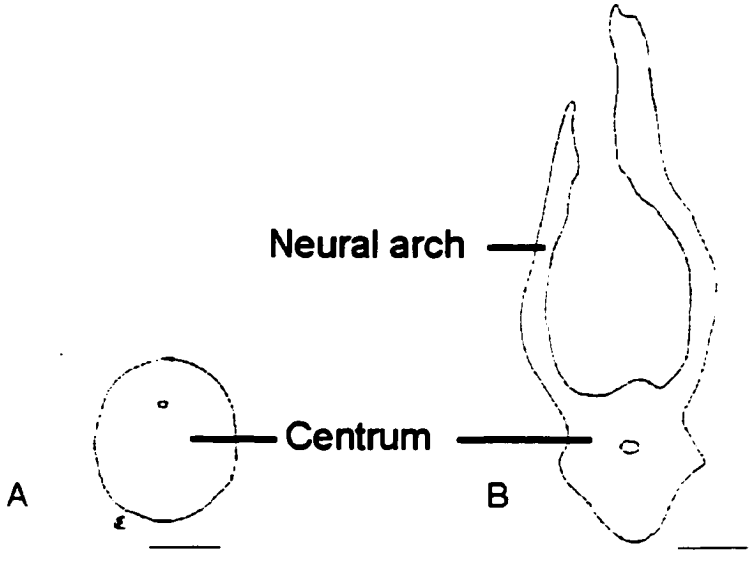

Fig. 78: Frontal view of the first caudal vertebra of A) *Psammodiscus ocellatus* CSIRO CA.1668 and B) *Oncopterus darwinii* INIDEP unregistered. Scale bars = 1 mm.

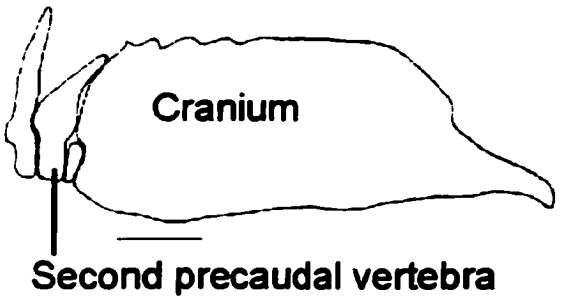

Fig. 79: Outline of the cranium and first three vertebrae of *Psammodiscus ocellatus* (CSIRO CA.3433) showing the anterior inclination of the second neural spine. Scale bar = 2 mm.

The family Paralichthodidae was added to the analysis. Since this taxon was not examined by Hoshino (2001b) its phylogenetic position has not been determined with the most recent data matrix available. The consensus cladogram (Fig. 77) shows that the family Paralichthodidae is the sister-group of a large clade including the flatfishes with a bothoid type of caudal skeleton (Hoshino's clade F) and the newly formed clade II (Fig. 77). Six homoplasies are shared by *Paralichthodes* and its sister-group: fusion of the hemal arch to preural centrum 2 (character 23) (Fig. 80), the blind side sphenotic bone is not in contact with the blind side lateral ethmoid (Character 29), uroneural 1 is absent in the caudal skeleton (character 35) (Fig. 80), one or no procurrent rays in the caudal fin (character 38), a stay is absent on the dorsal and anal pterygiophores (character 41 and hypochordal longitudinalis muscle absent (character 42). *Paralichthodes* is excluded from clade II because its interarcual cartilage is well developed and rod-like (character 31), it has a sensory canal in the supracleithrum (character 32) (Fig. 81) and the internal dorsolateral wing of the pelvic fin is present and bent towards the ocular side (character 33).

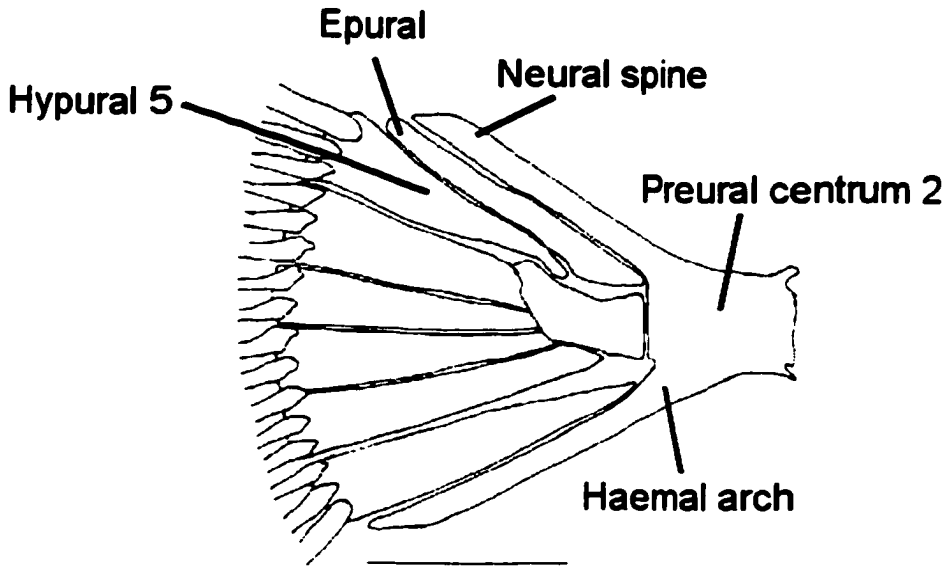

Fig. 80: Caudal skeleton of *Paralichthodes algoensis* ANSP 55218, scale bar = 3 mm.

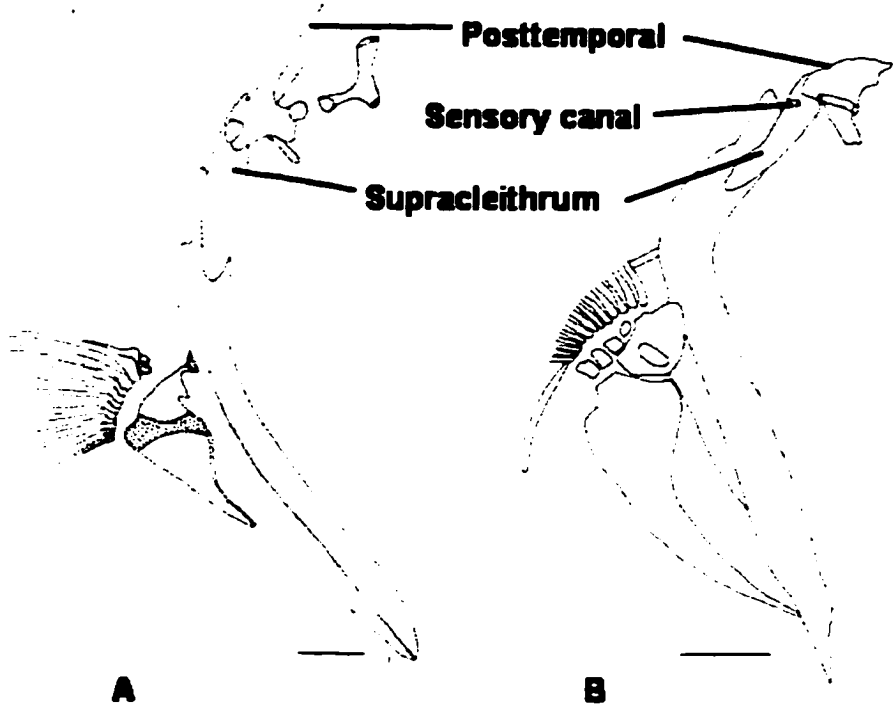

Fig. 81: Ocular side pectoral girdles of A) *Rhombosolea leporina* AMS I.27007-001, scale bar = 2 mm and B) *Paralichthodes algoensis* ANSP 55218, scale bar = 3 mm.

The genus *Azygopus* was removed from the Rhombosoleidae because it grouped with the outgroup in the preliminary analysis (Fig. 57). In the analysis of the family Rhombosoleidae three characters linked the genus *Azygopus* with the Achiropsettidae (*sensu* Evseenko, 1984). These characters are 1) position of the last ocular side pelvic fin rays on the ocular side, 2) high number of caudal vertebrae, and 3) absence of pterosphenoid bone on the ocular side. These three characters were not incorporated in the analysis of the order level relationships because character states could not be determined for all taxa in the data matrix. These similarities explain why the genus *Azygopus* is incorporated in the newly defined family Achiropsettidae in the order level analysis.

The family Achiropsettidae (including *Azygopus*) is the sister-group of clade VI (Fig. 77). Achiropsettidae shares one apomorphy: blind side coracoscapular complex and postcleithra reduced or absent (character 9) and two homoplasies: pterosphenoid bone absent (character 3) and almost parallel orientation over orbital region of the first proximal radial of the dorsal fin (character 10) with its sister-clade. Achiropsettidae is excluded from clade VI because its hyomandibular bone is articulated to the cranium with its posterodorsal margin (character 8).

Discussion

Intrarelationships of the Rhombosoleidae.-Sakamoto's (1984) (Appendix 1) phenetic study dealt with 11 species of six genera of the Rhombosoleidae (*sensu* Norman, 1934). Not surprisingly, his phenogram suggests relationships that differ from the cladisitic analysis (Fig. 58). The only congruence between both analyses is a clade formed by *Peltorhamphus* and *Rhombosolea*. Because the objectives of a phenetic and cladistic analyses differ in their purpose and their objectives, these differences are to be expected.

Based mainly on a comparative study of otolith morphology, Schwarzhans (1999) split the Rhombosoleidae (*sensu* Norman, 1934) into five different groups with various affinities within the flatfishes. However, Schwarzhans' analysis was ecclectic in nature without any formal quantitative analysis. Thus, it is not surprising that we find no congruence between his results and the conclusion of our cladistic analysis. Clearly, this study shows that the Rhombosoleidae (*sensu novo*) are monophyletic (Fig. 58).

Finally, this study corroborates, through a formal cladistic analysis, the suggestion made by Evseenko's (2000) regarding the phylogenetic position of the family Achiropsettidae as the sister-group of clade VI (Fig.77). However, contrary to the

conclusion of this study, Evseenko (2000) did not include *Azygopus* within the Achiropsettidae.

Unresolved relationships within the Rhombosoleidae.-The genera *Ammotretis* and *Colistium* are the most problematic group within the family because of their unresolved relationships. Within this clade eight different topologies are possible (Fig. 82). For the genus *Colistium*, in six of eight topologies (Fig. 82, A-E, G) it is found to be monophyletic but, in two of these topologies (F and H) it does not form a monophyletic group. Because these two topologies are part of the most parsimonious cladograms found by the analysis, it is possible that *Colistium* does not form a monophyletic group. In that case, *Colistium* would become a synonym of *Ammotretis* which was described earlier by Günther in 1862 (Eschmeyer *et al.*, 1998). Before *Colistium* is placed in synonymy with *Ammotretis* the multiple question marks (24 out of 68 characters) entered for the taxon *Colistium guntheri* in the data matrix should be replaced by the proper character states. In phylogenetic analyses, question marks increase the number of most parsimonious trees and decrease the resolution for the relationships (Kitching *et al.*, 1998). The uncertainty introduced by the question marks is reflected by the fact that *Colistium* is not monophyletic in only 25% of the topologies. For this reason, for the sake of stability, *Colistium* is kept as a valid genus until it is clearly shown not to be monophyletic.

