



uOttawa

L'Université canadienne  
Canada's university

FACULTÉ DES ÉTUDES SUPÉRIEURES  
ET POSTDOCTORALES



uOttawa

L'Université canadienne  
Canada's university

FACULTY OF GRADUATE AND  
POSTDOCTORAL STUDIES

Holly Rae Stephens

AUTEUR DE LA THÈSE / AUTHOR OF THESIS

M.Sc. (Biology)

GRADE / DEGREE

Department of Biology

FACULTÉ, ÉCOLE, DÉPARTEMENT / FACULTY, SCHOOL, DEPARTMENT

Taxonomic Revision of the Flatfish Genera *Zebrias* Jordan and Snyder, 1900 and *Pseudaesopia*  
Chabanaud, 1934 with Notes on *Aesopia* Kaup, 1858 (Pleuronectiformes: Soleidae)

TITRE DE LA THÈSE / TITLE OF THESIS

François Chapleau

DIRECTEUR (DIRECTRICE) DE LA THÈSE / THESIS SUPERVISOR

CO-DIRECTEUR (CO-DIRECTRICE) DE LA THÈSE / THESIS CO-SUPERVISOR

Guy Drouin

Lynn Gillespie

Kathleen Conlan

Gary W. Slater

Le Doyen de la Faculté des études supérieures et postdoctorales / Dean of the Faculty of Graduate and Postdoctoral Studies

Taxonomic revision of the flatfish genera *Zebrias* Jordan and Snyder, 1900 and  
*Pseudaesopia* Chabanaud, 1934 with notes on *Aesopia* Kaup, 1858 (Pleuronectiformes:  
Soleidae)

Holly R. Stephens

Thesis submitted to the Faculty of Graduate and Postdoctoral Studies

University of Ottawa

In partial fulfillment of the requirements for the M.Sc. degree in the

Ottawa-Carleton Institute of Biology

Thèse soumise à la Faculté des études supérieures et postdoctorales,

Université d'Ottawa

en vue de l'obtention de la maîtrise

L'Institut de biologie d'Ottawa-Carleton



Library and Archives  
Canada

Bibliothèque et  
Archives Canada

Published Heritage  
Branch

Direction du  
Patrimoine de l'édition

395 Wellington Street  
Ottawa ON K1A 0N4  
Canada

395, rue Wellington  
Ottawa ON K1A 0N4  
Canada

*Your file* *Votre référence*  
ISBN: 978-0-494-74168-9  
*Our file* *Notre référence*  
ISBN: 978-0-494-74168-9

**NOTICE:**

The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

**AVIS:**

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protègent cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

---

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

  
**Canada**

## ABSTRACT

The taxonomic status of the 25 nominal species of the Indo-Pacific flatfish genus *Zebrias* (Pleuronectiformes: Soleidae) was revised based on a morphological study of 531 specimens, including 36 type specimens. Two distinct, monophyletic groups were identified differing in the confluence and attachment of the caudal fin to adjacent dorsal and anal fins. Species most closely associated to the type species *Pleuronectes zebra* were included in the genus *Zebrias* while the remaining species were assigned to the genus *Pseudaesopia* to accommodate *Zebrias* species having a shallowly confluent caudal fin with adjacent fins, among other characters. Ten species are now recognized and re-described in *Zebrias* while six species are recognized and re-described in *Pseudaesopia*. Comprehensive generic definitions and identification keys to species are provided. In addition, the closely related and monospecific genus *Aesopia* is briefly discussed. Finally, potentially useful characters for a future phylogenetic study are discussed.

## RÉSUMÉ

Le statut taxinomique des 25 espèces nominales du genre indopacifique *Zebrias* (Pleuronectiformes: Soleidae) a été examiné suite à une étude morphologique de 531 spécimens incluant 36 spécimens types. Deux groupes monophylétiques ont été identifiés sur la base de la confluence et l'attachement de la nageoire caudale aux derniers rayons des nageoires anale et dorsale. Les espèces étroitement associées avec l'espèce type, *Pleuronectes zebra* ont été placées dans le genre *Zebrias*. Les autres espèces nominales ont été placées dans le genre *Pseudaesopia* pour accommoder les espèces ayant, entre autres caractères, une nageoire caudale peu confluyente avec les nageoires adjacentes. Dix espèces sont reconnues comme valides dans *Zebrias* alors que six espèces sont validées dans *Pseudaesopia*. Ces espèces sont re-décrites. Une définition exhaustive des genres ainsi que des clés d'identification des espèces sont présentées. Le statut du genre *Aesopia* est discuté brièvement. Finalement, des caractères potentiellement informatifs au niveau phylogénétique sont discutés.

## TABLE OF CONTENTS

<b>Acknowledgements</b> .....	vi
<b>List of Figures</b> .....	ix
<b>List of Tables</b> .....	xix
<b>Abstract</b> .....	1
<b>Résumé</b> .....	2
<b>General Introduction</b> .....	3
<b>Materials and Methods</b> .....	12
<b>Chapter 1: A revision of the flatfish genus <i>Zebrias</i> with notes on <i>Aesopia</i> (Pleuronectiformes: Soleidae)</b> .....	20
Abstract.....	21
Résumé.....	22
Introduction.....	23
Genus <i>Zebrias</i> .....	38
Descriptions	
<i>Zebrias altipinnis</i> .....	52
<i>Zebrias annularis</i> .....	59
<i>Zebrias cancellatus</i> .....	68
<i>Zebrias captivus</i> .....	77
<i>Zebrias craticula</i> .....	85
<i>Zebrias maculosus</i> .....	95
<i>Zebrias penescalaris</i> .....	100
<i>Zebrias quagga</i> .....	110

<i>Zebrias scalaris</i> .....	122
<i>Zebrias zebra</i> .....	131
Species Key.....	148
Genus <i>Aesopia</i> .....	151
References.....	159
<b>Chapter 2: A taxonomic revision of the flatfish genus <i>Pseudaesopia</i></b> <b>(Pleuronectiformes: Soleidae).....</b>	<b>185</b>
Abstract.....	186
Résumé.....	187
Introduction.....	188
Genus <i>Pseudaesopia</i> .....	196
Descriptions	
<i>Pseudaesopia callizona</i> .....	208
<i>Pseudaesopia cochinchinensis</i> .....	215
<i>Pseudaesopia japonica</i> .....	224
<i>Pseudaesopia lucapensis</i> .....	235
<i>Pseudaesopia regani</i> .....	242
<i>Pseudaesopia synapturoides</i> .....	251
Species Key.....	264
References.....	266
<b>General Conclusion.....</b>	<b>272</b>
<b>Phylogenetic Observations.....</b>	<b>274</b>
<b>Key to Genera.....</b>	<b>276</b>

**Appendix A**..... 280  
**Appendix B**..... 285  
**Appendix C**..... 290

## ACKNOWLEDGEMENTS

First and foremost, I would like to thank my supervisor, Dr. François Chapleau. I could not have asked for a better mentor. I thank him for his limitless patience and understanding, as well as his invaluable guidance over the years. His passion for flatfish is infectious and I am grateful to have had the opportunity to work with him.

I would also like to extend my sincerest thanks to the Smithsonian Institution in Washington, D.C. for granting me access to their facilities and collections, as well as the assistance I received during my visits. I am in deep gratitude to Dr. Thomas Munroe for his generous assistance throughout my thesis. His guidance and wealth of knowledge were of critical importance to my thesis and were greatly appreciated. Tom, it always brings a smile to my face when I recall your funny anecdotes. I would like to thank Martha for her wonderful hospitality; I had a wonderful time in Virginia with her and Tom and I will miss our breakfast excursions on Thursdays. I thank Cheryl Ames for leaving me with such wonderful memories of my time in Washington, particularly the Halloween spent in Old Virginia. I would also like to thank Sandra Raredon for training me in the use of x-ray equipment.

To the wonderful people in the Ichthyology Department at the Australian Museum, my exceptional experience in Australia was largely attributable to the wonderful staff I had the pleasure of working alongside. I thank Mark McGrouther, Amanda Hay, Michelle Yerman, Jeff Leis, John Paxton, Sally Reader, and Sascha Schulz for making me feel so welcome, and for all their help. I'd like to extend a special thank you to Amanda and James for their assistance in taking radiographs of my specimens.

In addition, I would like to thank my advisory committee members, Dr. Kathleen Conlan, Dr. Lynn Gillespie, and Dr. Keith Seifert. Their guidance, feedback, and expert advice were exceptionally helpful to me in structuring and focusing my study.

There are no words to describe how thankful I am for the endless support and encouragement of my friends and family. I am eternally grateful to my labmates, René Duplain, Krystal Lapierre, Josiane Vachon, our “unofficial labmate” Eric Young, and Matti Emery. I consider myself very lucky to have had the opportunity to work alongside such wonderful friends who were always available to assist me with my work or share in a laugh. Some of my best memories of this thesis are of the time we spent together. I would like to thank my mom, Charis, my father, Larry, and my twin sister, Carrie, for always believing in me, even at times when I doubted myself. The pride and encouragement they regularly expressed helped me continue to push forward and I will forever be grateful for that. I am also incredibly grateful to Monique Gaudreault for her invaluable support and assistance in making it through some of the more challenging aspects of my degree.

I am indebted to the institutions that provided the material examined over the course of this study and to the individuals who were so accommodating in arranging the loans that were crucial to this study: Lisa Palmer (USNM), Jeff Williams (USNM), Richard Vari (USNM), Kris Murphy (USNM), Jerry Finan (USNM), Jeff Clayton (USNM), Barbara Brown (AMNH), Mary Anne Rogers (FMNH), Mark Sabaj (ANSP), Phil Hastings (SIO), Dave Catania (CAS), Douglas Nelson (UMMZ), Jeff Seigel (LACM), Rick Feeney (LACM), Noel Alfonso (CMNFI, formerly NMC), Sylvie Laframboise (CMNFI, formerly NMC), Michael Bougaardt (SAM), Mark McGrouther (AMS), Amanda Hay (AMS), Dr. Jack Randall (BPBM), Dr. Leon Yun-Chih Liao (ASIZP), Alastair Graham (CSIRO), Dianne Bray (NMV), Dr. Helen Larson (NTM), Ralph

Foster (SAMA), Jeff Johnson (QM), and Sue Morrison (WAM). In addition, I am thankful to the following institutions for granting access to their facilities and collections: BMNH, CMNFI, MNHN, RMNH, and ZMB.

I would also like to thank the Ontario Student Assistance Program (OSAP) and the National Sciences and Engineering Research Council of Canada (NSERC) for providing funding for this research.

## LIST OF FIGURES

CHAPTER 1		PAGE
Fig. 1.1	Photograph of <i>Turahbuglossus cuvillieri</i> Chabanaud, 1937, MNHN 1942-2-2, a flatfish fossil from the Upper Lutetian of Egypt. Photograph obtained from the website: <a href="http://www.acanhoweb.fr/en/node/340">http://www.acanhoweb.fr/en/node/340</a> .	7
Fig. 1.2	Figure modified from Chapleau (1989) depicting the supracranial morphology of a specimen of <i>Zebrias craticula</i> .	16
Fig. 1.3	(A) Inverted x-ray of <i>Zebrias zebra</i> (AMS B67, 162 mm SL) depicting various osteological structures examined in the present study. (B) Magnified section shows details of the head region.	18
Fig. 1.4	(A) Photograph of <i>Pseudaesopia cochinensis</i> (USNM Uncatalogued, 138 mm SL) depicting the anatomical features that were examined in the present study. (B) Magnified section showing the external morphology of the head region.	19
Fig. 1.5	Photograph of <i>Phyllichthys munroi</i> , holotype, AMSI.15557063, 105 mm SL, Gulf of Carpentaria, Queensland, 17°29'S, 14°45'E.	30
Fig. 1.6	Photograph of <i>Pleuronectes zebra</i> Bloch 1787, lectotype, ZMB2423, 86 mm SL, "Indischer Ozean" (= Indian Ocean).	32
Fig. 1.7	Photographs depicting an abnormal band arrangement in specimens of A) <i>Zebrias fasciatus</i> (= <i>Z. zebra</i> ), ANSP89453, 134 mm SL, Thailand, Paknam, Siam, and B) <i>Zebrias zebra</i> , ANSP87490, 162	34

mm SL, China, Aberdeen, Victoria I.

- Fig. 1.8 Photograph of *Zebrias cancellatus*, WAM P.32578.002, 130 mm SL, 36  
Western Australia, Shark Bay, Cape Levillain, 21.17 km E of cape,  
25°32.04'S 113°13.247'E to 25°33.448'S 113°13.335'E, depth 19.3  
to 18.7 m, displaying ambicoloration.
- Fig. 1.9 Graph depicting the ratio between the length of the posteriormost 50  
anal-fin ray and the length of the caudal fin among recognized  
species of *Zebrias* (diamonds) and *Pseudaesopia* (squares). Ratio  
was examined in a subset of 155 specimens.
- Fig. 1.10 Diagram illustrating the generalized attachment of the posteriormost 51  
vertical fin rays to the caudal fin as observed in A) *Pseudaesopia* and  
B) *Zebrias*.
- Fig. 1.11 Photographs of *Zebrias altipinnis*, USNM uncatalogued, 200 mm SL, 52  
India, showing the ocular (above) and blind (below) sides.
- Fig. 1.12 Geographic distribution of *Zebrias altipinnis*. Star denotes locality of 57  
type material according to Alcock (1890).
- Fig. 1.13 Photographs of *Zebrias annularis*, holotype, USNM93095, 129 mm 59  
SL, Taiwan (Pacific Taiwan), China Sea, vicinity of Formosa  
(=Taiwan), 21°40'N, 116°58'E, depicting the ocular (above) and  
blind (below) sides.
- Fig. 1.14 Geographic distribution of *Zebrias annularis*. Stars denote locality of 64  
type material.

Fig. 1.15	Digital x-ray showing the supracranial structure of <i>Zebrias annularis</i> , AMSI.22828-015, 121 mm SL, NW Shelf.	67
Fig. 1.16	Photographs of <i>Zebrias cancellatus</i> , WAM P28613-006, 151 mm SL, Western Australia, King George Sound, 2km SE of Emu Pt., 35°01'S, 117°57'E.	68
Fig. 1.17	Geographic distribution of <i>Zebrias cancellatus</i> . Stars denote locality of type material.	74
Fig. 1.18	Photograph of <i>Synaptura cancellata</i> (= <i>Zebrias cancellatus</i> ), holotype, AMSI.13199, 152 mm SL, near Fremantle, Rockingham Western Australia.	76
Fig. 1.19	Photographs of <i>Zebrias captivus</i> , BPBM29478, holotype, 81 mm SL, Persian Gulf, off Bahrain, depicting the ocular (above) and blind (below) sides.	77
Fig. 1.20	Geographic distribution of <i>Zebrias captivus</i> . Stars denote locality of type material.	82
Fig. 1.21	Photograph depicting an ocular tentacle, diagnostic of <i>Zebrias captivus</i> , BPBM29478, holotype, 81 mm SL, Persian Gulf, off Bahrain.	84
Fig. 1.22	Photographs depicting the difference in band morphology between <i>Zebrias captivus</i> (above: BPBM29478, holotype, Persian Gulf, off Bahrain) and <i>Zebrias quagga</i> (below: MNHN1965-487, 110 mm SL, 10.35°S, 104.3°E).	84

Fig. 1.23	Photographs of <i>Synaptura craticula</i> (= <i>Zebrias craticula</i> ), holotype, AMSE.2700, 124 mm SL, 19 km NE Bowen, depicting the ocular (above) and blind (below) sides.	85
Fig. 1.24	Geographic distribution of <i>Zebrias craticula</i> . Stars denote locality of type material.	92
Fig. 1.25	<i>Zebrias maculosus</i> , as depicted in the original type description (Oommen, 1977), IFP F55a, holotype, 128 mm SL, Arabian Sea, 9°30'N, 75°50'E, depth 150 fathoms.	95
Fig. 1.26	Geographical distribution of <i>Zebrias maculosus</i> . Star denotes locality of type material, according to Oommen (1977).	98
Fig. 1.27	Photographs of <i>Zebrias penescalaris</i> , paratype, AMS I.20194-029, 119 mm SL, South Australia, Investigator Strait, showing the ocular (above) and blind (below) sides.	100
Fig. 1.28	Geographic distribution of <i>Zebrias penescalaris</i> . Stars denote locality of type material.	105
Fig. 1.29	Geographic distribution of <i>Zebrias scalaris</i> (stars) and <i>Zebrias penescalaris</i> (triangles). The number of lateral line scales is indicated for each specimen. It should be noted that the two <i>Z. scalaris</i> specimens indicated as having lateral line scale counts of 76 and 78 are missing many scales and therefore, these values are likely underestimates.	107
Fig. 1.30	Diagram depicting the direction of flow of the Leeuwin Current, as	108

illustrated by Waters et al. (2004).

- Fig. 1.31 Photographs of *Zebrias quagga*, MNHN1998-1307, holotype, 150 mm SL, Maharashtra, Bombay, India, 18°933'N, 72°85'E, depicting the ocular (above) and blind (below) sides. 110
- Fig. 1.32 Geographic distribution of *Zebrias quagga*. Star denotes locality of type material. 118
- Fig. 1.33 Photographs of *Z. quagga* depicting abnormal (left, center) and typical (right) caudal fin patterns. Left - QMI.14231, off Dampier, Western Australia, 20°39'S 116°43'E; Center - WAMP4508-001, Western Australia, Shark Bay, 25°21'S 113°44'E; Right - NTMS.10284-002, Shoal Bay, Darwin, N.T., 12°18'S 130°58'E. 121
- Fig. 1.34 Photographs of *Zebrias scalaris*, AMS E1792, 155 mm SL, NSW, 18 km ESE Clarence River, depicting the ocular (above) and blind (below) sides. 122
- Fig. 1.35 Geographic distribution of *Zebrias scalaris*. Star denotes locality of type material. The circles represent non-type material. 128
- Fig. 1.36 Photograph of *Zebrias scalaris*, holotype, AMS I.16281-001, 152 mm SL, Port Jackson, New South Wales, Australia, 33°50'S, 151°15'E. 130
- Fig. 1.37 Photographs of *Zebrias zebra*, SU61077, 109 mm SL, Hong Kong, China, depicting the ocular (above) and blind (below) sides. 131
- Fig. 1.38 Geographic distribution of *Zebrias zebra*. Star denotes locality of 139

type material. The lectotype of *Pleuronectes zebra* is not represented as the locality, listed as “Indian Ocean”, was imprecise and possibly incorrect (see Remarks).

- Fig. 1.39 Photographs of *Zebrias zebra* showing the barbels around the anterior end of the dorsal fin and on the blind side of the chin, a character that is diagnostic of the species; CAS224633, 150 mm SL, Suruga Bay, Japan. 145
- Fig. 1.40 Photograph of *Solea zebrina*, lectotype, RMNH1308, 277 mm SL, Japan. 146
- Fig. 1.41 Graph depicting the relationship between the head length (mm) and ocular-side pectoral fin length (mm) among specimens of *Zebrias zebra* (Bloch, 1787). N=102. 147
- Fig. 1.42 Photographs of *Aesopia cornuta*, WAM P.32293.001, 107 mm SL, Western Australia, Shark Bay, Point Quobba, 6.49 km WSW of 24°30.827'S, 113°21.721'E, depicting the ocular (above) and blind (below) sides. 151
- Fig. 1.43 Geographic distribution of *Aesopia cornuta*. Star denotes locality of the syntype for *A. cornuta*, according to Kaup (1858). 154
- Fig. 1.44 Radiograph showing the supracranial complex of *A. cornuta*, WAM P.32293.001, 107 mm SL, Western Australia, Shark Bay, Point Quobba, 6.49 km WSW of 24°30.827'S, 113°21.721'E to 24°31.431'S, 113°21.723'E. 157

Fig. 1.45	Photographs showing the striking similarity between <i>Aesopia cornuta</i> (Above: NSMT-P 6198, 210 mm SL, Sea of Japan, Nagasaki Pref., Tsushima Is., Tsutsu) and <i>Zebrias zebra</i> (Below: NSMT-P54002, 212 mm SL, Japan, Honshu, Chiba Pref., southern part of Boso Peninsula, Suno-saki Point).	158
-----------	--	-----

CHAPTER 2		PAGE
Fig. 2.1	Photographs of <i>Pseudaesopia callizona</i> , QM I. 28002, 84 mm SL, Gulf of Carpentaria, depicting the ocular (above) and blind (below) sides.	208
Fig. 2.2	Geographic distribution of <i>Pseudaesopia callizona</i> . Star denotes locality of type material.	213
Fig. 2.3	Photographs of <i>Pseudaesopia cochinensis</i> , USNM uncatalogued, 138 mm SL, India, depicting the ocular side (above) and the blind side (below).	215
Fig. 2.4	Geographic distribution of <i>Pseudaesopia cochinensis</i> . Star denotes locality of type material according to Rama-Rao (1967).	220
Fig. 2.5	Scans of photographs depicting holotypes of <i>Zebrias cochinensis</i> Rama-Rao, 1967 (above) and <i>Zebrias keralensis</i> Joglekar, 1976 (below), as presented in their original descriptions.	222
Fig. 2.6	Photographs of <i>Pseudaesopia japonica</i> , UMMZ159582, 126 mm SL, Sea of Japan, NE of Oki-No-Jima (off Miyazu), Kyoto-Fu (Miyazu Market), Japan, 40-70 fathoms, depicting ocular side (above) and	224

blind side (below).

- Fig. 2.7 Geographic distribution of *Pseudaesopia japonica*. The locality of the 230  
holotype of *P. japonica* is unknown. Stars denote locality of the  
holotype of *Synaptura smithii* (= *P. japonica*) and the two  
paralectotypes of *Solea zebrina* (Temminck and Schlegel, 1846) that  
actually represent *P. japonica* specimens.
- Fig. 2.8 Photograph depicting the holotype of *Synaptura smithii* 233  
(= *Pseudaesopia japonica*), BMNH1902.10.31.152, 113 mm SL,  
inland sea, Japan.
- Fig. 2.9 Photograph depicting one of the three ethanol-preserved 233  
paralectotypes of *Solea zebrina* (= *Pseudaesopia japonica*),  
RMNH3580, 75 mm SL, Japan.
- Fig. 2.10 An illustration of *Zebrias annandalei*, as depicted in the original type 234  
description (Talwar and Chakrapany, 1967), 97 mm SL, Puri Beach,  
Orissa, India.
- Fig. 2.11 Photographs of *Pseudaesopia lucapensis*, LACM37436-6, holotype, 235  
81 mm SL, Philippines, Lingayen Gulf, Pangasinan, Lucap Bay,  
depicting the ocular (above) and blind (below) sides.
- Fig. 2.12 Geographic distribution of *Pseudaesopia lucapensis*. Stars denote 240  
locality of type material.
- Fig. 2.13 Photographs of *Pseudaesopia regani*, syntype, BMNH 242  
1903.12.31.12, 102 mm SL, Western Indian Ocean, South Africa,

	Natal, depicting the ocular side (above) and blind side (below).	
Fig. 2.14	Geographic distribution of <i>Pseudaesopia regani</i> . Star denotes locality of type material.	247
Fig. 2.15	Photograph of <i>Pseudaesopia regani</i> , SAM15424, syntype, 116 mm SL, 2.5 miles off Umhlanga River Mouth, Natal, Sta. No: PF, 26 March 1901.	250
Fig. 2.16	Photograph of <i>Pseudaesopia sp.</i> , SAM28866, 97 mm SL, Off Tugela River, South Africa, Sta No: WT 231. Specimen displays abnormal meristics for this species. Note that caudal fin appears truncated because it is damaged.	250
Fig. 2.17	Photograph of <i>Pseudaesopia sp.</i> , ANSP145359, 109 mm SL, Somali Coast, 10°03'N, 51°15'E.	250
Fig. 2.18	Photographs of <i>Pseudaesopia synapturoides</i> , syntype, MNHN1976-0380, 106 mm SL, Ganjam, India, 19°28'1"N, 85°4'59"E, 44-55 m depth, depicting ocular (above) and blind (below) sides.	251
Fig. 2.19	Geographic distribution of <i>Pseudaesopia synapturoides</i> . Star denotes locality of a syntype for <i>P. synapturoides</i> . Asterisk denotes locality of holotype for <i>Z. crossolepis</i> , according to Zheng and Chang (1965).	256
Fig. 2.20	Radiograph showing the anterior region of the syntype <i>Solea synapturoides</i> , Jenkins, 1910, MNHN1976-0380, 106 mm SL, Ganjon Port, Calcutta, India. Urohyal is circled and denoted by a dotted line for enhanced visibility.	257

- Fig. 2.21      Photographs showing variation in banding pattern among a lot of      259  
*Pseudaesopia synapturoides* specimens from the Indian Ocean,  
 ANSP145382, 10(93 -111 mm SL), 9°13'N, 97°51'E. Photograph A  
 shows a specimen having paired body bands; Photograph B shows a  
 specimen with a mixture of paired and singular bands; Photograph C  
 shows a specimen with singular body bands.
- Fig. 2.22      Scan of the illustration of the holotype of *Zebrias crossolepis* (Zheng      260  
 and Chang, 1965) as presented in the original description, ASIZB  
 29861, 127 mm SL, Jieshi Harbor, Guangdong, China.
- Fig. 2.23      Photograph of *Pseudaesopia sp.*, BPBM38806, 56 mm SL, Indonesia,      262  
 Sulawesi, Lembah Strait, "Hairball" dive site, 56 feet. Note: the  
 membrane attaching the posteriormost vertical-fin rays to the caudal  
 fin appears to be damaged, giving the caudal fin the illusion of being  
 connected to the vertical-fin rays at its base.
- Fig. 2.24      Photographs depicting *Pseudaesopia sp.*, QMI.28792, 131 mm SL,      263  
 Gulf of Carpentaria, Australia, 11.26°S, 137.09°E, 47 m depth.
- Fig. 2.25      Photograph of *Soleichthys microcephalus*, AMSI.40868-015, 135 mm      279  
 TL, NSW, Chowder Bay, end of fuel wharf, east side, 33°51.58'S,  
 151°12.01'E, 14.4 m depth.

## LIST OF TABLES

CHAPTER 1		PAGE
Table 1.1	Frequency distribution of precaudal vertebrae among closely-related genera, <i>Zebrias</i> , <i>Pseudaesopia</i> , <i>Aesopia</i> , <i>Soleichthys</i> , and <i>Phyllichthys</i> . The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material.	44
Table 1.2	Frequency distribution of vertebral counts and haemapophyses on the abdominal vertebrae among recognized species of <i>Zebrias</i> . The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material.	45
Table 1.3	Frequency distribution of supracranial complex patterns of the dorsal fin and the number of supracranial pterygiophores of the dorsal fin on and anterior to the first neural spine among recognized species of <i>Zebrias</i> . The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material. See materials and methods for definition of supracranial complex.	46
Table 1.4	Frequency distribution of ocular-side pectoral- and pelvic-fin rays among recognized species of <i>Zebrias</i> and <i>Aesopia</i> . The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material.	47
Table 1.5	Frequency distribution of dorsal-, anal-, and caudal-fin rays among	48

recognized species of *Zebrias*. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote value for type material.

Table 1.6	Frequency distribution of lateral line scales among recognized species of <i>Zebrias</i> . The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote value for type material.	49
Table 1.7	Meristic and morphometric characteristics of type and non-type specimens of <i>Zebrias altipinnis</i> . Means and standard deviations are shown in parentheses. Data for <i>Synaptura altipinnis</i> holotype were obtained from the original species description (Alcock, 1890). 1: count from origin on snout to base of caudal fin; 2: 1/11 specimens with 7, rest with 9-12. Measurements and abbreviations are described in Appendix B.	56
Table 1.8	Meristic and morphometric characteristics of type and non-type specimens of <i>Zebrias annularis</i> . 1 = Fin damaged. Measurements and abbreviations are described in Appendix B.	63
Table 1.9	Meristic and morphometric characteristics of type and non-type specimens of <i>Zebrias cancellatus</i> . Means and standard deviations are shown in parentheses. Measurements and abbreviations are described in Appendix B.	73
Table 1.10	Meristic and morphometric characteristics of type and non-type specimens of <i>Zebrias captivus</i> . Means and standard deviations are	81

shown in parentheses. 1: pelvic fins damaged; 2: approximation as a few scales are missing. Measurements and abbreviations are described in Appendix B.

Table 1.11	Meristic and morphometric characteristics of type and non-type specimens of <i>Zebrias craticula</i> . Means and standard deviations are shown in parentheses. 1: n=43; 2: n=41. Measurements and abbreviations are described in Appendix B.	91
Table 1.12	Meristic and morphometric characteristics of type and non-type specimens of <i>Zebrias maculosus</i> , as reported in the original species description (Oommen, 1977). NT=Length of ocular anterior nasal tube. 1=Corresponding values for holotype and paratype were not indicated, only range provided. Measurements and abbreviations are described in Appendix B.	97
Table 1.13	Meristic and morphometric characteristics of type and non-type specimens of <i>Zebrias penescalaris</i> . Means and standard deviations are shown in parentheses. 1: n=12. 2: n=6; 3: n=11. Measurements and abbreviations are described in Appendix B.	104
Table 1.14	Meristic and morphometric characteristics of type and non-type specimens of <i>Zebrias quagga</i> . Means and standard deviations are shown in parentheses. 1: n=111; 2: n=112; 3: n=113; 4: n=108; 5: n=107; 6: n=106. Measurements and abbreviations are described in Appendix B.	117

Table 1.15	Frequency distribution of transverse band number and arrangement among specimens of <i>Zebrias quagga</i> . Asterisk denotes value of holotype; n = sample size.	121
Table 1.16	Meristic and morphometric characteristics of type and non-type specimens of <i>Zebrias scalaris</i> . Means and standard deviations are shown in parentheses. 1: n=31. 2: n=30; 3: Holotype devoid of pigmentation, pectoral fins absent, specimen in poor condition. Measurements and abbreviations are described in Appendix B.	127
Table 1.17	Meristic and morphometric characteristics of type and non-type specimens of <i>Zebrias zebra</i> . Means and standard deviations are shown in parentheses. Data for <i>Solea ommatura</i> were obtained from the original species description (Richardson, 1846). 1: n=3; 2: n=1; 3: n=2; 4: n=101; 5:n=99; 6:n=100; 7:n=120. Measurements and abbreviations are described in Appendix B.	138
Table 1.18	Table comparing the meristics and morphometrics of <i>Zebrias zebra</i> (Bloch, 1787) specimens found in Southeastern Asia (Thailand, Malaysia, Singapore, Indonesia) to those from Eastern Asia (China, Taiwan, North Korea, South Korea, Japan). These values are also compared to the lectotype of <i>Z. zebra</i> . Note that the singular fish having 41 vertebrae has several vertebral abnormalities. 1: n=22; 2: n=9; 3: n=93; 4: n=94; 5: n=95; 6: n=101; 7: n=102.	146
Table 1.19	Meristic and morphometric characteristics of type and non-type	153

specimens of *Aesopia cornuta*. Means and standard deviations are shown in parentheses. Data for type material were obtained from the original species description (Kaup, 1858). 1: n=20; 2: n=19. Measurements and abbreviations are described in Appendix B.