Looking at the relationships within the genus *Ammotretis*, we see in the first four possibilities (Fig. 82, A-D) that either *A. rostratus* or *A. macrolepis* can be the sister-group of the most advanced clade. The other two taxa follow this larger clade alternating between the sister-group of this large clade or the more primitive taxa of the genus. In the last two possibilities (E, G) *A. rostratus* is either the sister-group of the more advanced clade formed by *A. brevipinnis* and *A. lituratus* (Fig. 82, E) or the sister-group of all other species of the same genus (Fig. 82, G). In five topologies (A, B, E, F, H) out of eight, *A.*

rostratus is the sister-group of *A. brevipinnis* and *A. lituratus*. *A. rostratus* shares with the other two species progressively longer hemapophyses on the precaudal vertebrae and between 7 and 10 ocular side pelvic fin rays. This character is also shared with *C. nudipinnis*. If more characters were found *A. rostratus* would likely be the sister-group of *A. brevipinnis* and *A. lituratus* as shown in 63% of the most parsimonious topologies. The relationships between *A. elongatus*, *A. macrolepis* and the other species of the genus are unclear. In two topologies (E and G) *A. elongatus* and *A. macrolepis* are sister taxa. Only one character unites these two taxa: more than 11 ocular side pelvic fin rays. This character is also shared with *C. guntheri*. More characters will be needed to resolve the relationships between the species of this genus.

The relationships within the genus *Peltorhamphus* are also unresolved. Two different and equally parsimonious topologies (Fig. 83) show that *P. novaezeelandiae* can be the sister taxa of both *P. latus* and *P. tenuis* but can never be the most plesiomorphic taxon of the genus. More characters will be necessary to resolve these relationships.

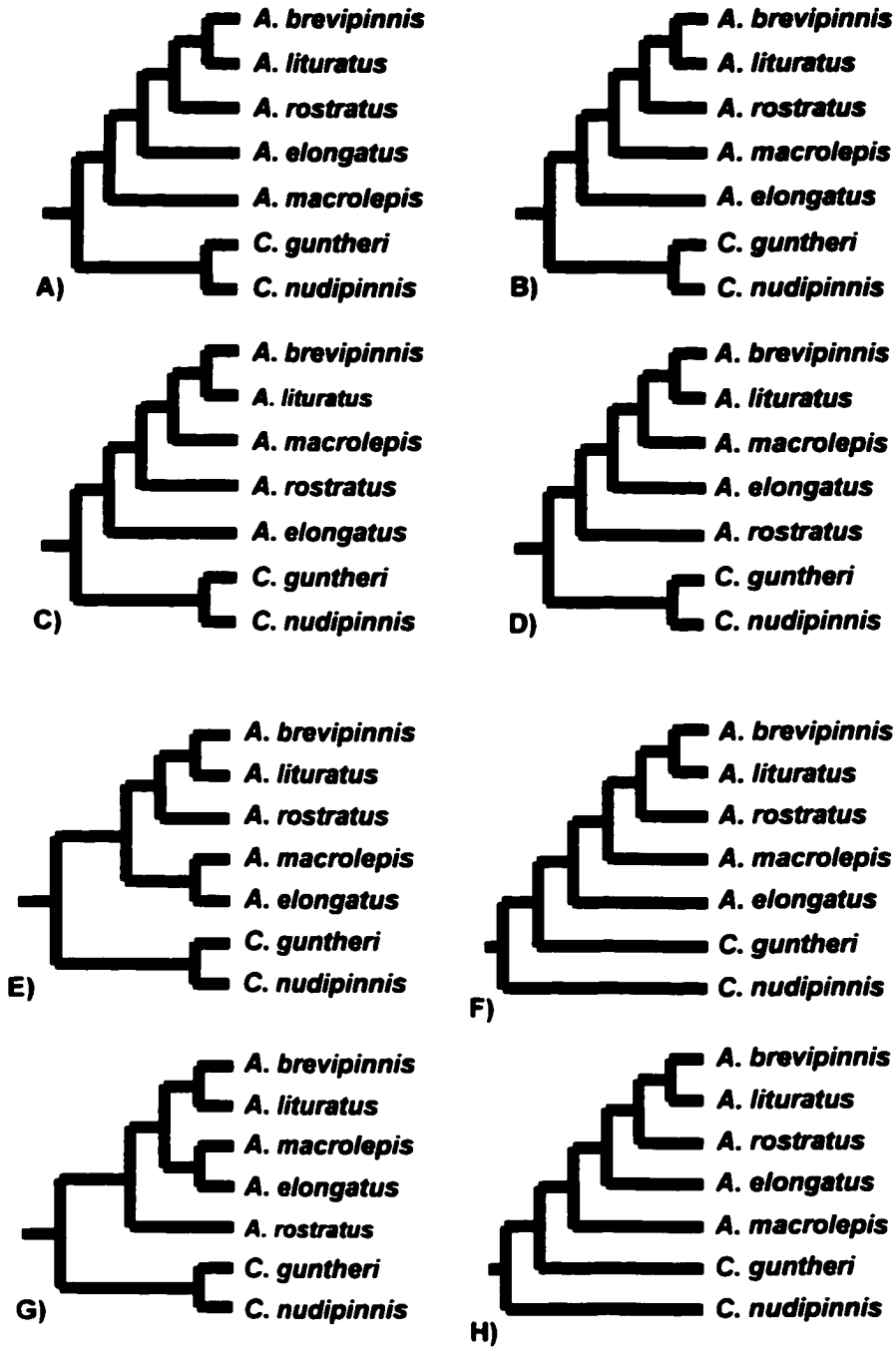

Fig. 82: Eight different equally parsimonious topologies involving the clade formed by the genera *Ammotretis* and *Colistium*.

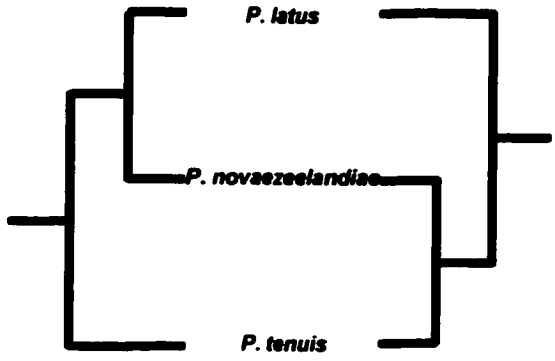

Fig. 83: Two equally parsimonious topologies between the species of the genus *Peltorhamphus*.

Classification of the Rhombosoleidae.-The phylogenetic analysis suggests that the new Rhombosoleidae are a monophyletic group when *Psammodiscus ocellatus*, *Oncopterus darwinii* and both subspecies of the genus *Azygopus* are removed from the rest of the family. Based on a branch and bound analysis, the strict consensus tree of all parsimonious trees demonstrates that the remaining genera, *Taratretis*, *Pelotretis*, *Colistium*, *Ammotretis*, *Peltorhamphus* and *Rhombosolea* now constitute a monophyletic group. Thus, it is recommended that minor changes in the classification should be done to reflect this new natural group. The new classification should be:

Family Rhombosoleidae:

Genus *Taratretis* (*T. derwentensis*)

Genus *Pelotretis* (*P. flavilatus*)

Genus *Colistium* (*C. guntheri* and *C. nudipinnis*)

Genus *Ammotretis* (*A. rostratus*, *A. elongatus*, *A. macrolepis*, *A. lituratus* and *A. brevipinnis*)

Genus *Peltorhamphus* (*P. latus*, *P. novaezeelandiae* and *P. tenuis*)

Genus *Rhombosolea* (*R. retiaria*, *R. leporina*, *R. plebeia* and *R. tapirina*)

Biogeography.-Few fossil Pleuronectiformes have been described. The oldest flatfish fossil is a bothid from the Middle Eocene (Chanet 1999). This fossil of approximately 43 MY can be placed in the family Bothidae. Bothids are relatively derived pleuronectiforms (Fig. 77). Their presence as far back as 43 MYA would make it possible for many other Pleuronectiformes (including Rhombosoleidae) to have been present earlier than 43 MYA since many flatfishes appeared before the bothids (Fig. 77). Only two fossils are known for the rhombosoleids, both are from the genus *Peltorhamphus* (Schwarzhans, 1999). These fossils date back to the Middle Miocene (23-5 MYA) and to the Pliocene (5-1.8 MYA) in New Zealand.

The area cladogram (Fig. 84) represents the distributions of taxa within the family Rhombosoleidae. Two possible biogeographic scenarios can be hypothesised to explain the current distribution of the family Rhombosoleidae. The first possibility (see 1 on Fig. 84) is that the ancestral rhombosoleid was found on a big island formed by Australia and New Zealand. When Australia and New Zealand separated, 80 MYA (Smith *et al.*, 1994), *Taratretis* evolved in Australia and its sister-group evolved in New Zealand. After this vicariant event, two dispersal events took place: the dispersal of the ancestor of the genus *Ammotretis* and of *Rhombosolea tapirina* to Australia (see 3 on Fig. 84). The second possible scenario (see 2 on Fig. 84) is the splitting of New Zealand and Australia shortly before the genus *Ammotretis* evolved. If that is the case, the absence of *Taratretis*, the most plesiomorphic taxon of the family, in New Zealand, could be explained by the fact that it was not able to survive there. Furthermore, when *R. tapirina* appeared it dispersed to Australia (see 3 on Fig. 84), explaining its distribution on both islands.

These two scenarios imply that at least some members of the Rhombosoleidae were present 80 MYA, before the separation of Australia and New Zealand, a hypothesis that cannot be ruled out by the pleuronectiform fossil record. Also, Waters *et al.* (2000) in their study on Galaxiidae (order Osmeriformes), present on almost all Gondwanan continents, could not rule out the possibility of a vicariant event to explain the distribution of this family. Even if the galaxiids are much older than the rhombosoleids (more than 135 MY) (Waters *et al.*, 2000), it is possible the Rhombosoleidae had already evolved at the time when Australia and New Zealand separated. More information is necessary before any one of the two proposed scenarios is excluded.

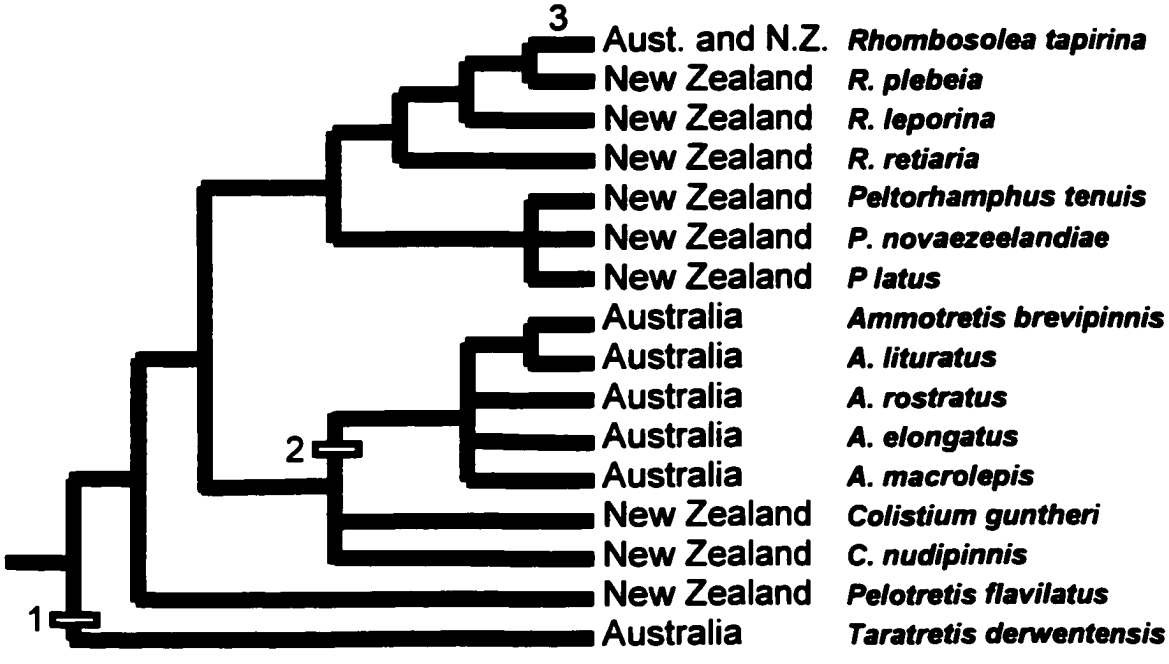

Fig. 84: Area cladogram showing the distribution of each species within the family Rhombosoleidae. White bars and numbers represent different biogeographic scenarios. See discussion.

Status of *Psammodiscus*, *Oncopterus*, Rhombosoleidae and Poecilopsettidae.-The phylogeny of the Pleuronectiformes has not changed considerably with the addition of four taxa (Paralichthodidae, Achiropsettidae, *Oncopterus* and *Psammodiscus*). The major changes are found within clade III (Fig. 77). *Psammodiscus* and *Oncopterus* are the most plesiomorphic taxa of this clade and their relationships are unresolved. The sister-group of these genera is a clade formed by the Rhombosoleidae, Poecilopsettidae, Achiropsettidae, Samaridae, Achiridae, Soleidae and Cynoglossidae (clade IV in Fig. 77).

Within clade IV the relationships between Rhombosoleidae and Poecilopsettidae are unresolved. Two equally parsimonious topologies are found at this node (Fig. 85). In one topology the family Rhombosoleidae is the sister-group of clade V (Fig. 85, A) and in the other topology the family Poecilopsettidae is the sister-group of clade V (Fig. 85, B). In the first topology the absence of a pterosphenoid bone (character 3) and the epioccipitals forming the dorsal margin of the foramen magnum (character 4) unite the family Rhombosoleidae with its sister-clade. In the second topology (Fig. 85, B) only one character unites the family Poecilopsettidae to its sister-clade: the absence of infraorbital bones on the blind side (character 6). The second topology is supported but only one character (compared to two for the first) but is still equally parsimonious because character 3, presence or absence of the pterosphenoid bone, was coded 0/1 for the Rhombosoleidae. The pterosphenoid bone is absent in only two genera of the Rhombosoleidae (*Peltorhamphus* and *Rhombosolea*). Since this character is coded with both character states it does not help to choose between one topology and the other.

The relationships between the Rhombosoleidae and the Poecilopsettidae remain unresolved even if the analysis performed by Hoshino (2001b) (Fig. 1) had resolved this relationship. In his analysis, the characters (1, 4, 30 and 31) supported the hypothesis that the Poecilopsettidae were the sister-group of the Rhombosoleidae. These characters are no longer found supporting that node. Character 1, the absence of teeth on the ocular

side premaxilla is optimised differently with the addition of Achiropsettidae in clade IV. Only two steps are needed when the absence of teeth is added on the branch leading to the Rhombosoleidae and when it is added on the branch leading to the clade Achiridae, Soleidae and Cynoglossidae. Any other position of this character would require more steps. Character 4 remains the only character supporting this topology (see above). Character 30 was coded 0/1 for the Rhombosoleidae. According to Sakamoto (1984), the arterial canal runs along the external surface of the anterior ceratohyal in the genera *Ammotretis* and *Taratretis*. Character 31 is also optimised differently when *Psammodiscus* and *Oncopterus* are added in the matrix. This explains why the relationships between Poecilopsettidae and Rhombosoleidae are still unresolved.

The results obtained by this analysis shows that more characters are needed in the analysis to be able to determine the relationships between closely related genera and families.

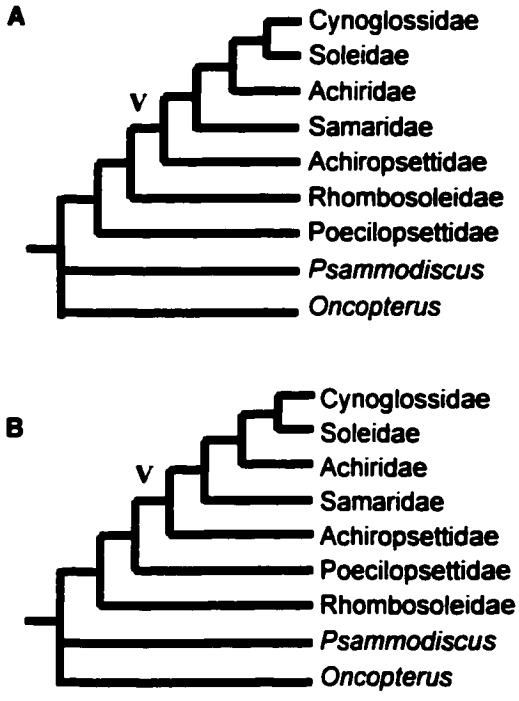

Fig. 85: Two equally parsimonious topologies between Rhombosoleidae and Poecilopsettidae and members of clade V.

Status of *Azygopus*.-The genus *Azygopus* is represented by one species with two subspecies *A. pinnifasciatus pinnifasciatus* and *A. p. flemingi*. These subspecies are allopatric. *A. p. pinnifasciatus* is found in deep waters off South East Australia while *A. p. flemingi* is found in deep waters off New Zealand. More than 2000 km separate the two subspecies geographically (Nielsen, 1961) and in between these geographic sites the water is more than 5000 m in depth.

The two subspecies are phenotypically very similar except for the coloration of the ocular side. *A. p. flemingi* has numerous small brown spots all along the body and on the dorsal and anal fins but not arranged in bands. *A. p. pinnifasciatus* has bands on the

dorsal and anal fins and sometimes irregular brown spots on the body. They can also be differentiated by the number of lateral line scales, number of rays in the dorsal fin, the size of the eyes and the maxilla on the ocular side. These characteristics were all found by Nielsen (1961) in his description of the subspecies *A. p. flemingi*. Furthermore, when a limited number of specimens were surveyed, the number of caudal vertebrae seemed to be different between the two subspecies (pers. obs.). These differences in morphology between the two subspecies will probably be sufficient to elevate them to the rank of species once a detailed examination of specimens belonging to both taxa is completed.

The family Achiropsettidae should now include the genus *Azygopus* in addition to *Achiropsetta*, *Mancopsetta*, *Pseudomancopsetta* and *Neoachiropsetta* (Evseenko, 1984, 1996, 2000). This revised family remains to be shown to be monophyletic with formal cladistic analysis. Nonetheless, some characters point toward the monophyly of this family: all the species have a curve in their ocular side pelvic fin, the posteriormost pelvic rays are located on the ocular side. This feature is unique within the clade where the achiropsettids are found. Also unique to the achiropsettids within the clade is the high number of caudal vertebrae (more than 34). The only exception is the samarid *Samariscus corallinus* (Sakamoto, 1984) and the Cynoglossidae (Munroe, 1998). A close examination of all the taxa involved in this family will undoubtedly enable the examiner to find more unique characters shared between the species of this group.

MATERIALS EXAMINED

Ingroup.-*Ammotretis brevipinnis*: **AMS I.16847-012**; 6, 1 C/S: 24-40 mm SL; radiograph only. **SAMA F5815**; 5, 1 C/S: 107-139 mm SL. *Ammotretis elongatus*: **AMS I.13207**; 1 C/S. **CSIRO H568-01**; 14: 85-98 mm SL. **NMV** unregistered; 1 C/S. *Ammotretis lituratus*: **CSIRO T1587-01**; 2, 1 C/S: 69-71 mm SL. **CSIRO T1589-01**; 2: 39-42 mm SL. **NMV A707**; 1: 105 mm SL; radiograph only. **SAMA F1933**; 1 C/S: 87 mm SL. *Ammotretis macrolepis*: **CSIRO T1585-01**; 4, 1 C/S: 76-91 mm SL. **CSIRO T1591-01**; 2, 1 C/S: 74-79 mm SL. *Ammotretis rostratus*: **AMS I.15859-004**; 12, 2 C/S: 13-29 mm SL. **AMS I.16847-012**; 5: 23.3-39.8 mm SL. **AMS I.16987-002**; 6, 1C/S: 58-76 mm SL. **CSIRO T1598-01**; 11, 1 C/S: 23-57 mm SL. **NMV** unregistered; 1 C/S. *Colistium guntheri*: **AMS I.14657**; 1: 148 mm SL; radiograph only. **AMS I.14775**; 4, 1 C/S: 36-43 mm SL. *Colistium nudipinnis*: **NMNZ P.1823**; 1: 128 mm SL. **NMNZ P.5290**; 1: 70 mm SL. **NMNZ P.34082**; 1: 420 mm SL. **NMNZ P.36909**; 1: 104 mm SL. **NMNZ P.36910**; 1 C/S: 59 mm TL. **NMNZ P.369111** C/S: 45 m TL. **NMNZ P.36912**; 1 C/S: 55 mm SL. **NMNZ P.36913**; 1: 86 mm SL. **NMNZ P.36914**; 1 C/S: 36 mm SL. *Pelotretis flavilatus*: **NMNZ P.7895**; 3, 2 C/S: 75-145 mm SL. *Peltorhamphus latus*: **NMNZ P.6004**; 8, 2 C/S: 40-124 mm SL. **NMNZ P.38321**; 1: 75.6 mm SL. *Peltorhamphus novaezeelandiae*: **AMS I.14666-075**; 1 C/S, 78 mm SL. **AMS I.14673**; 1 C/S. **AMS I.14674**, 2: 101-109 mm SL; radiograph only. **NMNZ P.37857**; 1 C/S; 86 mm SL. **NMNZ P.6080**; 6: 57-86 mm SL. **NMNZ P.6118**; 3, 1 C/S: 184-196 mm SL. *Peltorhamphus tenuis*: **AMS I.14069**; 2: 67-69 mm SL; radiograph only. **AMS I.14675**; 2: 72-75 mm SL; radiograph only. **NMNZ P.6017**; 3, 2 C/S: 144-154 mm SL. **NMNZ P.6081**; 8: 68-89 mm SL. *Rhombosolea leporina*: **AMS I.27007-001**; 10 C/S: 17-63 mm SL. **NMC 87-0494**; 28: 19-122 mm SL. **NMNZ P.5266**; 4: 64-142 mm SL. **ROM 53630**; 33: 14-111 mm SL. *Rhombosolea plebeia*: **AMS I.27003-001**; 1: 74mm SL. **AMS I.27006-001**; 7 C/S: 15-78 mm SL. **ANSP 122857**; 1 C/S: 73 mm SL. **NMC 87-0499**; 32: 14-39 mm SL. **NMNZ P.18237** 3: 56-82 mm SL. **ROM 53628**; 17: 21-49 mm SL;