<b>CHAPTER 2</b>	<b>PAGE</b>
Table 2.1	203
<p>Frequency distribution of vertebral counts and haemapophyses on the abdominal vertebrae among recognized species of <i>Pseudaesopia</i>. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material.</p>	
Table 2.2	204
<p>Frequency distribution of supracranial complex patterns of the dorsal fin and the number of supracranial pterygiophores of the dorsal fin on and anterior to the first neural spine among recognized species of <i>Pseudaesopia</i>. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material. See Materials and Methods for definition of supracranial complex.</p>	
Table 2.3	205
<p>Frequency distribution of ocular-side pectoral- and pelvic-fin rays among recognized species of <i>Pseudaesopia</i>. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material.</p>	
Table 2.4	206
<p>Frequency distribution of dorsal-, anal-, and caudal-fin rays among recognized species of <i>Pseudaesopia</i>. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote value for</p>	

type material.

Table 2.5	Frequency distribution of lateral line scales among recognized species of <i>Pseudaesopia</i> . The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote value for type material.	207
Table 2.6	Meristic and morphometric characteristics of type and non-type specimens of <i>Pseudaesopia callizona</i> . Means and standard deviations are shown in parentheses. 1: n=3. Measurements and abbreviations are described in Appendix B.	212
Table 2.7	Meristic and morphometric characteristics of type and non-type specimens of <i>Pseudaesopia cochinensis</i> . Means and standard deviations are shown in parentheses. Data for type material were obtained from the original species descriptions (Rama-Rao, 1967; Joglekar, 1976). 1: n=1; 2: n=7. Measurements and abbreviations are described in Appendix B.	219
Table 2.8	Meristic and morphometric characteristics of type and non-type specimens of <i>Pseudaesopia japonica</i> . Means and standard deviations are shown in parentheses. 1: 2/3 of the alcohol-preserved paralectotypes represent <i>P. japonica</i> , while the third specimen represents <i>Z. zebra</i> (Bloch, 1787); 2: n=44; 3: n=43; 4: n=42; 5: n=41.	229

Table 2.9	Meristic and morphometric characteristics of type and non-type specimens of <i>Pseudaesopia lucapensis</i> . Means and standard deviations are shown in parentheses. 1: approximation, a few scales missing. Measurements and abbreviations are described in Appendix B.	239
Table 2.10	Meristic and morphometric characteristics of type and non-type specimens of <i>Pseudaesopia regani</i> . Means and standard deviations are shown in parentheses. 1: n=2, other specimens devoid of pigmentation. Measurements and abbreviations are described in Appendix B.	246
Table 2.11	Meristic and morphometric characteristics of type and non-type specimens of <i>Pseudaesopia synapturoides</i> . Means and standard deviations are shown in parentheses. 1: Data obtained from original description (Zheng and Chang, 1965); 2: n=23; 3: n=24; 4: n=22; 5: n=21. Measurements and abbreviations are described in Appendix B.	255

## ABSTRACT

The taxonomic status of the 25 nominal species of the Indo-Pacific flatfish genus *Zebrias* Jordan and Snyder, 1900 (Pleuronectiformes: Soleidae) was revised based on a morphological study of 531 specimens, including 36 type specimens. Two distinct, monophyletic groups were identified differing in the confluence and attachment of the caudal fin to adjacent dorsal and anal fins. The genus was divided with the species most closely associated to the type species, *Pleuronectes zebra* Bloch 1787, being placed in the genus *Zebrias*. The remaining species were assigned to the genus *Pseudaesopia* Chabanaud, 1934, established by Chabanaud as a subgenus of *Zebrias* and later raised to the genus level to accommodate *Zebrias* species having a shallowly confluent caudal fin with adjacent fins, among other characters. Ten valid species are now recognized for the genus *Zebrias* (*Z. altipinnis*, *Z. annularis*, *Z. cancellatus*, *Z. captivus*, *Z. craticula*, *Z. maculosus*, *Z. penescalaris*, *Z. quagga*, *Z. scalaris* (*Synaptura fasciata*), and *Z. zebra* (*Solea fasciata*, *Solea ommatura*, *Solea zebrina*)), while six valid species are recognized for the genus *Pseudaesopia* (*P. callizona*, *P. cochinensis* (*Zebrias keralensis*), *P. japonica* (*Zebrias annandalei*, *Synaptura smithii*), *P. lucapensis*, *P. regani*, and *P. synapturoides* (*Zebrias crossolepis*)). A comprehensive generic definition and an identification key to species are provided for both genera. In addition, the closely-related, monospecific genus *Aesopia* Kaup, 1858 is briefly discussed. Finally, characters that might prove useful for a phylogenetic study of these species and genera are presented and discussed.

## RÉSUMÉ

Le statut taxinomique des 25 espèces nominales appartenant au genre Indo-Pacifique *Zebrias* Jordan et Snyder, 1900 (Pleuronectiformes: Soleidae) a été examiné suite à une étude morphologique de 531 spécimens, incluant 36 spécimens types. Deux groupes monophylétiques ont été identifiés sur la base de la confluence et l'attachement de la nageoire caudale aux derniers rayons des nageoires anale et dorsale. Le genre a été divisé en plaçant les espèces les plus étroitement associées avec l'espèce type, *Pleuronectes zebra* Bloch, 1787 dans le genre *Zebrias*. Les autres espèces nominales ont été placées dans le genre *Pseudaesopia* Chabanaud, 1934, un sous-genre établi par Chabanaud pour accommoder les espèces de *Zebrias* ayant, entre autres caractères, une nageoire caudale peu confluyente avec les nageoires adjacentes. Subséquemment, ce sous-genre a été élevé au rang de genre. Dix espèces sont reconnues comme étant valides dans le genre *Zebrias* (*Z. altipinnis*, *Z. annularis*, *Z. cancellatus*, *Z. captivus*, *Z. craticula*, *Z. maculosus*, *Z. penescalaris*, *Z. quagga*, *Z. scalaris* (*Synaptura fasciata*), et *Z. zebra* (*Solea fasciata*, *Solea ommatura*, *Solea zebrina*)), tandis que six espèces sont valides dans le genre *Pseudaesopia* (*P. callizona*, *P. cochinchinensis* (*Zebrias keralensis*), *P. japonica* (*Zebrias annandalei*, *Synaptura smithii*), *P. lucapensis*, *P. regani*, et *P. synapturoides* (*Zebrias crossolepis*)). Une définition exhaustive des genres et une clé d'identification des espèces de *Zebrias* et *Pseudaesopia* sont présentées. De plus, le genre monospécifique *Aesopia* Kaup, 1858, étroitement apparenté à *Zebrias*, est brièvement discuté. Finalement, des caractères qui seront probablement utiles dans le cadre d'une étude phylogénétique des espèces et des genres sont présentés et discutés.

## GENERAL INTRODUCTION

### **Flatfishes: A Diverse Group of Fishes**

The Pleuronectiformes form a very diverse group of fishes. Commonly known as flatfishes, the order currently comprises an estimated 1339 nominal species, of which approximately 716 are regarded as valid (Munroe, 2005). The valid species are distributed among 121 genera. New species are continuously being discovered (Randall and Desoutter-Meniger, 2007; Amaoka et al., 2008; Kawai et al., 2008; Randall and Munroe, 2008; Yokogawa et al., 2008; Lee et al., 2009a; Lee et al., 2009b; Ramos et al., 2009; Suzuki et al., 2009; Voronina, 2009; Kawai et al., 2010). There is currently an extensive body of literature on flatfish ecology and biology, a synthesis of which can be found in Gibson (2005).

Adult flatfishes are perhaps best known for their laterally-compressed, asymmetrical appearance, having both eyes on the same side of their head. It is a feature not present in any other living vertebrate. In larval stages, however, these fish are symmetrical, and it is only as they develop that one eye migrates from one side to the other in conjunction with additional cranial reconfiguration. This transformation is accompanied by the loss of the swim bladder and the transition to a flattened shape, at which point the fish adopts a benthic lifestyle. In their adult form, flatfish can range in size from a few centimeters, weighing about 2 g (e.g. *Tarphops oligolepis*) to 2.5 m, weighing 272,155 g (e.g. Atlantic Halibut, *Hippoglossus hippoglossus*). They are known to live in a diverse array of environments, including marine, freshwater, and brackish water habitats.

## Origin and Classification

Linnaeus (1758) first classified all known species of flatfish in the genus *Pleuronectes* (Order Thoracici, Class Pisces). It was not until many years later that Cuvier (1816) published “*Le Règne Animal*”, in which he raised *Pleuronectes* to the family level. Flatfish were subsequently promoted to a suborder, Pleuronectoidei, by Günther (1862) and later recognized as an order by Bonaparte (1846) and Cope (1871) under the name Heterosomata. The name Heterosomata was later (Berg, 1940) replaced by Pleuronectiformes.

Chapleau (1993) provided a synthesis of past studies dealing with the intra- and interrelationships of the Pleuronectiformes and conducted the first comprehensive cladistic analysis of Pleuronectiform relationships. He established the monophyletic status of the Order based on three synapomorphies: 1- cranial asymmetry resulting from ocular migration; 2- advanced position of the dorsal fin over the cranium; and 3- presence of a *recessus orbitalis*, a muscle that enables protrusion of the eyes. These derived characters are accompanied by numerous other features, including the ability of many species to camouflage with their environment, offering them concealment from predators and prey alike.

For nearly two centuries, scientists have been perplexed by the origin of flatfish asymmetry. While various hypotheses have been proposed to explain their asymmetry, the true origin remains shrouded in mystery. Even Darwin, who opposed Jean-Baptiste Lamarck’s theory of inheritance of acquired characters, resorted to a Lamarckian explanation of flatfish asymmetry (Chanet and Chapleau, 2004; Chanet and Chapleau, 2005). In his renowned “On the Origin of Species”, Darwin suggested that migration of the eye was an inherited character acquired by physically straining to look skyward in shallow waters in an attempt to remain vigilant for predators. Other scientists have since proposed different theories, including

evolution guided by a divine hand (Mivart, 1871), physical limitations in body structure which necessitated lying down while straining the lower eye to look upward (Malm, 1868), and the combination of genetic and environmental factors, the asymmetrical state being linked to an as-of-yet unidentified character (Policansky, 1982). Most recently, Friedman (2008) studied a 47 million year old fish fossil displaying intermediate stages of both cranial asymmetry and ocular migration. This fossil specimen suggests that the evolution of asymmetry in flatfish was gradual, as opposed to saltatory. He identifies the genera, *Amphistium* and *Heteronectes*, the latter being a new genus, as possible evolutionary intermediates between generalized fishes and living flatfishes.

Several authors have postulated a Perciform ancestor to the Order (Regan, 1910; Norman, 1934; Evseenko, 2000), while others have suggested that flatfishes may have originated before the Perciformes (Amaoka, 1969; Li and Wang, 1995). Despite numerous attempts at elaborating hypotheses regarding the origin of flatfishes, the search for the sister group of flatfishes remains active (Chapleau, 1993).

Recently, phylogenetic studies using molecular data have provided new insight in this search. Chen et al. (2003) conducted a phylogenetic analysis of acanthomorph fishes using molecular data (ribosomal 28S, rhodopsin gene, mitochondrial 12S and 16S). The Pleuronectiformes were grouped in a clade along with sister taxa Carangidae (jacks), Echeineidae (remoras), Sphyrnaeidae (barracudas), Menidae (moonfish), Polynemidae (threadfins), and Centropomidae (snooks). This clade was further supported by Dettai and Lecointre (2005) using the datasets provided by Chen et al. (2003) as well as partial sequences of exons of the MLL (Mixed Lineage Leukaemia-like) gene. Chen et al. (2003) interpreted their results as indicating the origin of flatfishes to be close to the origin of either carangoid or centropomid fishes, the

latter lending support to the percoid origin theory. Pardo et al. (2005) found a monophyletic origin for the Pleuronectiformes, but noted a closer relationship with the Cyclosquamata and Atherinomorpha using mitochondrial 16s rDNA sequences. Based on the primary nucleotide sequence of the cytochrome oxidase 1 gene, Sharina and Kartavtsev (2010) obtained a monophyletic origin for pleuronectiform families using two perciform species as the outgroup. The phylogenetic analysis of Azevedo et al. (2008), based on sequences of 12S and 16S mitochondrial genes, corroborated the monophyletic status of all but one family (Paralichthyidae) within the order Pleuronectiformes using the flatfish species *Psettodes erumei* Bloch and Schneider, 1801 as an outgroup. Berendzen and Dimmick (2002) designated the percomorphs and basal acanthopterygians as outgroups. Using nucleotide sequence data of the 12S and 16S mitochondrial ribosomal genes, they found strong support for a monophyletic origin of the Pleuronectiformes and identify *Psettodes* as the sister group to all other flatfishes.

Currently, the fossil record for *Zebrias* and *Pseudaesopia* is greatly lacking, making inferences about the age of these groups and their evolutionary histories difficult. Chanet (1997) estimates the origin of the Soleidae to be 45 million years ago. The earliest soleid fossils date from the Upper Lutetian of Djebbel Turah, Egypt. One of these fossils, *Turahbuglossus cuvillieri* Chabanaud, 1937 (Figure 1.1), was proposed by Chabanaud (1937; 1943b) to belong to *Zebrias*. Although the physical specimen could not be obtained for examination, a photograph of this fossil is available online at <http://www.acanthoweb.fr/en/node/340>. The skeletal structure exhibited by this fossil is consistent with meristics observed for *Zebrias* and *Pseudaesopia* species. Moreover, the elongate body shape is comparable to species within these genera. The cranial region is contorted, making an examination of the supracranial complex difficult, but there appear to be six supracranial pterygiophores present. *Zebrias* and *Pseudaesopia* species

typically have 3-5 supracranial pterygiophores (Tables 1.3 and 2.2, respectively), although *Zebrias altipinnis* (Alcock, 1890), found in Indian waters, typically has six. The two anteriormost neural spines are enlarged at their distal ends with the anteriormost neural spine apparently curving anteriorly over the posterior end of the cranium, which is consistent with *Zebrias* and *Pseudaesopia*. Unfortunately, the caudal fin region is not visible in the photograph, making the ratio between the length of the caudal fin and the length of the posteriormost dorsal- and anal-fin rays impossible to assess; however, it seems highly probable that this species does belong to either *Zebrias* or *Pseudaesopia*.



Figure 1.1. Photograph of *Turahbuglossus cuvillieri* Chabanaud, 1937, MNHN 1942-2-2, a flatfish fossil from the Upper Lutetian of Egypt. Photograph obtained from the website: <http://www.acanthoweb.fr/en/node/340>.

## **A valuable resource**

In 2007, flatfishes accounted for 2.5% (USD \$2,248 million) of the estimated value of the global fishery production (FAO, 2009). The economic importance of this resource necessitates proper management of fisheries and conservation of individual species. Knowledge of flatfish biodiversity is based on proper taxonomic and systematics studies that establish the validity of new and nominal species, clarify the biogeographic distribution and classification of these species, and offer hypotheses of relationships.

## **FAMILY SOLEIDAE**

The family Soleidae, collectively known as the soles, is a diverse group of dextral (right-eyed) flatfishes inhabiting temperate and tropical waters of the Indo-Pacific (with one species of *Aseraggodes* in the Eastern Pacific) and Eastern Atlantic oceans. Recent studies estimate the current soleid diversity to encompass 139 species distributed amongst 29 genera (Munroe, 2005). Nelson (1994) had estimated 89 species in 20 genera, indicating an increase in soleid diversity with the discovery of 50 new species over the span of a decade. According to Munroe (2005), species discovery is still very active for this family.