radiograph only. *Rhombosolea retiaria*: **AMS I.27004-001** 1 C/S: 70 mm SL. **AMS I.27005-001** 3 C/S: 29-70 mm SL. **NMC 87-0478**; 3: 89-120 mm SL; radiograph only. **NMNZ P.3459**; 1: 75 mm SL. **NMNZ P.3815**; 1: 53 mm SL. **NMNZ P.16205**; 1: 76 mm SL. **ROM 53627**; 2: 118-128 mm SL. **ROM 53631**; 1: 99 mm SL. *Rhombosolea tapirina*: **AMS I.17560-004**; 2 C/S: 21-124 mm SL. **CSIRO CA1595-01**; 4: 45-54 mm SL. **NMV** unregistered; 6 C/S: 16-50 mm SL. *Taratretis derwentensis*: **CSIRO B1525**; 15, 1 C/S: 63.8-87.5 mm SL. **NMV** unregistered; 5, 1 C/S: 56-67 mm SL; radiographs only.

Outgroup.-*Mancopsetta maculata*: **MNHN 1985-968**; 5, 1 C/S: 108.7-148.0 mm SL. **MNHN unregistered**; 1: 215 mm SL. *Poecilopsetta hawaiiensis*: **ANSP 176079**; 13: 1 C/S: 57.3-79.0 mm SL. *Poecilopsetta plinthus*: **AMS I.20918-016**; 12, 2 C/S: 77-99 mm SL.

Order level phylogeny.-*Paralichthodes algoensis*: **ANSP 55218**; 4, 1 C/S: 61-141 mm SL. *Oncopterus darwini*: **INIDEP4**; 1: 196 mm SL; **INIDEP** unregistered; 11, 6 C/S: 23-89 mm SL. **ISH 1639-1966**; 2: 186-196 mm SL; radiograph only. **MCZ 11398**; 2: 148-193 mm SL; radiograph only. **NSMT-P 44800**; 1 C/S.

Psammodiscus ocellatus.-**CSIRO CA 1668**; 1 C/S. **CSIRO CA 1670**; 1: 108 mm SL; radiograph only. **CSIRO CA 3432**; 1: 86 mm SL. **CSIRO CA 3433**; 1: 80 mm SL; radiograph only. **WAM P.5530-001**; 1: 93 mm SL.

Achiropsetta tricholepis: **MNHN** unregistered; 250 mm SL.

Azygopus pinnifasciatus pinnifasciatus: **AMS I.18839-003**; 1 C/S. **CSIRO CA3184**; 1 C/S: 118 mm SL. **CSIRO T1224**; 6: 121-148 mm SL.

Azygopus pinnifasciatus flemingi: **NMNZ P.5196**; 6: 104-112 mm SL. **NMNZ P.5808**; 4: 80-107 mm SL. **NMNZ P.5862**; 14: 85-115 mm SL. **NMNZ P.6747**; 2: 120-135 mm SL. **NMNZ P.7407**; 3, 2 C/S: 108-120 mm SL.

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GENERAL CONCLUSION

The present taxonomic revision of the species of the family Poecilopsettidae has revealed that from the initial 19 valid species, 18 are now considered valid. One species is described (*Poecilopsetta dorsialta*) and two species are synonymised: *Nematops chui* is a junior synonym of *N. macrochirus* and *Poecilopsetta megalepis* is a junior synonym of *P. plinthus*. Two species are found in the genus *Marleyella*, three in the genus *Nematops* and 13 in the genus *Poecilopsetta*. The genera *Marleyella* and *Nematops* are hypothesised to be monophyletic, but the genus *Poecilopsetta* is more problematic. No unique character is shared between the species of this genus. Larvae are described for the species *Poecilopsetta beani*, *P. colorata*, *P. hawaiiensis*, *P. inermis* and *P. plinthus*. No larvae are known for the other two genera within the family.

The monophyly of the Rhombosoleidae was determined using 87 morphological characters analysed with cladistic methodology. The Rhombosoleidae become monophyletic when the genera *Azygopus*, *Psammodiscus* and *Oncopterus* are removed. Eight synapomorphies support the monophyly of the newly defined Rhombosoleidae. The results of this analysis contradict those obtained by Schwarzhans (1999) on otolith morphology. *Rhombosolea* and *Peltorhamphus* are sister-taxa. These two genera are the sister-group of a clade formed by *Ammotretis* and *Colistium*. *Pelotretis* is the sister-group of a large clade formed by these last four genera. Finally, *Taratretis* is the most plesiomorphic genus within the family. The intrageneric relationships for the genus *Rhombosolea* are fully resolved but remain uncertain for *Ammotretis* and *Peltorhamphus*.

In the revised order level phylogeny, *Psammodiscus* and *Oncopterus* form a trichotomy with a large clade formed by the Poecilopsettidae, Rhombosoleidae, Achiropsettidae, Samaridae, Achiridae, Soleidae and Cynoglossidae (clade IV) (Fig. 77).

Azygopus is found to be sharing at least two characters with the Achiropsettidae: posteriormost ocular side pelvic fin rays located on the ocular side and a high number of caudal vertebrae. The family Achiropsettidae should now include both subspecies of the one species of the genus *Azygopus*. Within the order Pleuronectiformes, the family Achiropsettidae (including *Azygopus*) is the sister-group of clade V (Samaridae, Achiridae, Soleidae and Cynoglossidae). Finally, the relationship between the Poecilopsettidae and the Rhombosoleidae is still unresolved in the order level phylogeny. The node separating the family Poecilopsettidae from its sister-group (a large clade including the Rhombosoleidae, Samaridae, Achiridae, Soleidae and Cynoglossidae) (see Fig 1), found in the analysis performed by Hoshino (2001b), collapsed when taxa were added in that section of the cladogram.

APPENDIX 1

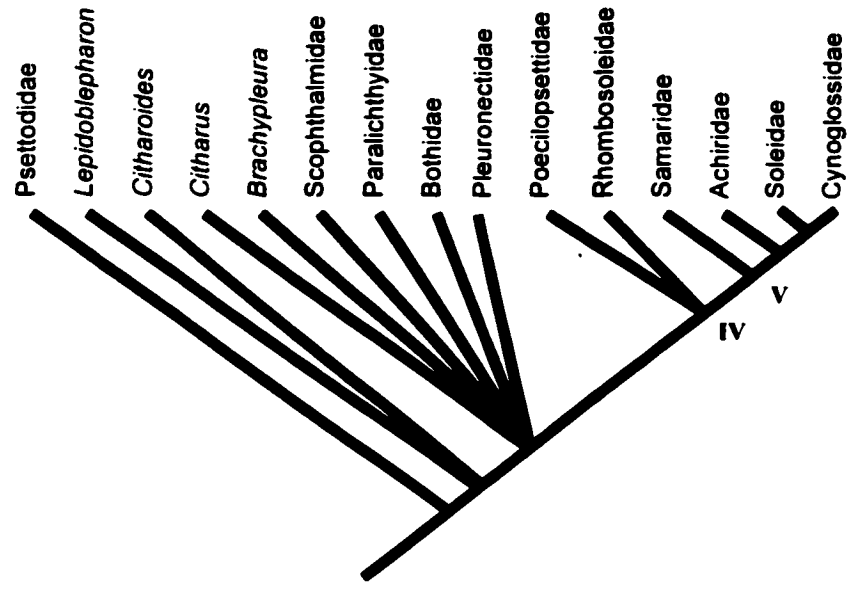


Fig. A1a: Phylogenetic relationships within the order Pleuronectiformes as defined by Chapleau (1993).

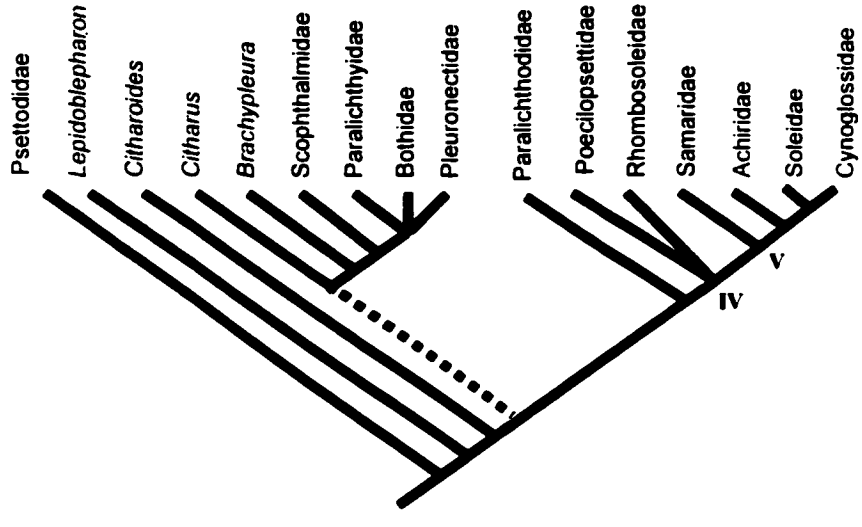


Fig A1b: Phylogenetic relationships within the order Pleuronectiformes as defined by Cooper and Chapleau (1998a).

APPENDIX 1 continued

Part of Sakamoto (1984) phenogram representing the relationships between the species of the subfamilies Poecilopsettinae, Rhombosoleinae and Samarinae.

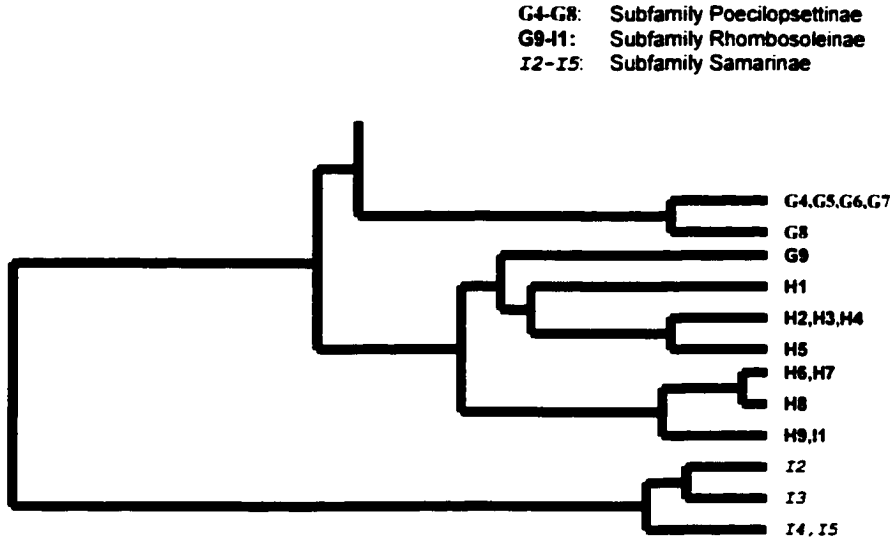
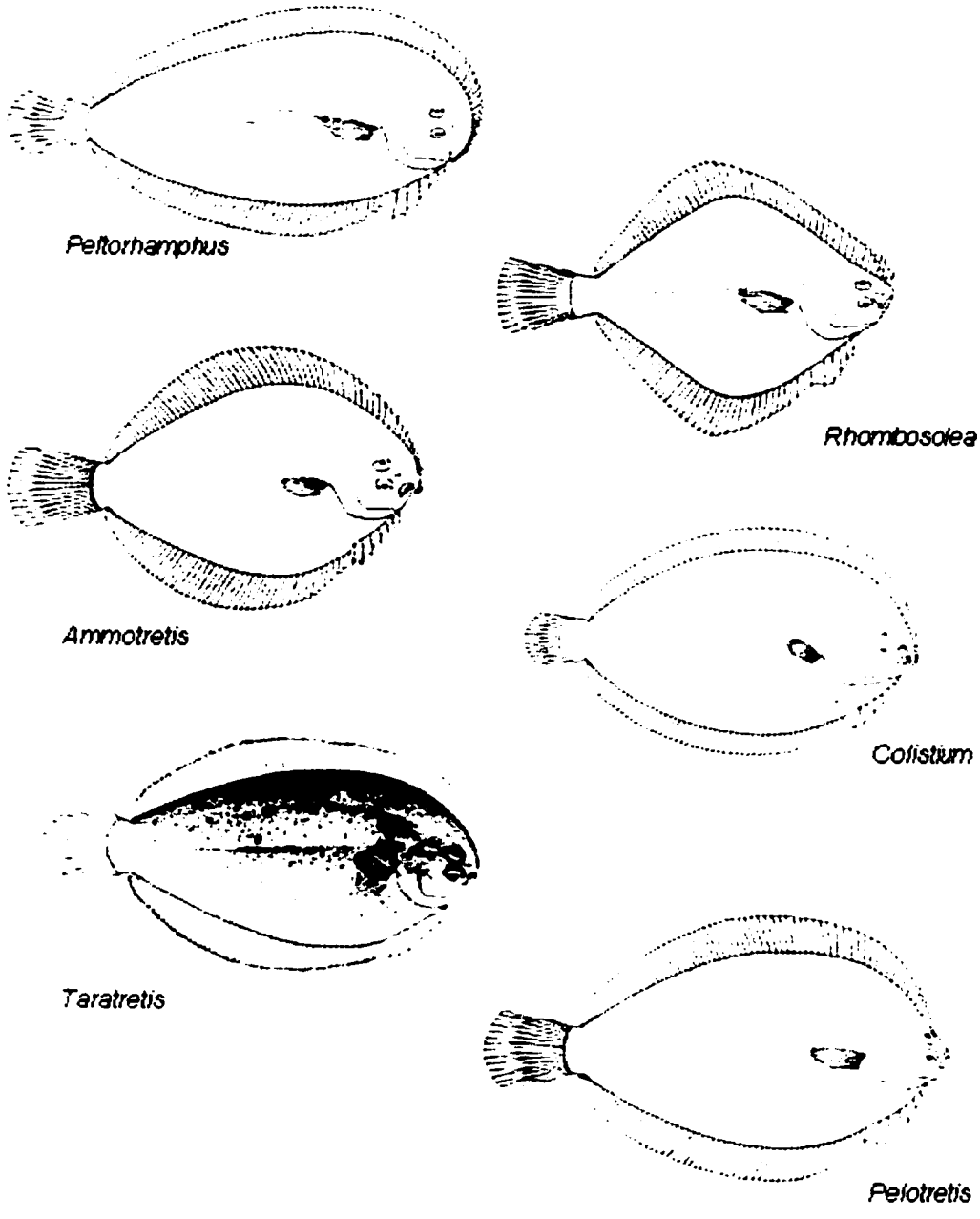
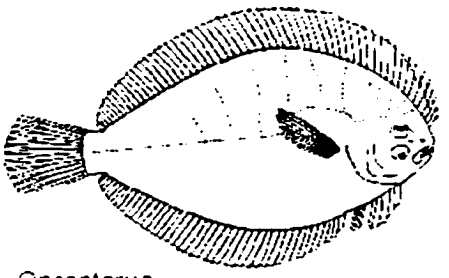


Fig. A1c: Tree representing the phenetic relationships found by Sakamoto (1984). G4, *Poecilopsetta beani*; G5, *P. praelonga*; G6, *P. plinthus*; G7, *P. albomarginata*; G8, *Nematops macrochirus*; G9, *Pelotretis flavilatus*; H1, *Azygopus pinnifasciatus pinnifasciatus*; H2, *Ammotretis rostratus*; H3, *A. lituratus*; H4, *A. elongatus*; H5, *Taratretis derwentensis*; H6, *Rhombosolea plebeia*; H7, *R. tapirina*; H8, *R. leporina*; H9, *Peltorhampus novaezeelandiae*; I1, *P. latus*; I2, *Samaris cristatus*; I3, *Plagiopsetta glossa*; I4, *Samariscus latus*; I5, *S. xenicus*. The upper part of the tree was truncated to keep only the species of interest.

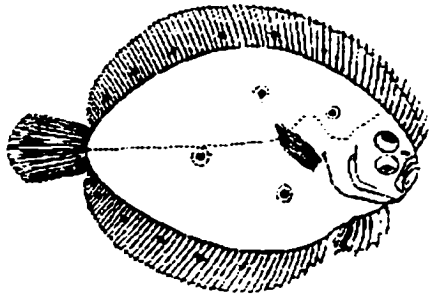
APPENDIX 2

General body outline of the genera hypothesised to belong to the family Rhombosoleidae

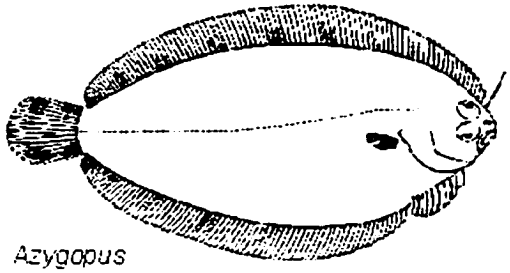




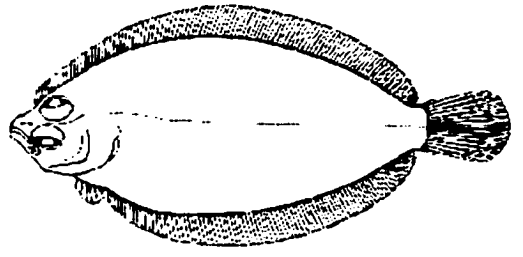
Oncopterus



Psammodiscus



Azygopus



Mancopsetta

APPENDIX 3

List of characters used for the order level phylogeny (modified from Hoshino 2001b, see Materials and methods):

Character 1: Teeth on ocular side premaxilla: (0) present; (1) absent.
Character 2: Vomerine teeth: (0) present; (1) absent.
Character 3: Pterosphenoid: (0) present; (1) absent.
Character 4: Epioccipitals and foramen magnum: (0) epioccipitals not forming margin of the foramen magnum; (1) epioccipitals forming margin of the foramen magnum.
Character 5: Ventral margin of foramen magnum and relation between zygapophyses: (0) exoccipitals forming the ventral margin of foramen magnum, with zygapophyses attached; (1) exoccipitals forming the ventral margin of the foramen magnum, but zygapophyses not mutually attached; (2) basioccipital forming ventral margin of foramen magnum.
Character 6: Blind side infraorbitals: (0) present; (1) absent.
Character 7: Ocular side infraorbitals: (0) present; (1) absent.
Character 8: Articulation of hyomandibular bone to cranium: (0) hyomandibula articulated to cranium with posterodorsal margin; (1) hyomandibula articulated with long posterodorsal process.
Character 9: Postcleithra and coracoscapular complex on the blind side: (0) developed; (1) reduced or absent.
Character 10: Shape and orientation of the first proximal radial of the dorsal fin: (0) first proximal radial without long anterior process; (1) almost parallel orientation over orbital region; (2) with long anterior process extending anteriorly.
Character 11: Teeth on epibranchial 3: (0) present; (1) absent.
Character 12: Shape of the anteriormost anal proximal radial: (0) short; (1) elongated.
Character 13: Pelvic fin spine: (0) present; (1) absent.
Character 14: Neural arch and spine on first abdominal vertebrae: (0) both present; (1) neural spine absent; (2) incomplete neural arch.
Character 15: Fusion of hypurals 1 and 2, and 3 and 4 respectively: (0) neither pair fused; (1) components of both pairs fused.
Character 16: Articulation of hypurals 1 and 2 to preural centrum 1: (0) hypural 1 and 2 in contact with preural centrum 1, lacking a large articulation surface; (1) with a tight and wide articulation surface.
Character 17: Fusion of hypurals 3 and 4 to preural centrum 1: (0) no fusion; (1) fusion.
Character 18: Fusion of proximal tip of hypurals to preural centrum 1: (0) No fusion; (1) fusion.
Character 19: Edge of preopercule: (0) visible; (1) concealed by skin.
Character 20: Blind side endopterygoid: (0) present; (1) absent.
Character 21: Fimbriation of opercular series: (0) absent; (1) opercular bones deeply fimbriated.
Character 22: Shape of the blind side dentary: (0) not markedly convex; short or deep (1) convex, short and deep.
Character 23: Fusion of the haemal arch to preural centrum 2: (0) absent; (1) present.
Character 24: Relationship of parhypural to preural centrum 1: (0) articulated; (1) detached.
Character 25: Branchiostegal membranes on both sides: (0) separated; (1) fused.
Character 26: Position of the opening of the blind side preopercular canal: (0) anteroventral tip of preopercle; (1) along the ventral margin of preopercle.
Character 27: Contribution of blind side frontal to margin of upper orbit: (0) contribution important; (1) contribution minimal; (2) contribution nil.