Recently, the soleids were identified as a family whose members were poorly differentiated and the family was considered to be in great need of revision (Heemstra and Gon, 1986; Hoese and Bray, 2006; Schwarzhans, 1999). In recent years, considerable progress has been made in elucidating the taxonomy of this family (for example, Desoutter, 1994; Desoutter-Meniger, 1997; Borsa and Quignard, 2001; Muchhala and Munroe, 2004; Randall and Munroe, 2008; Vachon et al., 2008). Despite this progress, the status of many species and genera, and their intra- and interrelationships, remain largely unknown.

The family Soleidae was recognized by Jordan and Evermann (1898) as one of two families within the order Heterosomata (now known as the Pleuronectiformes), the other being the Pleuronectidae. The Soleidae included three subfamilies: the tongue soles (Cynoglossinae), American soles (Achirinae), and eastern Atlantic, Mediterranean, and Indo-Pacific soles (Soleinae). The Soleinae and Cynoglossinae were later elevated to family status under the suborder Soleoidei (Hubbs, 1945); Achirinae was recognized as one of two subfamilies within the Soleidae, the other being the Soleinae. The Cynoglossidae were distinguished from the Soleidae by their sinistral (left-sided) eyes. Ochiai (1963) proposed that *Zebrias* Jordan and Snyder, 1900, along with closely-related genera *Soleichthys* Bleeker, 1860, *Aesopia* Kaup, 1858, and *Pseudaesopia* Chabanaud, 1934 be placed in the subfamily Soleinae. Chapleau and Keast (1988) were the first to conduct a comprehensive study to determine the monophyletic status of the Soleidae and its subfamilies, Soleinae and Achirinae. Based on their cladistic analysis, they determined that the family Soleidae was not monophyletic; the Soleinae were more closely related to the left-eyed Cynoglossidae with which they share more derived characters (apomorphies) than with the right-eyed Achirinae. Thus, the two former subfamilies were elevated to family level and the suborder Soleoidei was incorporated within the suborder Pleuronectoidei.

Chapleau and Keast (1988) defined the Soleidae on the basis of six autapomorphies: 1- vomer (nasal bone) protruding ventrally; 2- metapterygoid (portion of upper jaw that permits articulation) with high perpendicular lamina along its posterodorsal margin; 3- ascending process of blind-side premaxilla always directed toward ocular side and extending in front of rostral cartilage and opposing premaxilla; 4- maxillary spike of ocular-side maxilla covering rostral cartilage dorsally; 5- blind-side lateral ethmoid with posteroventral process attached to

sphenotic; and 6- basioccipital (cranial bone) with two distinct ventral processes for articulation of branchial arches. Recent studies (Schwarzhan, 1999) have also suggested that otolith morphology and structure of the supracranial complex (Chapleau, 1989) could be useful in distinguishing soleids from other Pleuronectiform families and to elucidate relationships within the Soleidae.

In addition to these diagnostic characters, the soles display other features. Within this family, the preopercular margin is covered by skin and is therefore inconspicuous. Teeth are minute and usually restricted to the blind-side jaws. Pectoral fins, when present, are small and asymmetrical, the ocular-side fin typically exceeding the length of the blind-side fin. The blind side of the head possesses numerous cirri, and the body is oval or elongate.

### **The Present Study**

Objectives of the present study are three-fold: 1- to establish the monophyletic status of the genera *Pseudaesopia* Chabanaud, 1934 and *Zebrias* Jordan and Snyder, 1900; 2- to provide comprehensive descriptions and diagnoses of these genera; and 3- to assess the validity of all nominal species of *Zebrias* and *Pseudaesopia* based on their morphology. A phylogenetic analysis of *Zebrias* is beyond the scope of this study but phylogenetic observations based on the distribution of presumed derived characters will be discussed in the conclusion of this thesis. The ultimate goal of this study is to resolve the taxonomic status of these two soleid genera and to evaluate the status of the nominal species assigned to each genus.

During the course of the present study, several specimens representing potentially undescribed species of *Pseudaesopia* were noted. It was beyond the scope of the present study to further investigate these potentially undescribed species; however, these specimens are briefly

discussed for the purposes of provoking and facilitating future research about their correct taxonomic placement.

## MATERIALS AND METHODS

### Acquisition of Specimens

Data are presented for 531 specimens, including 11 specimens of *Zebrias altipinnis* (Alcock, 1890), three *Z. annularis* (Fowler, 1934) (including holotype and the paratype), 35 *Z. cancellatus* (McCulloch, 1916) (including holotype and one paratype), two *Z. captivus* Randall, 1995 (including holotype and the paratype), 46 *Z. craticula* (McCulloch, 1916) (including holotype and the paratype), 21 *Z. penescalaris* Gomon, 1987 (including eight paratypes), 115 *Z. quagga* (Kaup, 1858) (including holotype), 34 *Z. scalaris* Gomon, 1987 (including holotype), 132 *Z. zebra* (Bloch, 1787) (including the lectotype of *Pleuronectes zebra* Bloch, 1787, the lectotype and three paralectotypes of *Solea zebrina* Temminck and Schlegel, 1846), five *Pseudaesopia callizona* (Regan, 1903) (including holotype), 50 *P. japonica* (Bleeker, 1860) (including the holotype of *Synaptura smithii* Regan, 1903 and two paralectotypes of *Zebrias zebrinus* (Temminck and Schlegel, 1846)), eight *P. cochinensis* (Rama-Rao, 1967), four *P. lucapensis* (Seigel and Adamson, 1985) (including holotype and the paratype), ten *P. regani* (Gilchrist, 1906) (including both syntypes), 24 *P. synapturoides* (Jenkins, 1910) (including one syntype) and 31 *Aesopia cornuta* Kaup, 1858. In addition, four type specimens including holotype and three paratypes of *Zebrias munroi* (Whitley, 1966) (= *Phyllichthys munroi*) and 26 specimens of *Pseudaesopia* spp. were examined and discussed, although data are not presented for these specimens. In the absence of, or lack of access to type material, identification of a nominal species was based on its original description. The statuses of all nominal species associated with the genera *Zebrias* and *Pseudaesopia* are summarized in Appendix A.

Institutions at which specimens were examined, or from which specimens were obtained on loan, include (abbreviations follow Leviton et al. 1985): American Museum of Natural History (AMNH), New York, U.S.A.; Australian Museum (AMS), Sydney, New South Wales, Australia; Academy of Natural Sciences (ANSP), Philadelphia, Pennsylvania, U.S.A.; Academia Sinica (ASIZP), Biodiversity Research Center, Taipei, Taiwan; Natural History Museum (BMNH), London, U.K.; Bishop Museum (BPBM), Honolulu, Hawai'i, U.S.A.; California Academy of Sciences (CAS), San Francisco, California, U.S.A.; The Australian National Fish Collection, Commonwealth Scientific and Industrial Research Organisation (CSIRO), Division of Marine and Atmospheric Research, Hobart, Tasmania, Australia; Division of Fishes, Department of Zoology, Field Museum of Natural History (FMNH), Chicago, Illinois, U.S.A.; Natural History Museum of Los Angeles County (LACM), Los Angeles, California, U.S.A.; Muséum National d'Histoire naturelle (MNHN), Systématique et Évolution, Laboratoire d'Ichthyologie Générale et Appliquée, Paris, France; Museum Victoria (NMV), Ichthyology, Melbourne, Victoria, Australia; Museums and Art Galleries of the Northern Territory, Northern Territory Museum of Arts & Sciences (NTM), Ichthyology, Northern Territory Government, Darwin, Northern Territory, Australia; Queensland Museum (QM), Centre for Biodiversity, Fishes, Brisbane, Queensland, Australia; Naturalis - National Natuurhistorisch Museum (RMNH), Leiden, Netherlands; South African Museum (SAM), Cape Town, South Africa; South Australian Museum (SAMA), Adelaide, South Australia, Australia; University of Michigan Museum of Zoology (UMMZ), Ann Arbor, Michigan, U.S.A.; Smithsonian Institution National Museum of Natural History (USNM), Washington D.C., U.S.A.; Western Australian Museum (WAM), Department

of Aquatic Zoology, Ichthyology, Perth, Western Australia, Australia; and Humboldt-Universität, Museum für Naturkunde, Zoologisches Museum (ZMB), Vertebraten (Wirbeltiere), Ichthyologie, Berlin, Germany. When only a subset of a particular collection could be obtained on loan, specimens were chosen to maximize representation of populations across the geographic range of each species.

## **Measurements**

Descriptions of meristic, morphological, and qualitative characters used in this study are presented in Appendix B. Note that only those measurements determined to be taxonomically relevant in distinguishing species of *Zebrias* and *Pseudaesopia* are presented in the body of the thesis. In addition, a glossary of anatomical and taxonomic terminology used throughout this study can be found in Appendix C. All observations were made on preserved specimens. Counts and measurements follow those of Hubbs and Lagler (1958), with exception of the following measurements: body thickness, preorbital head length, ocular-side mouth length, blind-side mouth length, nostril to snout distance, ventral eye diameter, and width of the orbits (see Appendix B for descriptions of these characters). All morphological measurements were taken with electronic calipers, sensitive to the nearest hundredth (0.01) of a millimeter. These measurements were subsequently rounded to the nearest tenth of a millimeter for analysis and tabulations. Meristics were obtained by analyzing digital and film radiographs, the majority of which were taken by the author at the Canadian Museum of Nature (CMNFI, formerly NMC), the Smithsonian Institution (USNM), the Australian Museum (AMS), the Muséum National d'Histoire naturelle (MNHN), and the Museum für Naturkunde

(ZMB). Radiographs of type material currently housed at the Natural History Museum (BMNH) and the Nationaal Natuurhistorisch Museum (RMNH) were kindly supplied by these institutions.

Measurements are expressed as percentages of standard length (% SL) or head length (% HL). Measurements may also be expressed as means ( $\bar{x}$ ) and standard deviations (SD). Acronyms used in tables can be found in Appendix B and Appendix C. Counts of ctenii were obtained using the scales at the posterior end of the ocular and blind sides of the fish, ventral to the lateral line. For some specimens, only x-ray data were collected, thus accounting for the infrequent discrepancy between sample sizes for morphological and meristic data presented in tables. Other such discrepancies may have resulted from an inability to take certain measurements on particular specimens as a result of damage or loss of pigmentation. Additional discrepancies in sample sizes may be the result of measurements or qualitative observations that were incorporated later on in the study after variations or trends were noted and access to previous collections was no longer available.

### **Supracranial Complex Pattern (Figure 1.2)**

The supracranial complex (SCC) pattern (Chapleau, 1989) was calculated as follows: the first number in the pattern represents the number of pterygiophores that are directly attached to the erisma. The second number represents the number of pterygiophores found between the erisma and the anteriormost neural spine (referred to as the first neural spine) of the second precaudal vertebra (note that the pterygiophores are not directly anchored to the cranium, and the first precaudal vertebra is represented solely

by a centrum). The third number represents the number of pterygiophores that are attached to the first neural spine. If a fourth number is present in the pattern, it represents the number of pterygiophores found between the neural spines of the second and third precaudal vertebrae (referred herein as the first and second neural spines).

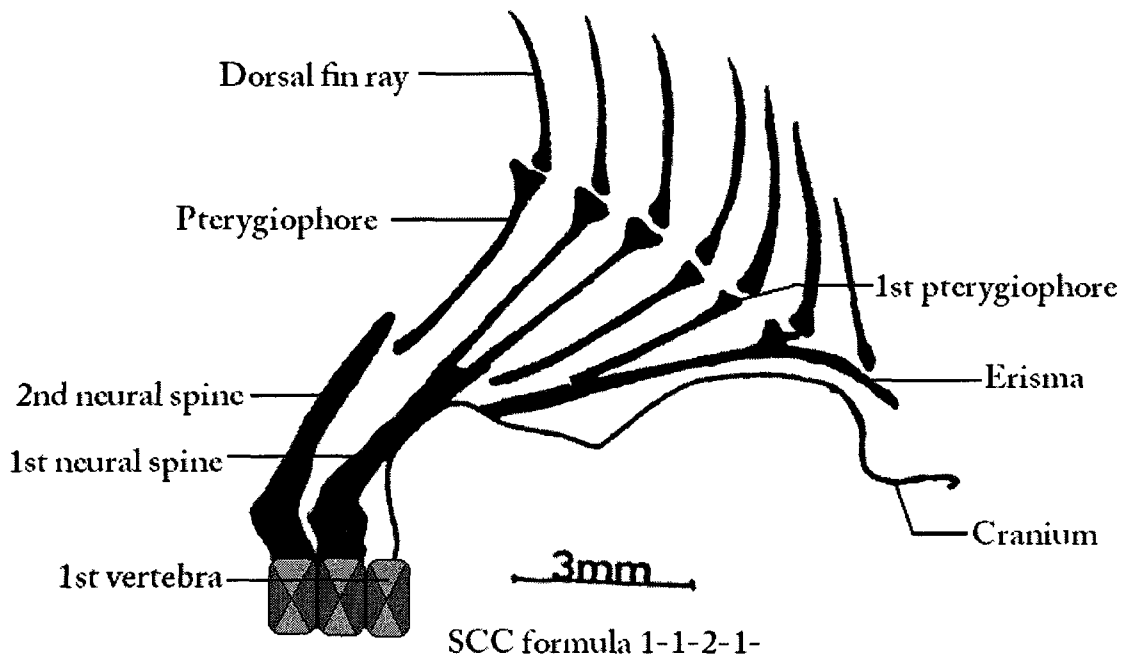


Figure 1.2. Figure modified from Chapleau (1989) depicting the supracranial morphology of a specimen of *Zebrias craticula*.

### Mapping

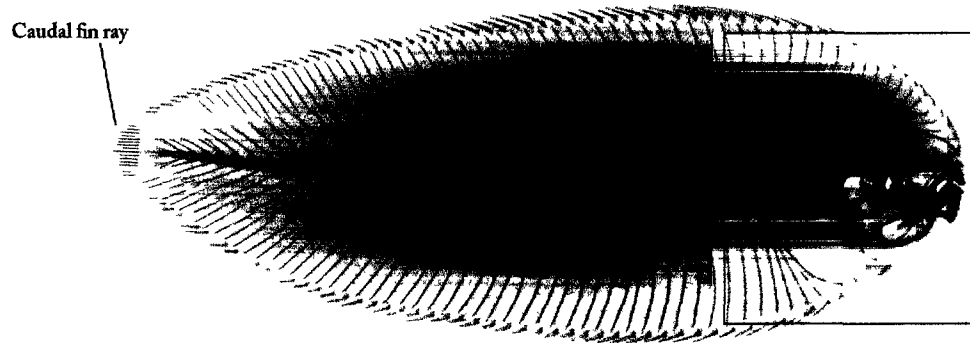
Species occurrence maps were created using ArcGIS (ArcMap 9.2) (ESRI 2006). To ensure accuracy, occurrence data are only presented for specimens that were examined in the present study, unless otherwise indicated. Geographic coordinates, when provided as part of the collection data, were entered into Google Earth 5.0 and converted into decimal degrees to be compatible with ArcMap. In the absence of this information, geographic

coordinates were approximated using Google Earth 5.0 based on the recorded locality. If no locality information was available, the specimen was not represented in the occurrence map. Locations that were deemed to be too vague for an accurate estimate of their geographic coordinates (e.g. “Pacific Ocean”) were also excluded from the maps.

### **Species Concept**

The species concept used in the present study is the phylogenetic species concept as modified by Nixon and Wheeler (1990). This concept considers a species to be a population sample diagnosable by a unique combination of character states.

A



B

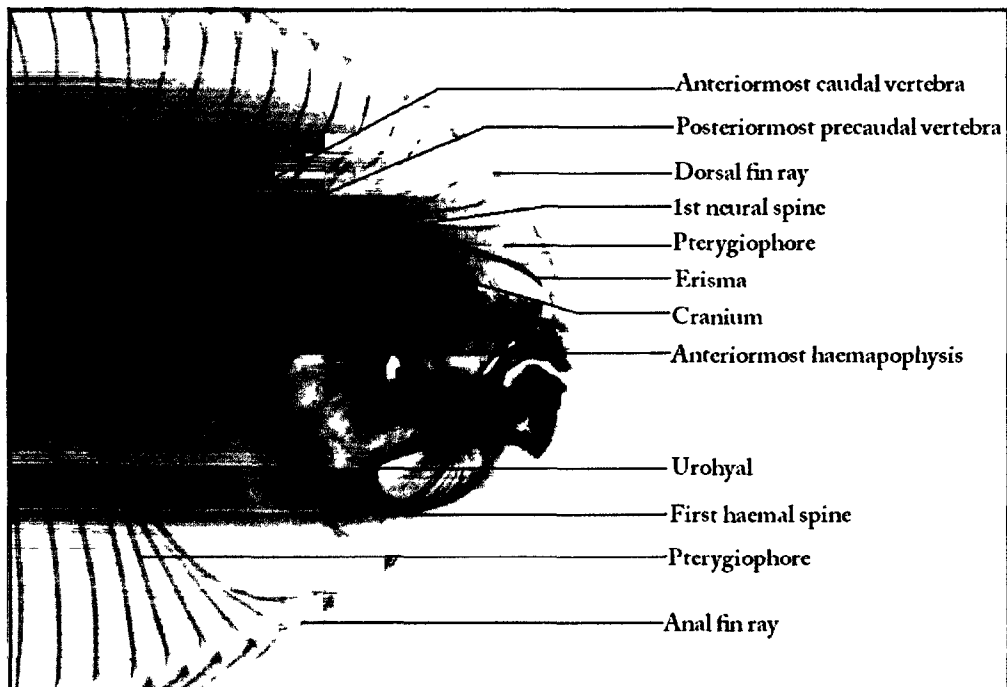
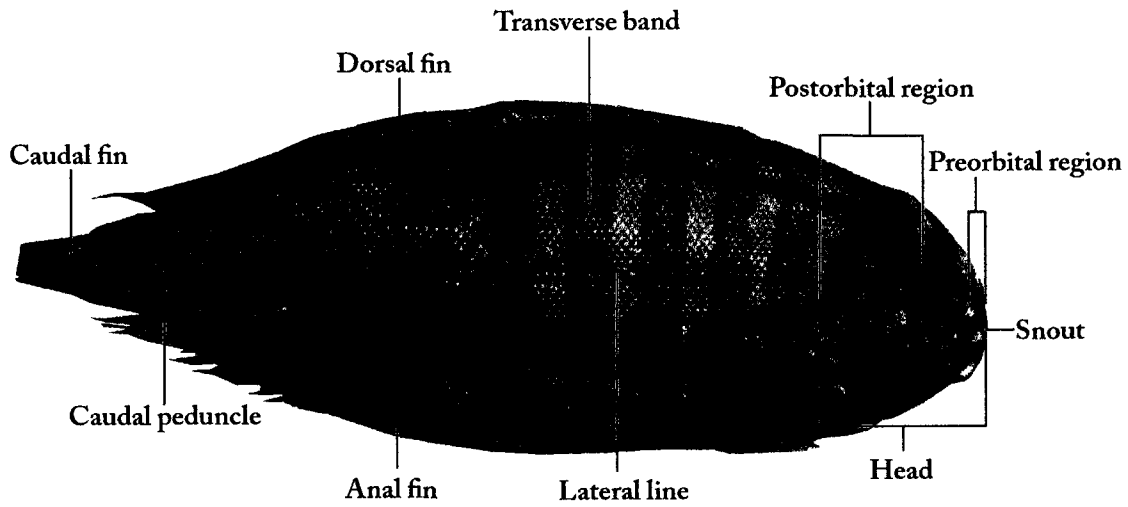


Figure 1.3. (A) Inverted x-ray of *Zebrias zebra* (AMS B67, 162 mm SL) depicting various osteological structures examined in the present study. (B) Magnified section shows details of the head region.

A



B

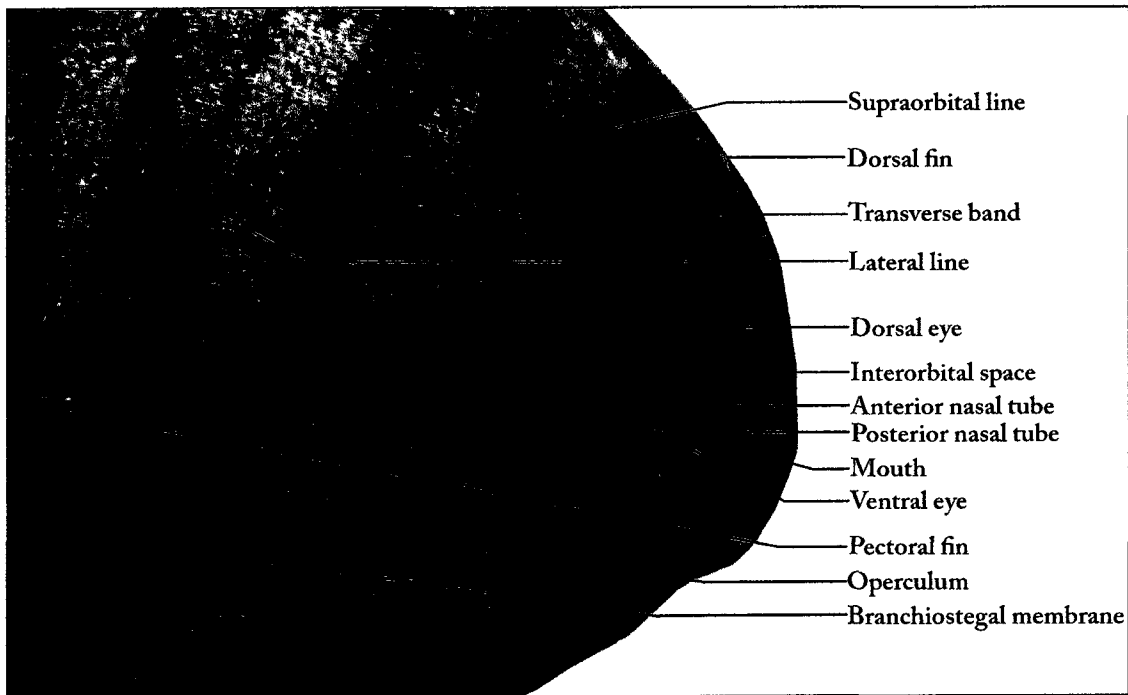


Figure 1.4. (A) Photograph of *Pseudaesopia cochinensis* (USNM Uncatalogued, 138 mm SL) depicting the anatomical features that were examined in the present study. (B) Magnified section showing the external morphology of the head region.

## **CHAPTER 1**

**A revision of the flatfish genus *Zebrias* Jordan and Snyder,  
1900 with notes on *Aesopia* Kaup, 1858 (Pleuronectiformes:  
Soleidae)**

## ABSTRACT

The flatfish genus *Zebrias* Jordan and Snyder, 1900 (Pleuronectiformes: Soleidae) is re-described and the taxonomic status of its nominal species is revised based on a morphological study of 399 specimens including 23 type specimens. The genus is diagnosed by the combination of the presence of a confluent caudal fin attached to the posteriormost anal- and dorsal-fin rays along their entire lengths; the supracranial morphology, characterized by one pterygiophore attached directly to the erisma, one pterygiophore found between the erisma and the first neural spine, and 1–4 pterygiophores attached directly to the first neural spine; the presence of irregular spots or transverse bands on the ocular side; and the attachment of the pectoral fins to the branchiostegal membrane. Of the 15 nominal species examined, 10 were recognized as valid and are re-described. These species, along with their synonyms in parentheses, are as follows: *Z. altipinnis* Alcock, 1890, *Z. annularis* Fowler, 1934, *Z. cancellatus* McCulloch, 1916, *Z. captivus* Randall, 1995, *Z. craticula* McCulloch, 1916, *Z. maculosus* Oommen, 1977, *Z. penescalaris* Gomon, 1987, *Z. quagga* Kaup, 1858, *Z. scalaris* Gomon, 1987 (*Synaptura fasciata* Macleay, 1882), and *Z. zebra* Bloch, 1787 (*Solea fasciata* Basilewsky, 1855, *Solea ommatura* Richardson, 1846, *Solea zebrina* Temminck and Schlegel, 1846). In addition, the closely-related and superficially similar genus *Aesopia* Kaup, 1858 is briefly discussed. An identification key to the species of *Zebrias* is provided.

## RÉSUMÉ

Le genre de poisson plat *Zebrias* Jordan and Snyder, 1900 (Pleuronectiformes: Soleidae) est décrit et le statut taxinomique des espèces nominales a été examiné suite à une étude morphologique de 399 spécimens incluant 23 spécimens-types. Les caractères diagnostiques du genre incluent la présence d'une nageoire caudale confluyente avec les derniers rayons des nageoires dorsale et anale; la morphologie particulière de la portion supracrânienne de la nageoire dorsale, caractérisée par un ptérygiophore attaché directement à l'érisme, un ptérygiophore placé entre l'érisme et la première épine neurale, et 1–4 ptérygiophores attachés directement à la première épine neurale; la présence de taches irrégulières ou de bandes transversales; et l'attachement des nageoires pectorales à la membrane branchiostège. Des 15 espèces nominales, dix espèces sont valides et sont re-décrites. Les espèces valides et leurs synonymes (entre parenthèses), sont: *Z. altipinnis* Alcock, 1890, *Z. annularis* Fowler, 1934, *Z. cancellatus* McCulloch, 1916, *Z. captivus* Randall, 1995, *Z. craticula* McCulloch, 1916, *Z. maculosus* Oommen, 1977, *Z. penescalaris* Gomon, 1987, *Z. quagga* Kaup, 1858, *Z. scalaris* Gomon, 1987 (*Synaptura fasciata* Macleay, 1882), and *Z. zebra* Bloch, 1787 (*Solea fasciata* Basilewsky, 1855, *Solea ommatura* Richardson, 1846, *Solea zebrina* Temminck and Schlegel, 1846). De plus, le genre superficiellement similaire et étroitement apparenté *Aesopia* Kaup, 1858 est brièvement discuté. Une nouvelle clé d'identification des espèces de *Zebrias* est élaborée.

## INTRODUCTION

There has been a long history of taxonomic confusion regarding what diagnostic features define genera within the Soleidae and how closely related and superficially similar genera are distinguished. This confusion has been especially problematic for soles featuring (among other characters) a conspicuous striped colour pattern. Since the mid-1800s, these species have been assigned to one of a group of related genera, including *Aesopia* Kaup, 1858, *Soleichthys* Bleeker, 1860, *Zebrias* Jordan and Snyder, 1900, *Pseudaesopia* Chabanaud, 1934, and *Phyllichthys* McCulloch, 1916.

Chabanaud (1930a) distinguished *Zebrias* Jordan and Snyder, 1900, *Aesopia* Kaup, 1858 (species belonging to the genus at that time have since been re-distributed among the genera *Soleichthys* Bleeker, 1860 and *Zebrias*), *Coryphaesopia* Chabanaud, 1930a (Chabanaud erected this genus to accommodate *Aesopia cornuta* Kaup, 1858) and *Phyllichthys* McCulloch, 1916 from other genera belonging to the Soleinae (once a subfamily of Soleidae) by the absence of the hypacoracoid bone (a bone of the pectoral girdle); the presence of simple, parallel pectoral-fin rays; the membranous attachment of both pectoral fins to the opercular membrane; a short blind-side anterior nasal tube not surrounded by a naked furrow; and the longest vertical-fin rays typically being the posteriormost rays, which are attached, at least basally, to the caudal fin.

Other researchers examining supracranial structures (Chapleau, 1989) and otoliths (Schwarzahns, 1999) have also suggested close relationships among nominal genera containing species of striped soles. As previously mentioned, it has been suggested that the supracranial structure (Figure 1.2; Chapter 1) may be useful in distinguishing soleids from other pleuronectiform families and elucidating intra-relationships within the Soleidae. Wu (1932), Chabanaud (1943) and Chapleau (1989) have discussed variation in supracranial morphology

amongst soleids. Chapleau (1989) organized this variation into four broad morphological types. He suggested that the supracranial complex could be useful in distinguishing genera and species among the Soleidae, as the variability in the structure at these taxonomic levels is minimal. Chabanaud (1943) established groupings based on supracranial morphology as well; these are roughly in accordance with the morphological types established by Chapleau (1989), although there are some differences. Because Chabanaud doesn't specify which species he examined, only genera, it is difficult to make comparisons between the two studies. The genera *Phyllichthys*, *Zebrias*, *Pseudaesopia*, *Aesopia*, and *Soleichthys* exhibit similar supracranial complex patterns (see Methods). These genera typically have 3-6 supracranial pterygiophores, with slight variation in their arrangement.

Schwarzahns (1999) suggested a phylogeny (without a quantitative analysis) of *Zebrias* and closely-related genera based on otolith morphology. He suggests that *Phyllichthys* could represent the most plesiomorphic genus with respect to *Zebrias*, *Pseudaesopia*, *Aesopia*, *Soleichthys*, and *Typhlachirus*. Within this group, Schwarzahns notes synapomorphic features of otolith morphology and postulates that these genera represent specialized offshoots from another group of genera having a different otolith morphology, including *Heterobuglossus*, *Dexillichthys*, *Brachirus*, *Anisochirus*, and *Phyllichthys*, the latter being a morphologically intermediate genus. Schwarzahns' preliminary conclusions based on otolith morphology will have to be examined in light of additional characters to determine the usefulness of otolith morphology for delineating monophyletic groups within the Soleidae.

To date, a phylogenetic study encompassing a comprehensive evaluation and osteological study of all nominal species presently assigned to *Zebrias* Jordan and Snyder, 1900 and related genera has not been published. The genera within this group of soleids are still not well defined;

consequently, taxonomic assignment of nominal species associated with these genera is still problematic.

The genus *Zebrias* was established by Jordan and Snyder (1900) based on *Solea zebrina* Temminck and Schlegel, 1846. In their listing of this genus, Jordan and Snyder (1900) did not provide any detailed description of their new genus, nor any comments on their decision to erect a new genus, but merely commented in a footnote that the new genus is distinguished from *Synaptura* Cantor, 1849 in having a rudimentary blind-side pectoral fin. In their preliminary checklist of the fishes of Japan, Jordan and Snyder (1901a) again listed this genus and species. In that paper, they mentioned (again in a footnote) the single defining character that distinguishes this genus from *Synaptura* and also stated (in that same footnote) that the type species of *Zebrias* is *Solea zebrina* (Temminck and Schlegel). Jordan and Snyder (1901a) also assigned two additional nominal species to *Zebrias*, *Aesopia quagga* Kaup, 1858 and *Aesopia japonica* Bleeker, 1860.

Recognition of the genus *Zebrias* Jordan and Snyder was not universally accepted by other researchers studying nominal species that shared characters with those of the species these authors assigned to *Zebrias*. For example, following Jordan and Snyder's works (1900; 1901a), at least three nominal species with distinct striped color patterns were described and assigned to two other soleid genera including, *Solea synapturoides* (Jenkins, 1910), and *Synaptura cancellata* and *Synaptura craticula* (McCulloch, 1916).