Character 28: Continuity of skin on lower jaw and interopercle: (0) not continuous ventrally; (1) continuous.
Character 29: Relationship between blind side sphenotic and blind side lateral ethmoid: (0) generally detached; (1) mutually attached.
Character 30: Arterial canal on anterior ceratohyal: (0) canal generally running along external surface of anterior ceratohyal; (1) perforating anterior ceratohyal.
Character 31: Interarcual cartilage: (0) interarcual cartilage well developed, rodlike; (1) tiny and granular or absent.
Character 32: Sensory canal in supracleithrum: (0) sensory canal of lateral line system present in supracleithrum; (1) absent.
Character 33: Internal dorsolateral wing of pelvic plate: (0) pelvic plate with internal dorsolateral wing posterodorsally positioned, that on blind side not bent toward ocular side; (1) that on blind side bent toward ocular side.
Character 34: Anterior inclination of the second neural spine: (0) second neural spine erect, generally detached from cranium; (1) inclined anteriorly with distal part overlying the cranium.
Character 35: Uroneural 1: (0) present; (1) absent.
Character 36: Uroneural 2: (0) autogenous uroneural 2 present; (1) absent.
Character 37: Number of principal caudal fin rays: (0) 17; (1) fewer than 17.
Character 38: Number of procurrent rays: (0) 3 procurrent rays in each lobe of caudal fin; (1) two; (2) one or absent.
Character 39: Relationship between first dorsal proximal radial and blind side lateral ethmoid: (0) First dorsal proximal radial generally detached distally from blind side lateral ethmoid; (1) firmly wedged into notch of blind side lateral ethmoid.
Character 40: Anterior dorsal proximal radials: (0) anterior dorsal proximal radials generally not mutually attached; (1) tightly mutually attached.
Character 41: Stay of the dorsal and anal pterygiophores: (0) stay present; (1) absent.
Character 42: Hypochordal longitudinalis: (0) Hypochordal longitudinalis with tow tendons inserted onto two uppermost principal rays; (1) with one tendon inserted onto uppermost principal ray; (2) absent.
Character 43: Interradialis between principal ray and procurrent ray: (0) a bundle of interradialis present between outermost principal ray and a most medial procurrent ray in each lobe; (1) absent.
Character 44: Pseudo-interradialis: (0) pseudo-interradialis generally absent; (1) present.
Character 45: Blind side posterior nostril: (0) blind side posterior nostril generally moderate in size; (1) considerably enlarged.

APPENDIX 4

List of characters used in the analysis of the interrelationships of the Rhombosoleidae

Character 1. Shape of hypural plates: undivided plates (state 0), subdivided plates (state 1). Apomorphic state found in *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, and *R. tapirina*. (Sakamoto, 1984)

Character 2. Hypural plates and last caudal vertebra: hypural plates not fused to the centrum of the last caudal vertebra (state 0), fused to the centrum of the last caudal vertebra (state 1). Apomorphic state found in *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, and *R. tapirina*. (Hensley and Ahlstrom, 1984; Sakamoto, 1984; Chapleau, 1993)

Character 3. Number of caudal fin rays: generally 20 rays (state 0), generally 18 rays (state 1). Apomorphic state found in: *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Caudal fin rays in Rhombosoleidae.-Sakamoto (1984), the author of a phenetic study of the interrelationships between the subfamilies (elevated to the family level by Cooper and Chapleau, 1998) of the Pleuronectidae gathered a wealth of information on the taxa studied. Among this information was the phenotypes found for the fin rays on the caudal skeleton within the family Rhombosoleidae. Table A6.1 and A6.2 show the phenotype (unsegmented, segmented and branched) and their distribution among the family. Table A6.1 show the data collected by Sakamoto (in bold) and data collected on specimens observed for this analysis. From this table, it is obvious that there is a wide range of phenotypes observed within the family Rhombosoleidae. Furthermore, some species show great variability in the number and distribution of caudal fin rays (*Oncopterus*, for example) while others are highly conserved (*Ammotretis elongatus*, *A. lituratus* and *Pelotretis*). From the absence/presence data (Table A6.2) it is possible to see that three caudal fin patterns are mainly found in the Rhombosoleidae, all of them have a total of 18 caudal fin rays. Since some species within the group could be found to show the three patterns, it was decided to use the total number of caudal fin rays (mainly 18) for the analysis.

Hoshino (2001a) wrote about the homology of the caudal fin rays in the Pleuronectiformes. He insists on the fact that caudal fin rays and their phenotype have been used in phylogenies without proper testing of their homology. One conclusion of the paper is that principal rays should be separated from total fin rays and that procurrent rays should be separated from total number of caudal fin rays in a cladistic analysis. The definitions of those procurrent and principal rays are based on association of these rays with muscles of the caudal fin. As mentioned earlier, the paper deals with caudal fin rays homology at the level of order. Every family is represented within the order but the Rhombosoleidae are represented by only three species out of 20 historically included in the family. This is understandable due to the limited number of specimens available to the author and to the enormous amount of work necessary to study most of the species in the order.

For this study of the Rhombosoleidae, the procurrent and principal rays were not separated. The total number of caudal fin rays was used since the number of principal and procurrent rays were not known for the majority of taxa within the family.

Character 4. Ocular side pelvic and anal fin: not united by a membrane (state 0), united by a membrane (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*. (Sakamoto, 1984)

Character 5. Number of pelvic fin rays on the blind side: 5-7 fin rays (state 0), 3-4 fin rays (state 1), 0 fin ray (state 2). First apomorphic state found in *Ammotretis elongatus*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae* and *P. tenuis*. Second apomorphic state found in *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*. This character was ordered.

Character 6. Number of pelvic fin rays on the ocular side: 5-6 fin rays (state 0), 7-10 fin rays (state 1), 11+ fin rays (state 2). First apomorphic state found in *Ammotretis brevipinnis*, *A. lituratus*. *A. rostratus* and *Colistium nudipinnis*. Second apomorphic state *A. elongatus*, *A. macrolepis* and *C. guntheri*. This character was ordered.

Character 7. Cartilage on the pelvic fin on the ocular side: uniform cartilage (state 0), basic radials only (state 1) and multiple cartilaginous blocs (state 2). Unordered. First apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis* and *A. rostratus*. Second apomorphic state found in *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 8. Number of pterygiophores over the cranium: 1-2 (state 0), 6-14 (state 1), 15-23 (state 2), 23+ (state 3). First apomorphic state found in *Pelotretis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*. Second apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri* and *C. nudipinnis*. Third apomorphic state found in *Peltorhamphus latus*, *P. novaezeelandiae* and *P. tenuis*.

Character 9. Postcleithral bone of the pectoral fin on the ocular side: two bones (state 0), one bone (state 1), absence of bone (state 2). Unordered. First apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, and *Pelotretis*. Second apomorphic state found in *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*. (Hensley and Ahlstrom, 1984; Sakamoto, 1984)

Character 10. Bony tubercle on the tip of the first pectoral fin ray on the blind side: absent (state 0) present (state 1). Apomorphic state found in *A. brevipinnis* and *A. lituratus*.

Character 11. Sensory canal in the preorbital bone on the blind side: present (state 0), absent (state 1). Apomorphic state found in *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *R. plebeia* and *R. tapirina*.

Character 12. Relationship between coracoid and cleithrum on the ocular side: coracoid does not touch the cleithrum for most of its length (state 0), coracoid touches the cleithrum for most of its length (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 13. Projection of the first anal fin pterygiophore: thick and short projection (state 0), thin and long projection (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 14. Olfactory papilla: with central rachis (state 0), without central rachis (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 15. Fringed lower lip on the ocular side: absence (state 0), present and short fringes (state 1), present and long fringes (state 2). Unordered. First apomorphic state found in *A. brevipinnis*, *A. macrolepis*, *A. rostratus* and *Taratretis*. Second apomorphic state found in *A. elongatus*, *A. lituratus*, *Colistium guntheri* and *C. nudipinnis*.

Character 16. Scales on the eyes: absent (state 0) present (state 1). Apomorphic state found in *Pelotretis*. (Sakamoto, 1984)

Character 17. Gill rakers on the second epibranchial bone: present (state 0), absent (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 18. Second row of gill rakers on 3rd and 4th ceratobranchials: absent (state 0), present (state 1). Apomorphic state found in *P. latus*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 19. Scales on the dorsal fin rays: absent (state 0) present (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus* and *Pelotretis*. (Sakamoto, 1984)

Character 20. Scales on the ocular side: cycloid (state 0), ctenoid (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, and *Taratretis*.

Character 21. Lateral line on the ocular side: with a strong curve over the pectoral fin (state 0), without a strong curve over the pectoral fin (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina*, and *Taratretis*.

Character 22. Hyomandibular foramen on the ocular side: small (state 0) or large (state 1). Apomorphic state found in *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 23. Orientation of the hemapophyses of the 4th abdominal vertebra: anterodorsal orientation (state 0) or anteroventral orientation (state 1). Apomorphic state found in *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 24. Foramen on the labial portion of the head of the maxilla of the ocular side: absent (state 0), present (state 1). Apomorphic state found in *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 25. Flap of skin covering the jaws on the ocular side: absent (state 0), present (state 1). Apomorphic state found in *Peltorhamphus latus*, *P. novaezeelandiae* and *P. tenuis*.

Character 26. Elongation of the second pectoral fin ray on the ocular side: absent (state 0), present (state 1). Apomorphic state found in *Peltorhamphus latus*, *P. novaezeelandiae* and *P. tenuis*.

Character 27. Nasal bone on the blind side: opens on the blind side (state 0) opens on both sides (state 1) opens on ocular side (state 2). Unordered. First apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*. Second apomorphic state found in *Colistium nudipinnis*.

Character 28. Shape of the nasal bone of the blind side: I-shaped (state 0), Y-shaped (state 1), U-shaped (state 2). Unordered. First apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium nudipinnis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis* and *Taratretis*. Second apomorphic state found in *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 29. Teeth on ocular side dentary: present (state 0), absent (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*. (Chapleau, 1993)

Character 30. Bony projection on the articular bone of the blind side: present (state 0) absent (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 31. Urinary papilla: on the ocular side (state 0) on the mid-ventral line (state 1). Apomorphic state found in *R. leporina*, *R. plebeia* and *R. tapirina*. (Hensley and Ahlstrom, 1984)

Character 32. Dentary bone on the blind side: elongated under the articular bone (state 0), not elongated under the articular bone (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 33. Lower jaws: symmterical (state 0), asymmetrical (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Peltorhamphus latus*, *P. novaezeelandiae* and *P. tenuis*. (Sakamoto, 1984)

Character 34. Posterodorsal flange on the ocular side articular bone: big (state 0), small or absent (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 35. Posterodorsal flange on the blind side articular bone: big (state 0), small or absent (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 36. Foramen magnum and both epioccipital bones: epioccipitals not forming the dorsal portion of the foramen magnum (state 0), epioccipitals forming the dorsal portion of the foramen magnum (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Azygopus pinnifasciatus flemingi*, *A. p. pinnifasciatus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*. (Sakamoto, 1984; Chaleau 1993)

Character 37. Pterosphenoid bone on the blind side: present (state 0), absent (state 1). Apomorphic state found in *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*. (Sakamoto, 1984; Chapleau, 1993)

Character 38. Sensory canal in the epioccipital on the ocular side: absent (state 0) present (state 1). Apomorphic state found in *Peltorhamphus latus*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 39. Blind side frontal in interorbital process: present (state 0) absent (state 1). Apomorphic state found in *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 40. Sensory canal between both frontal bones: presence of a canal (state 0), absence of canal (state 2). Apomorphic state found in *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 41. Number of caudal vertebrae: 21-29 (state 0), 30-34 (state 1), 35+ (state 2). Unordered. First apomorphic state found in *Pelotretis* and *Peltorhamphus tenuis*. Second apomorphic state found in *Mancopsetta*. *Poecilopsetta* is coded 0/1 for this character.