In 1934, Chabanaud conducted the only complete revision of the genus *Zebrias* (the only such study to date). In that study, Chabanaud recognized seven valid species in *Zebrias*, including *Pleuronectes zebra* Bloch, 1787, *Aesopia quagga* Kaup, 1858, *Synaptura fasciata* Macleay, 1882, *Synaptura altipinnis* Alcock, 1890, *Solea synapturoides* Jenkins, 1910,

*Synaptura cancellata* McCulloch, 1916, and *Synaptura craticula* McCulloch, 1916. Chabanaud (1934) synonymized *Solea zebrina* Temminck and Schlegel, 1846 under the senior synonym *Pleuronectes zebra* Bloch, 1787.

Paul Chabanaud did extensive work in the field of flatfish taxonomy and systematics (see for example: Chabanaud 1928a, 1928b, 1930b, 1931, 1934, 1935, 1936, 1940, 1943a, 1947, 1948, 1949, 1950, 1954). His anatomical terminology is unique and complex, so much so, that it prompted a recent publication of a glossary of his terms by Chanet and Desoutter (2008). In addition to his unique jargon, Chabanaud also often used unconventional taxonomical methods based on Berg (1935), which resulted in the establishment of a plethora of taxon names and categories, many of which have dubious validity.

Chabanaud (1936) contended that multiple unique characters displayed by *Solea synapturoides* Jenkins, 1910 warranted the establishment of the subgenus *Holonodus* within *Zebrias*, to which *Solea synapturoides* would be assigned as the type species. The characters he used to define the subgenus include: absence of teeth; elongate ctenii, the lamellose portion of the scale measuring no more than half the total length of the scale; a long ocular-side anterior nasal tube that reaches the anterior margin of the ventral eye when depressed posteriorly; a long caudal fin that extends at least twice as far as the posteriormost dorsal- and anal-fin rays; and a membrane that runs the entire length of the posteriormost dorsal- and anal-fin rays and extends straight across to attach to the adjacent caudal-fin rays.

Chabanaud (1943a) partitioned the genus *Zebrias* into three new genera (*Haplozebrias*, *Nematozebrias*, *Strabozebrias*) and continued to recognize two subgenera (*Pseudaesopia* Chabanaud 1934; *Holonodus* Chabanaud 1936) he had created earlier.

In Chabanaud (1943a), *Haplozebias* was assigned the type species *Synaptura fasciata* Macleay, 1882 (a homonym replaced by *Zebrias scalaris* Gomon 1987; see discussion under account for *Zebrias scalaris*) and was differentiated from *Zebrias* in having simple, undivided fin rays, although Chabanaud pointed out that some of the more developed fin rays appeared to show signs of branching. Examination of *Z. scalaris* and its closely-related congener *Z. penescalaris* Gomon, 1987 in the present study revealed no conspicuous branching of the dorsal- or anal-fin rays.

Chabanaud (1943) assigned the type species *Aesopia quagga* Kaup, 1858 to his new genus *Nematozebias*, which he distinguished from *Zebrias* by the presence of nearly contiguous eyes, each having an ocular tentacle and an elevated interorbital space. *Zebrias quagga* and *Z. captivus* Randall, 1995 are the only species within the genus that display the character of having ocular tentacles.

Chabanaud (1943) distinguished the genus *Strabozebias* from *Zebrias* by the presence of perfectly contiguous eyes surrounded by a common membrane. Chabanaud describes the eyes of this species as being distinctly stalked while at rest. He assigned *Synaptura cancellata* McCulloch, 1916 as the type species and also placed *Synaptura craticula* McCulloch, 1916 in the genus.

With exception of *Pseudaesopia*, the genera and subgenera created by Chabanaud have not been widely used in the literature and have hitherto been designated by most authors dealing with these taxa as synonyms of *Zebrias*. The genera *Haplozebias*, *Nematozebias*, *Strabozebias* and the subgenera *Pseudaesopia* Chabanaud 1934 and *Holonodus* Chabanaud 1936 are presently considered as synonyms of *Zebrias* Jordan and Snyder in Eschmeyer (2010).

Although most genera and subgenera (with the exception of *Pseudaesopia*; see Chapter 2) proposed by Chabanaud have been considered as synonyms of *Zebrias*, there are still some authors (Ochiai, 1963; Whitley, 1966) who support their validity. Ochiai (1963), for example, states that *Zebrias* is easily distinguished from the genera *Haplozebrias* and *Strabozebrias* by the presence of branched vertical-fin rays and a flat interorbital space.

In the present study, evaluation of characters Chabanaud used to distinguish these nominal genera and subgenera do not support recognizing so many taxa among these fishes. Only *Zebrias* Jordan and Snyder and *Pseudaesopia* Chabanaud (see Chapter 2) are recognized. Possibly, after a phylogenetic analysis of all nominal species now recognized in *Zebrias* and related genera has been conducted, other genera and subgenera created by Chabanaud may be resurrected to accommodate a classification that reflects the resulting phylogeny.

Since Chabanaud's studies, relatively little revision work has been done on this genus, with most current references on the genus referring to new species descriptions. Ochiai (1963) provided a more detailed description of the genus, but his study was based only on species occurring in Japanese waters. Zheng and Chang (1965) also provided a preliminary revision of *Zebrias*, but again this provincial study was based only on those species occurring in Chinese waters.

Since Chabanaud's revision, the taxonomic diversity of *Zebrias* has also increased with the description of nine additional nominal species including: *Z. crossolepis* Zheng and Chang, 1965; *Strabozebrias munroi* Whitley, 1966; *Zebrias annandalei* Talwar and Chakrapany, 1967; *Z. cochinensis* Rama-Rao, 1967; *Z. keralensis* Joglekar, 1976; *Z. maculosus* Oommen, 1977; *Z. lucapensis* Seigel and Adamson, 1985; *Z. penescalaris* Gomon, 1987; and *Z. captivus* Randall, 1995. Many of these descriptions are brief and are based on relatively few specimens.

Additionally, *Synaptura callizona* Regan, 1903, (which was examined after its similarity to other species of *Zebrias* was noted while examining type material in the British Museum of Natural History) and *Aesopia japonica* Bleeker, 1860, both of which were assigned to the genus *Aesopia* at the time of Chabanaud's (1934) revision of *Zebrias*, are now also assigned to *Zebrias* (see below). Currently (Eschmeyer, 2010), lists 23 nominal species within the genus *Zebrias* (*Synaptura smithii* Regan, 1903 is listed as a synonym of *Pseudaesopia japonica* Bleeker, 1860 and the current status of *Synaptura callizona* Regan, 1903 is not indicated).

The species, *Strabozebias munroi* Whitley, 1966 (Figure 1.5) was among the nominal species of *Zebrias* examined in the present study. An examination of type material for this species indicates *Strabozebias munroi* would be better placed in the genus, *Phyllichthys* McCulloch, 1916, a genus allied to *Synaptura* Cantor, but distinguishable in having the ocular-side pelvic fin attached to the anal fin. This species has a few superficial characters that also occur in some species of *Zebrias*, including conjoined dorsal, anal and caudal fins and stripes on the body; however, this species possesses other features not present in any species of *Zebrias*, including opercula that are nearly completely sealed against the body, the only opening being found at the base of the pectoral fin; an anal fin that is attached to the ocular-side pelvic fin; a highly irregular band morphology; and proportionately miniscule eyes (14.2-15.0% HL for *munroi*, n = 4; 13-40% HL for *Zebrias*, n = 366,  $\bar{x}$  = 24%, SD = 0.05). Munroe (2001) and Hutchins (2001) also associate this species with the genus, *Phyllichthys*.

Discovery of additional species, re-assignment to *Zebrias* of species previously described in other genera, and removal of *Strabozebias munroi* from *Zebrias* necessitates a more contemporary, comprehensive revision of the genus.



Figure 1.5. Photograph of *Phyllichthys munroi*, holotype, AMSI.15557063, 105 mm SL, Gulf of Carpentaria, Queensland, 17°29'S, 14°45'E.

#### **Determining the type species of *Zebrias* Jordan and Snyder**

There is some confusion concerning the type species of this genus. Several authors have suggested that Bloch's (1787) *Pleuronectes zebra* represents the type species by original designation (Bleeker, 1870-75; Chabanaud, 1934; Ochiai, 1963; Shen and Lee, 1981; Lindberg and Federov, 1993; Li and Wang, 1995), while others contend that Temminck and Schlegel's (1846) *Solea zebrina* represents the type species of the genus (McCulloch, 1929; Jordan and Hubbs, 1925).

Part of the confusion is due to the nature of the types themselves. The types of *Solea zebrina* actually represent a composite species, with two of five paralectotypes corresponding to the species *Pseudaesopia japonica* (Bleeker, 1860) and three paralectotypes being synonymous with *Zebrias zebra* (Bloch, 1787).

Bloch (1787) based his description of *Pleuronectes zebra* on two specimens, one for which he designated the type locality as "Indian Ocean" (ZMB2423, lectotype), and the other for which he recorded the type locality as "Tranquebar" (ZMB7406, paralectotype). Bloch's

original description includes an illustration that was based on the specimen from “Tranquebar”. Presently, only the lectotype exists, the other specimen having gone missing. Like many of Bloch’s alcohol-preserved specimens (Paepke, 1999), the lectotype is in very poor condition; it is almost completely devoid of pigmentation, and a large portion of the abdomen has been destroyed (Figure 1.6). Upon examination of the lectotype, it is evident that Bloch’s illustration depicting the paralectotype is inaccurate. The illustration depicts a fish having nearly twice as many dorsal-fin rays as anal-fin rays, 10 caudal-fin rays, and 6 pelvic-fin rays. Not only are these meristics considerably different from the lectotype, but no species belonging to the genus has comparable meristics; *Zebrias* species have a minimum of 14 caudal-fin rays (more commonly 16-18), a maximum of 5 pelvic-fin rays, and a dorsal to anal fin ratio of 1.1-1.3 ( $\bar{x}$  = 1.2, SD = 0.04). The illustration does, however, depict the transverse bands and confluent caudal fin that are characteristic of the genus. Cantor (1849) also points out the inaccuracy of this figure and describes the dorsal fin as commencing opposite the anterior angle of the upper orbit for this species, as opposed to the end of the snout. In addition to the depicted insertion of the dorsal fin at the tip of the muzzle, the dense assemblage of dorsal-fin rays at the anterior end of the head is not consistent with the dorsal fin observed for the lectotype. In the latter specimen, the fin rays are more or less evenly spaced. The lectotype was observed to have a comparatively narrow body width to that depicted in the illustration of the missing paralectotype; however, this narrow width was not observed in any non-type material (Table 1.17) and could be the result of contraction due to preservation in a strong alcoholic solution, as suggested by Temminck and Schlegel (1846). Based on the illustration of the paralectotype and an examination of the lectotype, it is evident that Bloch based his description on an inaccurate illustration. According

to Paepke (1999), many of Bloch's fish illustrations have been criticized for their inaccurate depictions of fin rays, body proportions, and pigmentation.



Figure 1.6. Photograph of *Pleuronectes zebra* Bloch 1787, lectotype, ZMB2423, 86 mm SL, "Indischer Ozean" (= Indian Ocean).

In addition to the original illustration of *Pleuronectes zebra*, the recorded type locality may have also been inaccurate. Paepke (1999) noted that the geographic location from which Bloch's type specimens were described was often inaccurate. He suggests that Bloch seemed to be under the impression that Japan was actually much farther south, and that he may have mistaken it for Java (Paepke, 1999). Paepke (1999) indicates that Bloch sometimes made errors in recording the habitat of his described species and erroneously designated Tranquebar as the locality on more than one occasion. For example, in his handwritten catalog, Bloch recorded the origin of the species *Anthias macrophthalmus* as "Japan in Tranquebar" (Paepke, 1999). Bloch also incorrectly listed the habitat of the American species, *Trinectes maculatus*, as Tranquebar (Bloch and Schneider, 1801); an obvious error.

The paralectotype of *Z. zebra* was reported (Bloch and Schneider, 1801) from Tranquebar, however, this is most likely an error, as all examined specimens were recorded from

Japan to Indonesia (Figure 1.38). Moreover, no species of *Zebrias* found around India corresponds to the lectotype of this species, which has separate eyes devoid of ocular tentacles, 49 vertebrae, 16 caudal-fin rays, 108 scales along the lateral line, the supracranial complex pattern 1-1-2-, 8 pectoral-fin rays, and a relatively long pectoral fin (55% HL) with the upper three rays elongate.

Despite the aforementioned inaccuracies, the lectotype of Bloch's *Pleuronectes zebra* undoubtedly belongs to the genus, *Zebrias*, as evidenced by the completely confluent caudal fin, supracranial structure, and transverse bands (original illustration), making it the type species by original designation.

### **Abnormal Band Morphology and Arrangement**

Abnormal banding patterns are not uncommon within *Zebrias* and *Pseudaesopia*. Taki (1938) conducted a study on the abnormal arrangement of scales and transverse bands of "*Zebrias japonicus*" (Bleeker, 1860) (= *Pseudaesopia japonica*) and one specimen of "*Zebrias zebrius*" (Temminck and Schlegel, 1846) (= *Zebrias zebra* (Bloch, 1787)). For one of the *Pseudaesopia japonica* specimens, Taki (1938) noted two bands arranged in abnormal, semicircular patterns at the vertical fin margins. He suggested a correlation between the irregular banding pattern and abnormally directed scales. In his study, he found that the bands were oriented perpendicularly to abnormally directed scales. He observed the transverse bands of the *Zebrias zebra* specimen to be irregularly arranged around the middle of its body, however, the scales appeared to be oriented normally. Taki (1938) suggested the degree of variability in colour patterns may be a species-specific character and that the mechanism of band formation may not actually differ interspecifically. He concludes that while banding will be affected when

the scales are abnormally arranged, abnormal pigmentation does not necessarily indicate abnormal scale arrangement.

Abnormal banding was noted in three specimens examined over the course of the present study (Figure 1.7): ANSP87490, *Z. zebra*, West Pacific, China, Aberdeen, Victoria I; ANSP89453, *Z. fasciatus* (= *Z. zebra*), West Pacific, Thailand, Paknam, Siam (at the mouth of the Me Nam Chao Phya, south of Bangkok); SU4615, *Z. zebra*, NW and Central Pacific, Japan, Sea of Japan, Nazaki, off Sand Coast of Japan.

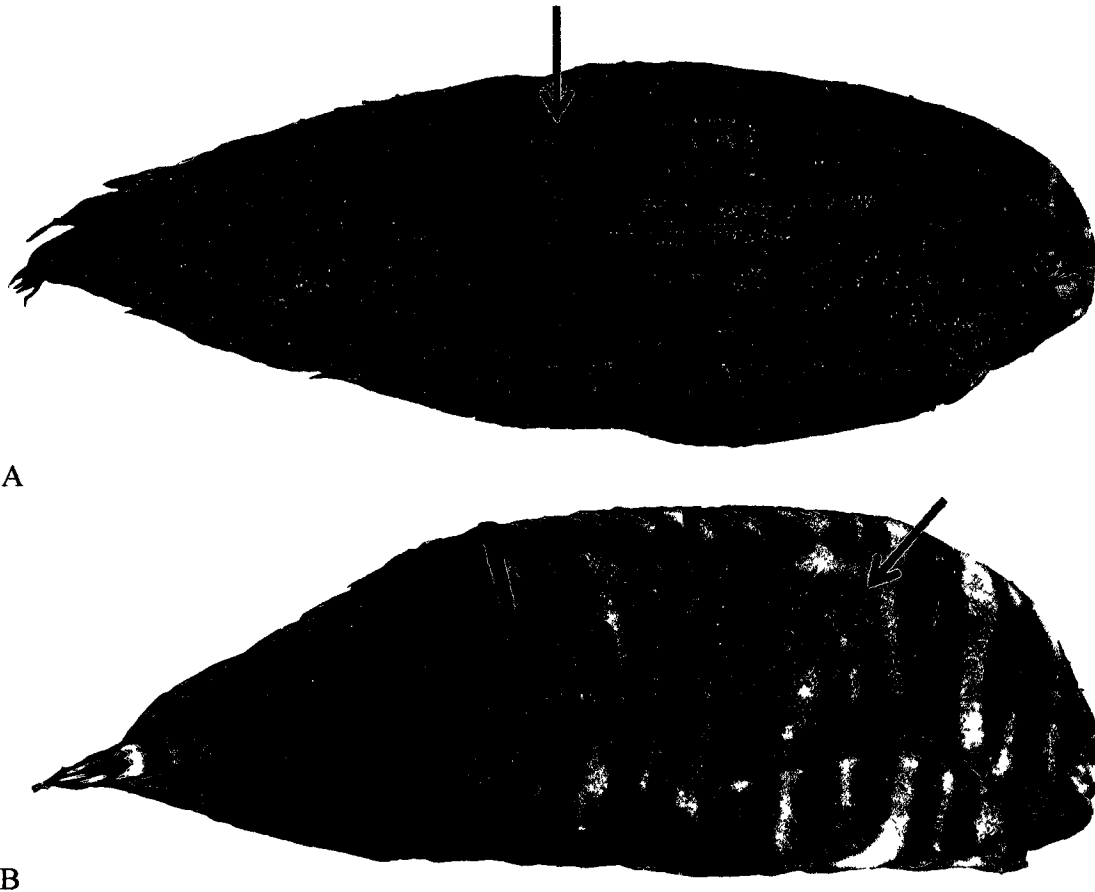


Figure 1.7. Photographs depicting an abnormal band arrangement in specimens of A) *Zebrias fasciatus* (= *Z. zebra*), ANSP89453, 134 mm SL, Thailand, Paknam, Siam, and B) *Zebrias zebra*, ANSP87490, 162 mm SL, China, Aberdeen, Victoria I.

Other band abnormalities have been observed within *Zebrias*. Infrequently, a banding pattern identical to the one found on the ocular side of a specimen was observed along the posterior end of its blind side (Figure 1.8). This type of band abnormality, referred to as ambicoloration, has been previously observed in other species of flatfish (Sivaprakasam, 1965; Pradhan and Pradhan, 1962; Love and Vucci, 1973). Wu (1932), who refers to this phenomenon as “*la coloration double*” (double coloration), states that it is quite common among flatfish and may arise in association with an abnormal origin of the dorsal fin, the vertical position of the dorsal eye, or the excessive growth of the pectoral fin. Wu observed double coloration on the posterior two thirds of a specimen of *Z. zebra* having an enlarged blind-side pectoral fin of comparable size to the ocular-side fin. Wu hypothesizes that the blind side of the abnormal *Zebrias* specimen was likely exposed to light for such a period of time as to enable the formation of bands. This exposure would have required the fish to be oriented so that its blind side was not directly adjacent the substrate, thereby providing more room for the blind-side pectoral fin to develop. Among the specimens presenting double coloration in the present study, the size and positioning of the dorsal fin, blind-side pectoral fin, and dorsal eye were not found to be abnormal, suggesting that another factor, or factors, may be responsible for the double coloration phenomenon.

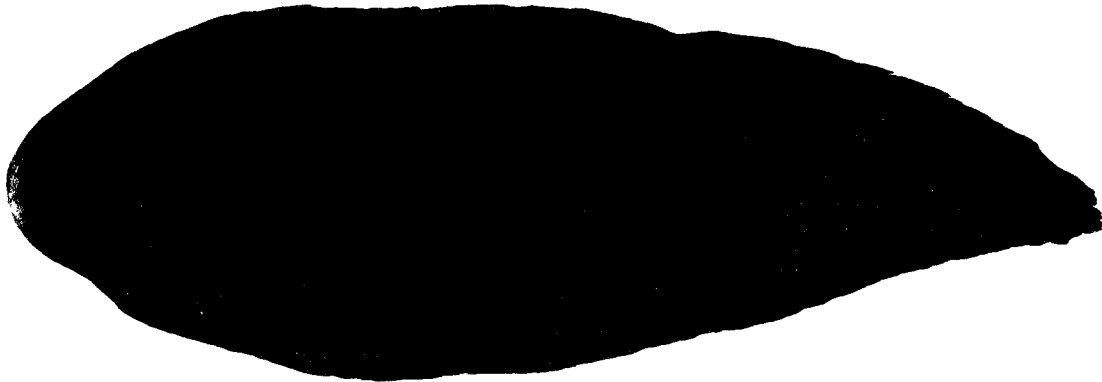


Figure 1.8. Photograph of *Zebrias cancellatus*, WAM P.32578.002, 130 mm SL, Western Australia, Shark Bay, Cape Levillain, 21.17 km east of cape, 25°32.04'S 113°13.247'E to 25°33.448'S 113°13.335'E, depth 19.3 to 18.7 m, displaying ambicoloration.

In addition to the aforementioned banding abnormalities, it is not uncommon for bands to be incomplete, branched, partially split down the center, or conjoined. These types of band abnormalities were observed by Apte and Rao (1991), who examined specimens of *Z. quagga*. As Taki (1938) suggested, the degree of variability in colour patterns does appear to be a species-specific character. Among specimens of *Zebrias scalaris* Gomon, 1987 and *Zebrias penescalaris* Gomon, 1987, for example, it is common to observe incomplete bands that fail to traverse the entire depth of the fish. In the present study, bands arranged into semi-circles were exclusively observed among specimens of *Z. zebra*, although it has been reported in specimens of *Pseudaesopia japonica* (Taki, 1938). The latter species also frequently exhibits bands that bifurcate at their distal end.

## Biological Studies

To date, few studies outside the field of taxonomy have been conducted on species of *Zebrias* and consequently, little is known of their behaviour and ecology. Wu (1932) conducted a study on the physiology of several species of flatfish found in Chinese waters, including *Z. zebra*; Taki (1938) published a study on the abnormal arrangement of scales and transverse bands in a specimen of *Z. zebra*; Apte and Rao (1991) conducted studies on the feeding habits of *Z. quagga*, as well as the eye lens and muscle proteins of this species (1992); Venkataramanujam et al. (1988) published a study on the egg and larval stages of *Z. quagga* reared in the laboratory; and Dou (1996) studied the life history cycle of flatfish species in the Bohai Sea, China, including *Z. zebra*.

## Nominal Species

The present chapter will consider the following nominal species that fit the current definition of *Zebrias*: *Synaptura altipinnis* Alcock, 1890; *Brachirus annularis* Fowler, 1934; *Synaptura cancellata* McCulloch, 1916; *Zebrias captivus* Randall, 1995; *Synaptura craticula* McCulloch, 1916; *Solea fasciata* Basilewsky, 1855; *Synaptura fasciata* Macleay, 1882; *Zebrias maculosus* Oommen, 1977; *Solea ommatura* Richardson, 1846; *Zebrias penescalaris* Gomon, 1987; *Aesopia quagga* Kaup, 1858; *Zebrias scalaris* Gomon, 1987; *Pleuronectes zebra* Bloch, 1787; *Solea zebrina* Temminck and Schlegel, 1846.

## Genus *Zebrias* Jordan and Snyder, 1900

**Synonym(s):** *Haplozebrias* Chabanaud, 1943a; *Holonodus* (subgenus of *Zebrias*) Chabanaud, 1936; *Nematozebrias* Chabanaud, 1943a; *Strabozebrias* Chabanaud, 1943a

**Common name(s):** Zebra sole.

**Type species:** *Pleuronectes zebra* Bloch, 1787: 27 (original designation)

**Type locality:** Lectotype: Indian Ocean; paralectotype: Tranquebar, India (type missing). Note that, as previously mentioned, the type locality is potentially incorrect.

**Diagnosis:** Caudal fin completely or nearly confluent with dorsal and anal fins, posteriormost vertical- (= dorsal and anal) fin rays extending 59-95% relative to caudal-fin length (Figure 1.10); membrane connecting posteriormost vertical-fin rays to adjacent caudal-fin rays extends along their entire lengths; pectoral-fin ray count usually 4-8, one species with 9-12; transverse bands usually present, two species with irregular spots; branchiostegal membrane connected to upper pectoral-fin rays; supracranial morphology with 1-2 pterygiophores attached directly to erisma, 1-2 pterygiophores in space between cranium and first neural spine (not directly anchored to either), and 1-4 pterygiophores attached to first neural spine (= neural spine of the second precaudal vertebra).

**Description:**

Epicranial morphology with 3-6 ( $\bar{x}$  = 4.0, SD = 0.6) supracranial pterygiophores (Table 1.3): one pterygiophore attached directly to erisma, one pterygiophore between erisma and first neural spine (not directly anchored to either), and 1-4 pterygiophores attached to first neural spine. Commonly observed supracranial pattern is 1-1-2. Erisma in close proximity to first neural spine without being in contact. First neural spine either curving anteriorly over posterior portion of cranium or straight with enlarged distal end. Precaudal vertebrae have a neural spine except for anteriormost, which is just a centrum. Precaudal vertebrae typically 9, infrequently 10 (Table 1.1). Vertebrae 38-53 (Table 1.2). Haemapophyses observed on last 4-6 precaudal vertebrae; usually 5 (Table 1.2). Lateral-line scales from opercular margin to caudal peduncle 67-133 (Table 1.6). Dorsal-fin rays 63-97 (Table 1.5); anal-fin rays 51-86 (Table 1.5); caudal-fin rays 16-18 (14-15 rays rarely observed and probably resulting from physical abnormalities or damage) (Table 1.5). Ocular-side pectoral-fin rays 4-12; blind-side pectoral-fin rays 4-12 (Table 1.4). Pelvic-fin rays 3-5 (typically 4-5; 3 rays probably resulting from abnormality or damage) (Table 1.4).

Small-sized group of soles, attaining total lengths to about 33 cm. Body oblong with greatest depth and thickness just posterior to opercular margin; body tapering at posterior end. Head shape somewhat wider than long.

Eyes may be separate or contiguous. Ventral eye nestled in posterior groove of upper lip. Dorsal eye more or less in alignment with ventral eye, or situated slightly anterior to it. Ocular tentacles in two species, but absent from all others.

Ocular-side anterior nostril a posteriorly oriented, elongate tube. When flattened posteriorly, tube reaching no farther than anterior margin of ventral eye; frequently, not reaching

beyond posterior nasal tube. Anterior nasal tube aperture less wide than its base. Ocular-side posterior nostril a short, ventrally oriented, circular tube, situated directly adjacent to ventral eye; its length typically two to three times shorter than anterior tube. Blind-side anterior nostril a short, uneven tube; higher end of tube covering nasal aperture. Anterior nasal tube often inconspicuous, hidden amidst a dense patch of cirri; situated slightly dorso-anteriorly to dorsalmost point of mouth, at vertical through anterior third of mouth. Blind-side posterior nasal tube dorso-posterior relative to anterior nasal tube, at vertical through posterior edge of mouth and at posterior margin of dense patch of cirri on anterior region of head. Posterior tube narrowing slightly toward distal end; slightly larger than ocular-side counterpart. Posterior nasal tube oriented posteriorly.

Mouth longer and less strongly curved on ocular side, posterior margin of jaws extending no farther posteriorly than vertical through posterior margin of ventral eye. Ocular-side lips smooth. Blind-side lower lip plicate. Teeth minute, villiform, restricted to blind-side jaws; often restricted to posterior end of jaws.

Anterior margin of blind-side head with nearly continuous patch of conspicuous cirri, originating near anterior end of dorsal fin and curving ventrally around posterior margin of mouth, cirri also covering chin and opercular margin. Cirri sometimes associated with blind-side lateral line. Mid-head region on blind side occasionally with sparsely distributed cirri between scales posterior to dense patch on anterior end of head. Cirri often present along a small portion of lateral line in region posterior to opercular margin. When present, ocular-side cirri restricted to opercular margin.

Branchiostegal membrane attaching to upper rays of pectoral fin on both sides.

Lateral line well developed on both sides. On ocular side, mediolateral line extending along middle of body from point slightly anterior to opercular margin to caudal peduncle. On head, supraorbital line curving around dorsal eye before straightening towards snout. Blind-side mediolateral line extending horizontally from opercular margin to caudal peduncle; absent or inconspicuous on head.

Scales moderately to strongly ctenoid on both sides. Lateral-line scales cycloid. Scales present or absent in interorbital space. When present, scales smaller than body scales. Body scales of comparable size on ocular and blind sides; number of ctenii comparable on both sides.

Anterior end of dorsal fin at, or slightly anterior to, vertical at anterior margin of dorsal eye. First anal-fin ray just posterior to anus, near distal ends of pelvic fins. Vertical-fin rays increasing in length posteriorly in fins; longest rays situated directly adjacent to caudal fin. Caudal fin rounded or squarish; completely or nearly confluent with dorsal and anal fins, posteriormost vertical-fin ray length 59% to 95% relative to caudal fin length (Figure 1.10). Thin connective membrane attaching posteriormost vertical-fin rays to adjacent caudal-fin rays along their entire lengths. Scales smaller than those on body extending onto dorsal, anal and caudal fins on both ocular and blind sides.

Scales present on base of ocular-side pectoral fin; scales absent on blind-side fin. Pectoral fins typically asymmetrical, ocular-side fin longer than blind-side counterpart. Pectoral fins generally rudimentary; fin rays decreasing in length toward ventral end. Pectoral-fin rays simple, arranged in parallel.

Pelvic fins inserted just anterior to anus, often partially or completely covering it. Pelvic fins not attached to anal fin; generally asymmetrical, ocular-side fin slightly longer. Blind-side pelvic fin may be covered in cirri.

Anus on midline of body or slightly submedian on blind side. Genital papilla submedian on ocular side or adjacent to posteriormost ocular-side pelvic-fin ray; often connected to posteriormost ocular-side pelvic-fin ray by thin membrane.

**Pigmentation of preserved specimens:** Ocular side with series of transverse bands or darkly-demarcated spots. Bands may be arranged in pairs, as singular bands, or a combination of these two. Band morphology and arrangement varies interspecifically and, to a lesser degree, intraspecifically. Bands typically relatively uniform in width across body, those on head becoming narrower. Ocular-side pigmentation ranging from light to dark- grey or brown. Blind side typically pale, whitish, with no conspicuous pigmentation. Minute, almost inconspicuous dark spots frequently present on blind side along posterior median-fin margins; spots may be found in higher concentration and extend onto head, creating a dusky appearance. Ocular-side anterior nasal tube pigmented; ocular-side posterior nasal tube typically whitish with few dark spots. Blind-side nostrils whitish. Interior of mouth typically pale but may be peppered with minute, dark spots, or uniformly charcoal. Bands extending onto dorsal and anal fins, becoming darker and bending posteriorly to follow direction of vertical-fin rays. Ocular-side caudal fin pigmentation varying interspecifically with subtle intraspecific variations. Ocular-side pectoral fin darkly pigmented; blind-side pectoral fin transparent or mostly transparent with minute, dark spots. Pelvic fins whitish.

**Geographic distribution:** *Zebrias* is an Indo-Pacific genus, ranging from the Persian Gulf and extending to India, Indonesia, Australia, China, and Japan.