Character 42. Supraoccipital over upper orbit: no projection of the supraoccipital over the upper orbit (state 0), projection of the supraoccipital over the orbit (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina*, and *Taratretis*.

Character 43. Bony support for the dorsal fin pterygiophore over the cranium: absent (state 0) present (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P.*

novaezeelandiae, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 44. Occipital condyle: formed by a round basioccipital (state 0), formed by the zygapophyses of both exoccipitals and the basioccipital (state 1). Apomorphic state found in *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.
Occipital condyle in Pleuronectiformes: Poecilopsetta, the most plesiomorphic outgroup was coded 1 for this character because this type of occipital condyle, formed by the exoccipitals and the basioccipital seems to be apomorphic for the order.

Character 45. Supratemporal section of the lateral line on the ocular side: bones absent (state 0), one bone (state 1), more than one bone (state 2). First apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis* and *R. retiaria*. Second apomorphic state found in *R. leporina*, *R. plebeia*, *R. tapirina* and *Taratretis*. This character was ordered.

Character 46. Shape of the bone in the supratemporal section of the lateral line: tube-shape (state 0), larger than the tube (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *P. latus* and *P. novaezeelandiae*.

Character 47. Supratemporal section of the lateral line on the blind side: bones absent (state 0), one or more bones (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 48. Orbital series (excluding lachrymal) on the ocular side: one or two bones (state 0), no bones (state 1). Unordered. Apomorphic state found in *Pelotretis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 49. Orbital series on the blind side: orbitals and lachrymal (state 0), no orbitals and lachrymal (state 1). Apomorphic state found in *Achiropsetta*, *Mancopsetta* and *Poecilopsetta*.
Orbital bones in Rhombosoleidae: For this character the outgroups are coded as the apomorphic state since the absence of orbitals is apomorphic at the order level.

Character 50. Relationship between exoccipital and prootic on the ocular side: exoccipital touching the prootic (state 0), exoccipital not touching the prootic (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 51. Cartilage between the basioccipital and the prootic: big and round cartilage (state 0), small cartilage (state 1). Apomorphic state found in *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae* and *P. tenuis*.

Character 52. Sensory canal on the parietal on the blind side: absent (state 0), present (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*,

A. macrolepis, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *P. latus*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 53. Length of the sciatic part of the urohyal: short or not extending beyond the main part of the bone (state 0), long, extending anteriorly in front of the main part of the bone (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 54. Length of hemapophyses on precaudal vertebrae: progressively longer posteriorly (state 0), all of equal length (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. lituratus*, and *A. rostratus*.

Character 55. Contact between elongated hemapophyses of last precaudal vertebrea and anterior margin of the first pterygiophore of the anal fin: no contact (state 0), contact (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 56. Radials on both pectoral girdles: present (state 0) absent (state 1). Apomorphic state found in *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 57. Fin rays on anteriormost pterygiophore of dorsal fin: two (state 0), one (state 1). Apomorphic state found in *R. plebeia* and *R. tapirina*.

Character 58. Scales on ocular side pectoral fin: absent on most of the fin (state 0), present on most of the fin (state 1). Apomorphic state found in *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae* and *P. tenuis*.

Character 59. Cardiac part of urohyal: split (state 0), straight (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 60. Size of ethmoid: moderate (state 0), small (state 1). Apomorphic state found in *Rhombosolea leporina*, *R. plebeia*, *R. retiaria* and *R. tapirina*.

Character 61. Blind side palatine bone: with a projection under the ectopterygoid (state 0), without a projection under the ectopterygoid (state 1). Apomorphic state found in *Peltorhamphus latus*, *P. novaezeelandiae* and *P. tenuis*.

Character 62. Ocular side palatine bone: with a projection under the ectopterygoid (state 0), without a projection under the ectopterygoid (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 63. Branchiostegal membranes: fused (state 0), not fused (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Branchiostegal membranes: The fusion of the branchiostegal membranes is assumed to be apomorphic at the order level, this is why *Poecilopsetta* is coded 1.

Character 64. Number of anal fin rays associated with cartilaginous radials under the modified pterygiophore of the anal fin: one ray (state 0), two or more rays (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae*, *P. tenuis*, *Rhombosolea leporina*, *R. plebeia*, *R. retiaria*, *R. tapirina* and *Taratretis*.

Character 65. Labial portion of ocular side premaxilla: longer than rostral portion (state 0), shorter than the rostral portion (state 1). Apomorphic state found in *Pelotretis*, *Peltorhamphus latus*, *P. novaezeelandiae* and *P. tenuis*.

Character 66. Dorsal fin: not prolonged in front of mouth (state 0), prolonged in front of mouth (state 1). Apomorphic state found in *Ammotretis brevipinnis*, *A. elongatus*, *A. lituratus*, *A. macrolepis*, *A. rostratus*, *Colistium guntheri*, *C. nudipinnis*, *Peltorhamphus Peltorhamphus latus*, *P. novaezeelandiae* and *P. tenuis*. (Sakamoto, 1984)

Character 67. Neuromasts on the blind side of the head: absent (state 0), present (state 1). Apomorphic state found in *A. brevipinnis*, *A. elongatus*, *A. lituratus*, *A. rostratus*, *C. nudipinnis*, *Peltorhamphus latus*, *P. novaezeelandiae* and *P. tenuis*.

Character 68. Gill rakers on the 1st epibranchial bone: present (state 0), absent (state 1). Apomorphic state found in *Ammotretis brevipinnis, A. elongatus, A. lituratus and A. macrolepis*.

Appendix 5

Characters used only in the preliminary analysis to determine the monophyly of the Rhombosoleidae.

A5-1: Fusion of hypural plates: hypurals 1+2+3+4 not fused together (state 0), hypurals 1+2+3+4 fused together (state 1), hypurals 2+3+4 fused together (state 2). Unordered. First apomorphic state found in: *Peltorhamphus* and *Rhombosolea*. Second apomorphic state found in *Psammodiscus*.

A5-2: Caudal fin ray articulating on neural spine of PU2 and on the epural: present on neural spine (state 0), absent on neural spine but present on epural (state 1), absent on both neural spine and epural (state 2). First apomorphic state found in *Azygopus* and *Mancopsetta*. Second apomorphic state found in *Psammodiscus* and *Oncopterus*. This character was ordered.

A5-3: Elongation of the first dorsal fin ray: absent (state 0), present (state 1). Apomorphic state found in *Azygopus*.

A5-4: Last pelvic fin rays of the ocular side: on the mid-ventral line (state 0), on the ocular side (state 1). Apomorphic state found in *Azygopus*, and *Mancopsetta*.

A5-5: Pterosphenoid bone on the ocular side: present (state 0), absent (state 1). Apomorphic state found in *Azygopus* and *Mancopsetta*.

A5-6: Position of the vomer: the vomer is the anteriormost bone in the cranium (state 0), the vomer is not the anteriormost bone in the cranium (state 1). Apomorphic state found in *Oncopterus* and *Pelotretis*.

A5-7: Foramen in ethmoid bone: absent (state 0), present (state 1). Apomorphic state found in *Oncopterus* and *R. leporina*.

A5-8: Teeth on 3rd hypobranchial: absent (state 0), present (state 1). Apomorphic state found in *Oncopterus* and *Psammodiscus*.

A5-9: Toothed bony plates on 3rd ceratobranchials: present (state 0), absent (state 1). Apomorphic state found in *Ammotretis*, *Azygopus*, *C. nudipinnis*, *Mancopsetta*, *Pelotretis*, *Peltorhamphus*, *Rhombosolea* and *Taratretis*.

A5-10: Caudal fin ray articulating on the hemal spine of PU2: present (state 0), absent (state 1). Apomorphic state found in *Psammodiscus*

A5-11: Teeth on third epibranchial bone: absent (state 0) present (state 1). Apomorphic state found in *Psammodiscus*.

A5-12: Sensory canal on the sphenotic on the blind side: absent (state 0), present (state 1). Apomorphic state found in *Oncopterus*.

A5-13: Relationship between sphenotic and lateral ethmoid on the blind side: sphenotic not in contact with lateral ethmoid (state 0), sphenotic in contact with lateral ethmoid (state

1). Apomorphic state found in *Oncopterus*.

A5-14: Position of the vomer: the vomer is the anteriormost bone in the cranium (state 0), the vomer is not the anteriormost bone in the cranium (state 1). Apomorphic state found in *Oncopterus* and *Pelotretis*.

A5-15: Angle in the sensory canal in the ocular side pterotic: more than 90° (state 0), less than 90° (state 1). Apomorphic state found in *Pelotretis*

A5-16: Ethmoid in relation to upper orbit: ethmoid forming part of the upper orbit (state 0), ethmoid not forming part of the upper orbit (state 1). *Ammotretis*, *Azygopus*, *C. nudipinnis*, *Mancopsetta*, *Peltorhamphus*, *Psammodiscus*, *Rhombosolea Taratretis*, and *Poecilopsetta*.

A5-17: Shape of urohyal: fishhook shape (state 0), plate-like with small anterodorsal hook (state 1). Apomorphic state found in *Oncopterus*.

A5-18: Small bony protuberance on dorsal margin of sciatic part of urohyal: absent (state 0) present (state 1). Apomorphic state found in *A. macrolepis*.

A5-19: Ribs on the last precaudal vertebra: absent (state 0), present (state 1). Apomorphic state found in *Psammodiscus*,.

Characters kept in the final analysis but that were modified (see appendix 1 for their modification in the final analysis):

Character A5-40: Sensory canal between both frontal bones: canal is V-shaped (state 0), canal is I-shaped (state 1), no canal (state 2). Unordered. First apomorphic state found in *Azygopus*. Second apomorphic state found in *Rhombosolea*.

Character A5-41: Number of caudal vertebrae: 21-29 (state 0), less than 20 (state 1), 30-34 (state 2), 35+ (state 3). First apomorphic state found in *Oncopterus*. Second apomorphic state found in *Pelotretis* and *Peltorhamphus tenuis*. Third apomorphic state found in *Achiropsetta*, *Azygopus* and *Mancopsetta*.

APPENDIX 5 continued
Character states for characters used only in the preliminary analysis.

	A5-1	A5-2	A5-3	A5-4	A5-5	A5-6	A5-7	A5-8	A5-9	A5-10	A5-11	A5-12
Azygopus p. p.	0	1	1	1	1	0	0	0	1	0	0	0
Azygopus p. f.	0	1	1	1	1	0	0	0	1	0	0	0
Oncopterus	0	2	0	0	0	1	1	1	0	0	0	1
Psammodiscus	1	2	0	0	0	0	0	1	0	1	1	0
Ammotretis brevipinnis	0	0	0	0	0	0	0	0	1	0	0	0
A. elongatus	0	0	0	0	0	0	0	0	1	0	0	0
A. lituratus	0	0	0	0	0	0	0	0	1	0	0	0
A. macrolepis	0	0	0	0	0	0	0	0	1	0	0	0
A. rostratus	0	0	0	0	0	0	0	0	1	0	0	0
Colistium guntheri	0	0	0	0	0	0	0	0	?	0	?	?
C. nudipinnis	0	0	0	0	0	0	0	0	1	0	0	0
Pelotretis flavilatus	0	0	0	0	0	1	0	0	1	0	0	0
Peltorhamphus latus	1	0	0	0	0	0	0	0	1	0	0	0
P. novaezeelandiae	1	0	0	0	0	0	0	0	1	0	0	0
P. tenuis	1	0	0	0	0	0	0	0	1	0	0	0
Rhombosolea leporina	1	0	0	0	0	0	1	0	1	0	0	0
R. plebeia	1	0	0	0	0	0	0	0	1	0	0	0
R. retiaria	1	0	0	0	0	0	0	0	1	0	0	0
R. tapirina	1	0	0	0	0	0	0	0	1	0	0	0
Taratretis	0	0	0	0	0	0	0	0	1	0	0	0
Mancopsetta	0	1	0	1	1	0	0	0	1	0	0	0
Poecilopsetta	0	0	0	0	0	0	0	0	0	0	0	0

	A5-13	A5-14	A5-15	A5-16	A5-17	A5-18	A5-19
Azygopus p. p.	0	0	0	1	0	0	0
Azygopus p. f.	0	0	0	1	0	0	0
Oncopterus	1	1	0	1	1	0	0
Psammodiscus	0	0	0	1	0	0	1
Ammotretis brevipinnis	0	0	0	1	0	0	0
A. elongatus	0	0	0	1	0	0	0
A. lituratus	0	0	0	1	0	0	0
A. macrolepis	0	0	0	1	0	1	0
A. rostratus	0	0	0	1	0	0	0
Colistium guntheri	0	?	?	?	0	0	0
C. nudipinnis	0	0	0	1	0	0	0
Pelotretis flavilatus	0	1	1	0	0	0	0
Peltorhamphus latus	0	0	0	1	0	0	0
P. novaezeelandiae	0	0	0	1	0	0	0
P. tenuis	0	0	0	1	0	0	0
Rhombosolea leporina	0	0	0	1	0	0	0
R. plebeia	0	0	0	1	0	0	0
R. retiaria	0	0	0	1	0	0	0
R. tapirina	0	0	0	1	0	0	0
Taratretis	0	0	0	1	0	0	0
Mancopsetta	0	0	0	1	0	0	0
Poecilopsetta	0	0	0	1	0	0	0

APPENDIX 5 continued

Character states for taxa removed from the final analysis of the Rhombosoleidae. For characters 40 and 41 see characters A5-40 and A5-41.

	1	2	3	4	5	6	7	8	9	10	11	12
Azygopus p. p.	0	0	1	0	0	0	1	1	1	0	0	1
Azygopus p. f.	0	0	1	0	0	0	1	1	1	0	0	1
Oncopterus	0	0	1	0	0	0	0	1	1	0	0	0
Psammodiscus	1	1	2	0	0	0	0	1	0	0	0	0

	13	14	15	16	17	18	19	20	21	22	23	24
Azygopus p. p.	1	0	0	1	0	0	0	1	1	0	0	0
Azygopus p. f.	1	0	0	1	1	0	0	1	1	0	0	0
Oncopterus	0	0	0	0	0	0	0	1	0	0	0	0
Psammodiscus	0	0	0	0	0	0	1	0	0	0	0	0

	25	26	27	28	29	30	31	32	33	34	35	36
Azygopus p. p.	0	0	0	0	0	0	0	0	0	1	1	1
Azygopus p. f.	0	0	0	0	0	0	0	0	0	1	1	1
Oncopterus	0	0	0	0	0	0	0	0	0	0	0	0
Psammodiscus	0	0	0	0	0	0	0	0	0	0	0	0

	37	38	39	42	43	44	45	46	47	48	49	50
Azygopus p. p.	1	0	1	1	0	0	1	0	0	1	0	1
Azygopus p. f.	1	0	1	1	0	0	1	0	0	1	0	1
Oncopterus	0	0	0	0	1	0	1	0	1	0	0	0
Psammodiscus	0	0	0	1	1	0	2	0	1	0	0	1

	51	52	53	54	55	56	57	58	59	60	61	62
Azygopus p. p.	1	1	1	0	0	0	0	0	0	0	0	1
Azygopus p. f.	1	1	1	0	0	0	0	0	0	0	0	1
Oncopterus	0	1	0	0	0	0	0	0	0	0	0	0
Psammodiscus	1	0	1	0	1	0	0	0	1	0	0	0

	63	64	65	66	67	68
Azygopus p. p.	0	1	0	0	0	0
Azygopus p. f.	0	1	0	0	0	0
Oncopterus	0	0	0	0	0	0
Psammodiscus	0	1	0	0	0	0

APPENDIX 6

Table A6.1: Distribution of caudal fin rays in the Rhombosoleidae.

	16 1+1+11+2+1	16 0+2+12+2+0	16 0+1+14+1+0	17 1+1+12+2+1	17 1+2+12+1+1	17 1+1+13+1+1	18 1+4+8+4+1	18 1+3+10+3+1	18 1+2+11+3+1
Oncopterus					**2**				1
Psammodiscus		**5**							
Pelotretis									
Azygopus p. p.									
A. pinnifasciatus flemingi									1
Ammotretis rostratus									
A. brevipinnis									
A. lituratus									
A. macrolepis									
A. elongatus									
Taratretis	**1**			**1**					
Colistium nudipinnis									
C. guntheri									
Rhombosolea retiaria									
R. plebeia									
R. tapirina									
R. leporina									
Peltorhamphus novaezeelandiae								**1 + 5**	**2 + 1**
P. latus							**1**	**5 + 4**	1
P. tenuis								**2**	
Mancopsetta			**1**			**1**			
Totals	1	5	1	1	2	1	1	17	6

Numbers in bold represent data taken from Sakamoto (1984).

	18 1+3+11+2+1	18 1+2+12+2+1	18 1+2+12+3+0	18 0+3+12+3+0	18 0+3+12+2+1	18 1+1+13+2+1	18 1+2+13+1+1	18 0+3+13+2+0	18 0+1+13+4+0
Oncopterus		3				1			
Psammodiscus									
Pelotretis									
Azygopus p. p.						3 + 1			
A. pinnifasciatus flemingi	1	3				3			
Ammotretis rostratus		8 + 5				1			
A. brevipinnis		4							
A. lituratus		4 + 3							
A. macrolepis		1				1			
A. elongatus								1	1
Taratretis		1 + 2				1	1		
Colistium nudipinnis						1	1		
C. guntheri		3							
Rhombosolea retiaria		5		1					
R. plebeia		3		1 + 4		1			
R. tapirina	1	1 + 6	1	1		1	1		
R. leporina		5 + 6	1	10	1		2		
Peltorhamphus novaezeelandiae		2							
P. latus		1							
P. tenuis		1							
Mancopsetta		1				1			
Totals	2	68	2	17	1	15	5	1	1

	18 0+2+13+3+0	18 1+1+14+1+1	18 0+2+14+1+1	18 0+2+14+2+0	18 ?	19 1+1+14+2+1	19 1+4+10+3+1	Totals
Oncopterus		1						3
Psammodiscus								5
Pelotretis		14 + 1						15
Azygopus p. p.		2 + 5						11
A. pinnifasciatus flemingi		8						1
Ammotretis rostratus		1						15
A. brevipinnis					1			0
A. lituratus								7
A. macrolepis		2			1			0
A. elongatus				4 + 6				12
Taratretis		5				1		13
Colistium nudipinnis		1 + 2						5
C. guntheri	1			1				0
Rhombosolea retiaria		1						0
R. plebeia								9
R. tapirina	1		1					14
R. leporina						1		26
Peltorhamphus novaezeelandiae								11
P. latus								12
P. tenuis							1	4
Mancopsetta								4
Totals	2	43	1	11	2	2	1	167

Table A6.2: Presence/absence data on caudal fin rays in Rhombosoleidae.

	16 1+1+11+2+1	16 0+2+12+2+0	16 0+1+14+1+0	17 1+1+12+2+1	17 1+2+12+1+1	17 1+1+13+1+1	18 1+4+8+4+1	18 1+3+10+3+1	18 1+2+11+3+1
Oncopterus					1				1
Psammodiscus		1							
Pelotretis									
Azygopus p. p.									
A. pinnifasciatus flemingi									1
Ammotretis rostratus									
A. brevipinnis									
A. lituratus									
A. macrolepis									
A. elongatus									
Taratretis	1			1					
Colistium nudipinnis									
C. guntheri									
Rhombosolea retiaria									
R. plebeia									
R. tapirina									
R. leporina									
Peltorhamphus novaezeelandiae								1	1
P. latus							1	1	1
P. tenuis								1	
Mancopsetta			1			1			
Totals	1	1	1	1	1	1	1	3	4

	18 1+3+11+2+1	18 1+2+12+2+1	18 1+2+12+3+0	18 0+3+12+3+0	18 0+3+12+2+1	18 1+1+13+2+1	18 1+2+13+1+1	18 0+3+13+2+0	18 0+1+13+4+0
Oncopterus		1				1			
Psammodiscus									
Pelotretis									
Azygopus p. p.						1			
A. pinnifasciatus flemingi	1	1				1			
Ammotretis rostratus		1				1			
A. brevipinnis		1							
A. lituratus		1							
A. macrolepis		1				1		1	1
A. elongatus									
Taratretis		1				1			
Colistium nudipinnis						1	1		
C. guntheri		1							
Rhombosolea retiaria		1		1					
R. plebeia		1		1		1			
R. tapirina	1	1	1	1		1	1		
R. leporina		1	1	1	1		1		
Peltorhamphus novaezeelandiae		1							
P. latus		1							
P. tenuis		1							
Mancopsetta		1							
Totals	2	16	2	4	1	9	3	1	1

	18 0+2+13+3+0	18 1+1+14+1+1	18 0+2+14+1+1	18 0+2+14+2+0	18 ?	19 1+1+14+2+1	19 1+4+10+3+1	
Oncopterus		1						2
Psammodiscus								1
Pelotretis		1						0
Azygopus p. p.		1						0
A. pinnifasciatus flemingi		1						1
Ammotretis rostratus		1						0
A. brevipinnis					1			0
A. lituratus								0
A. macrolepis		1			1			0
A. elongatus				1				0
Taratretis		1				1		2
Colistium nudipinnis		1						0
C. guntheri	1			1				0
Rhombosolea retiaria		1						0
R. plebeia								0
R. tapirina	1		1					0
R. leporina						1		0
Peltorhamphus novaezeelandiae								2
P. latus								3
P. tenuis							1	1
Mancopsetta								2
Totals	2	9	1	2	2	2	1	