**Comparisons:** *Zebrias* is most closely allied to *Pseudaesopia* Chabanaud, 1934, with which it shares similar meristic values. The caudal fin among species of *Zebrias* is completely or nearly confluent with the dorsal and anal fins, whereas the caudal fin is quite rounded and distinct among species of *Pseudaesopia* (Figure 1.10). Within *Zebrias*, the posteriormost anal-fin ray extends 59% to 95% of the caudal-fin length, while within *Pseudaesopia*, this ray extends 30% to 62% of the caudal-fin length. The longest dorsal- or anal-fin ray of *Zebrias* species is 67% HL on average (standard deviation = 0.09); the corresponding value for *Pseudaesopia* species is 54% HL (standard deviation = 0.06).

*Zebrias* can be distinguished from *Aesopia* Kaup, 1858 by the presence of moderately to strongly ctenoid scales (*Aesopia* with weakly ctenoid scales), the absence of a modified first dorsal-fin ray (*Aesopia* with an enlarged, detached first dorsal-fin ray), an inconspicuous blind-side anterior nasal tube (*Aesopia* with conspicuous blind-side anterior nasal tube of comparable length to the posterior tube), and a lower number of pectoral-fin rays (*Aesopia* with 10-19 pectoral-fin rays; see Table 1.4). In addition, *Zebrias* typically has five haemapophyses and nine precaudal vertebrae, whereas *Aesopia* typically has six and ten, respectively (Table 1.1 and Table 1.2).

*Zebrias* is readily distinguished from *Phyllichthys* (McCulloch, 1916) by the detachment of the anal fin to the ocular-side pelvic fin (attached for *Phyllichthys*). In addition, *Zebrias* species have regular transverse bands or large, darkly-demarcated spots, both of which are absent from *Phyllichthys* (*P. munroi* has highly irregular, wavy bands; Figure 1.5).

*Zebrias* differs from *Soleichthys* Bleeker, 1860 in the attachment of the caudal fin (*Soleichthys* with a distinct caudal fin, attached only basally to the adjacent vertical-fin rays).

*Zebrias* can also be distinguished by its shorter ocular-side anterior nasal tube (*Soleichthys* with anterior nasal tube extending beyond the middle of ventral eye when flattened posteriorly).

Table 1.1. Frequency distribution of precaudal vertebrae among closely-related genera, *Zebrias*, *Pseudaesopia*, *Aesopia*, *Soleichthys*, and *Phyllichthys*. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material.

Genus	Precaudal Vertebrae						n	Mean	SD
	5	7	8	9	10	11			
<i>Aesopia</i>				7	23	1	31	9.8	0.5
<i>Pseudaesopia</i>			9*	83*	3		95	9.0	0.3
<i>Zebrias</i>	1	1	16*	355*	12		385	9.0	0.4
<i>Soleichthys</i>				12			12	9.0	0.0
<i>Phyllichthys</i>				6*	1		7	9.1	0.4

Table 1 2. Frequency distribution of vertebral counts and haemapophyses on the abdominal vertebrae among recognized species of *Zebrias*. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material.

Species	Vertebrae															n	Mean	SD	
	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52				53
<i>Z altipinnis</i>											6	3	2				11	48.6	0.8
<i>Z annularis</i>					1*	2*											3	42.7	0.6
<i>Z cancellatus</i>								4	8	9	11*	3					35	47.0	1.2
<i>Z captivus</i>	1*	1*															2	38.5	0.7
<i>Z craticula</i>	1			3	27*	12*											43	42.1	0.9
<i>Z penesularis</i>						6*	12*	3									21	43.9	0.7
<i>Z quagga</i>	1	19	47	32	9	3	1*										112	40.4	1.0
<i>Z scalaris</i>						1	7	20	5								33	44.9	0.7
<i>Z zebra</i>				1	2	1	5	18	26	12	6	10*	11	14	11	7	124	47.9	2.9

Species	Haemapophyses			n	Mean	SD
	4	5	6			
<i>Z altipinnis</i>		11		11	5	0
<i>Z annularis</i>		3*		3	5	0
<i>Z cancellatus</i>		35*		35	5	0
<i>Z captivus</i>		2*		2	5	0
<i>Z craticula</i>	1	41*	1	43	5	0.2
<i>Z penesularis</i>		19*	2*	21	5.1	0.3
<i>Z quagga</i>		107*	7	114	5.1	0.2
<i>Z scalaris</i>		28*	5	33	5.2	0.4
<i>Z zebra</i>	2	112*	11	125	5.1	0.3

Table 1.3. Frequency distribution of supracranial complex patterns of the dorsal fin and the number of supracranial pterygiophores of the dorsal fin on and anterior to the first neural spine among recognized species of *Zebrias*. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material. See materials and methods for definition of supracranial complex.

Species	Supracranial Pattern										n
	0-1-2-	1-0-1-	1-0-2-	1-1-1-	1-1-2-	1-1-3-	1-1-4-	1-2-1-	1-2-2-	1-2-3-	
<i>Z craticula</i>				6*	36*			1			43
<i>Z captivus</i>				1*	1*						2
<i>Z quagga</i>	1			11	98*	2					112
<i>Z cancellatus</i>		3	3	12*	16*	1					35
<i>Z penescalaris</i>					14	6	1				21
<i>Z zebra</i>	1			16	102*	3			1	1*	124
<i>Z scalaris</i>				1	19	12				1	33
<i>Z annularis</i>						2*			1*		3
<i>Z altipinnis</i>						2	9				11

Species	Number Supracranial Pterygiophores					n	Mean	SD
	2	3	4	5	6			
<i>Z craticula</i>		6*	37*			43	3.9	0.4
<i>Z captivus</i>		1*	1*			2	3.5	0.7
<i>Z quagga</i>		12	98*	2		112	3.9	0.3
<i>Z cancellatus</i>	3	15*	16*	1		35	3.4	0.7
<i>Z penescalaris</i>			14*	6*	1*	21	4.4	0.6
<i>Z zebra</i>		17	102*	4	1	124	3.9	0.4
<i>Z scalaris</i>		1	19	12	1	33	4.4	0.6
<i>Z annularis</i>				3*		3	5	0
<i>Z altipinnis</i>				2	9	11	5.8	0.4

Table 1.4. Frequency distribution of ocular-side pectoral- and pelvic-fin rays among recognized species of *Zebrias* and *Aesopia*. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material.

Ocular-Side Pectoral-Fin Rays																					
Species	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	n	Mean	SD		
<b><i>Zebrias</i></b>																					
<i>Z. altipinnis</i>				1		2	3	4	1								11	10.8	0.9		
<i>Z. annularis</i>	1*			1*	1												3	7.3	1.2		
<i>Z. cancellatus</i>		3	9	18*	4			1									35	7.5	1.0		
<i>Z. captivus</i>			2*														2	5.5	0.7		
<i>Z. craticula</i>		1	12*	30*	3												46	7.6	0.7		
<i>Z. penescalaris</i>		10*	7*	3*													20	5.7	0.7		
<i>Z. quagga</i>	1	10	42	47	9				1*								110	7.2	0.8		
<i>Z. scalaris</i>	1	6	13	9	1												30	6.0	0.9		
<i>Z. zebra</i>		2	6	17	34*	32*	11										102	8.8	1.0		
<b><i>Aesopia</i></b>																					
<i>A. cornuta</i>									1	2	5	3	5	2	1	1	20	14.9	1.7		
Ocular-Side Pelvic-Fin Rays																					
	3	4	5																n	Mean	SD
<i>Z. altipinnis</i>		1	10															11	5.0	0	
<i>Z. annularis</i>		1	2*															3	5.0	0	
<i>Z. cancellatus</i>	2	32*	1															35	4.0	0.2	
<i>Z. captivus</i>		2*																2	4.0	0	
<i>Z. craticula</i>	1	45*																46	4.0	0.1	
<i>Z. penescalaris</i>		21*																21	4.0	0	
<i>Z. quagga</i>	5	103*	1															109	4.0	0.2	
<i>Z. scalaris</i>		32*																32	4.0	0	
<i>Z. zebra</i>	3	97*	1															101	4.0	0.2	

Table 1.5. Frequency distribution of dorsal-, anal-, and caudal-fin rays among recognized species of *Zebrias*. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote value for type material.

Species	Dorsal-Fin Rays																												n	Mean	SD												
	58	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89				90	91	92	93	94	95	96	97				
<i>Z altipinnis</i>																		1	1	1	1	1	1	2		3										11	83.6	2.9					
<i>Z annularis</i>										2*		1																											3	72.0	1.7		
<i>Z cancellatus</i>							1	1		2	5	4	2	5*	6	1	3	2	1	2*																				35	74.9	3.2	
<i>Z captivus</i>	1*				1*																																		2	64.5	2.1		
<i>Z craticula</i>										1	4	9*	6	5	8	4	2	2*	2																					43	75.0	2.3	
<i>Z penesularis</i>									3*	4*	5*		4*	1*	1	1	1*		1*																					21	75.0	3.0	
<i>Z quagga</i>		2	2	9	9	12	18	20	11	13	6	3	4*	1	2																									112	69.8	2.7	
<i>Z scalaris</i>											2		2	5	3*	4	4	2	2	2	2	5	2	1																34	79.1	3.3	
<i>Z zebra</i>						1	2	3	2	1	7	8	11*	10	5	7*	3	6*	4	1	3	6	6	4	10	2	4	4	6	4	1	2	2	1	1				127	81.2	7.2		
Species	Anal-Fin Rays																												n	Mean	SD												
	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78				79	80	81	82	83	86						
<i>Z altipinnis</i>													1	1	1	2	1	2		3																					11	67.0	2.4
<i>Z annularis</i>					1*		1*			1																														3	57.3	2.5	
<i>Z cancellatus</i>										3	3	5	4	6	3	3*	4	1	3*																						35	65.1	2.7
<i>Z captivus</i>	1*			1*																																				2	52.5	2.1	
<i>Z craticula</i>											5	6*	4	7	8	6	4	2*	1																					43	64.3	2.1	
<i>Z penesularis</i>									1*	1	4*		4*	7*	1	1*	1*	1																							21	64.3	2.2
<i>Z quagga</i>		3	3	4	7	8	22	27	14	9	8*	3	3	1																											112	57.8	2.4
<i>Z scalaris</i>										2	2		6	6*	4	3	6	3	1				1																	34	65.9	2.8	
<i>Z zebra</i>							1	3	2	3	9	8	10*	13	4	7*	4	3	3	2	7*	5	5	6	5	6	4	8	1	1	1	3	1	1					126	69.7	6.7		
Species	Caudal-Fin Rays							n	Mean	SD																																	
	13	14	15	16	17	18	19																																				
<i>Z altipinnis</i>							11																																11	18.0	0		
<i>Z annularis</i>							3*																																	3	18.0	0	
<i>Z cancellatus</i>	1	1	1*	1	6	25*																																		35	17.4	1.2	
<i>Z captivus</i>						2*																																		2	18.0	0	
<i>Z craticula</i>				1	2	39*	1																																	43	17.9	0.4	
<i>Z penesularis</i>			1	18*	1	1																																		21	16.1	0.5	
<i>Z quagga</i>				2	3	107*	1																																	113	17.9	0.3	
<i>Z scalaris</i>		1	2	26*	2	1																																		32	16.0	0.6	
<i>Z zebra</i>		3	13	100*	2	6																																		124	16.0	0.6	

Table 1.6. Frequency distribution of lateral line scales among recognized species of *Zebrias*. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote value for type material.

Species	Count of Scales Along Lateral Line																							
	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	
<i>Z altipinnis</i>																								
<i>Z annularis</i>																								
<i>Z cancellatus</i>																								
<i>Z captivus</i>									1*	1*														
<i>Z craticula</i>												1		1	2	3	1	2	3	5*	5	3*	5	
<i>Z penesularis</i>	1	1*	1	3*	2*	2	1	1		3*	2	2*												
<i>Z quagga</i>											1	2*		2	6	2	6	2	7	6	8	8	4	
<i>Z scalaris</i>										1	1	2		2	3		1	6	4	6*		4		
<i>Z zebra</i>																								
	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	
<i>Z altipinnis</i>												1		2	3	1	1	1						
<i>Z annularis</i>					1				1*		1*													
<i>Z cancellatus</i>																	1		1		1*	1		
<i>Z captivus</i>																								
<i>Z craticula</i>	3	7	1	2		1																		
<i>Z penesularis</i>																								
<i>Z quagga</i>	5	8	9	4	4	3	5	3	3	3	3	1		2	1	1								
<i>Z scalaris</i>			1		1																			
<i>Z zebra</i>		1			2	5	3	6*	4	3	1	7*	2	1	5	4*	3	4	7	3*	3	2	2	
	112	113	114	115	116	117	118	119	120	121	122	123	124	125	127	129	131	133				n	Mean	SD
<i>Z altipinnis</i>		2																				11	104.9	4.3
<i>Z annularis</i>																						3	96.7	3.5
<i>Z cancellatus</i>	2	5	1	1	3	3	3	2	2*	2	3		1	1	1	1						35	116.9	5.4
<i>Z captivus</i>																						2	74.5	0.7
<i>Z craticula</i>																						45	86.2	3.8
<i>Z penesularis</i>																						19	71.9	3.5
<i>Z quagga</i>																						109	88.8	6.2
<i>Z scalaris</i>																						32	84.0	3.8
<i>Z zebra</i>	5	3	1	7	4		2	1	4	2	2	2	1				1	1				104	107.1	9.4

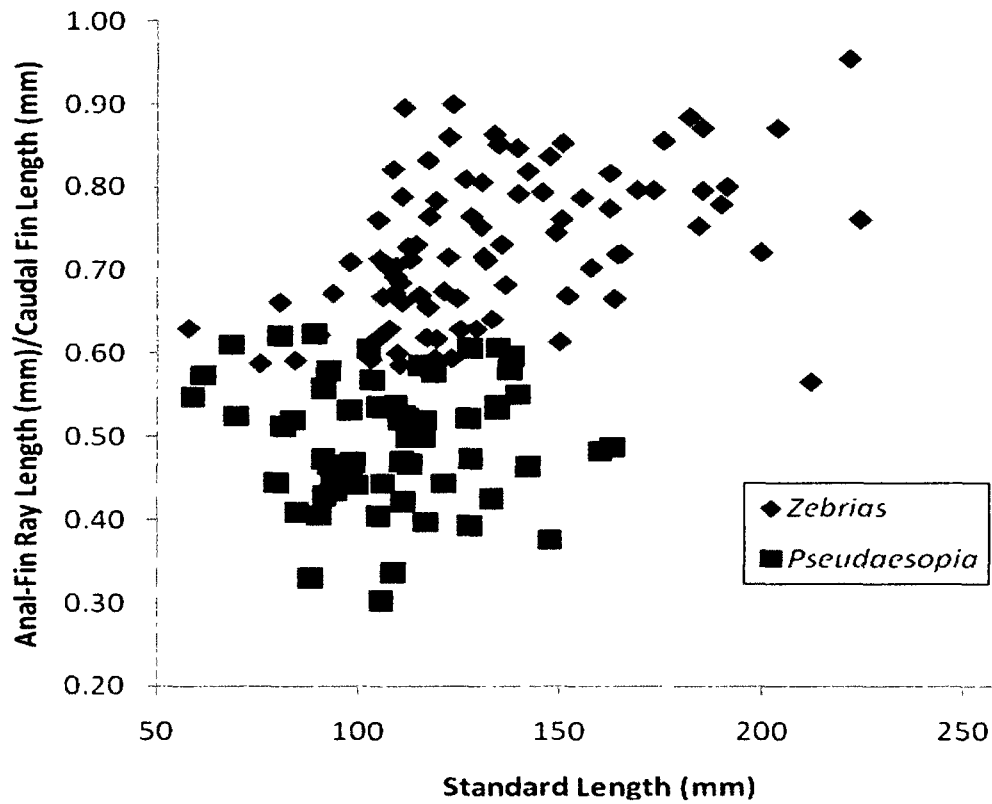
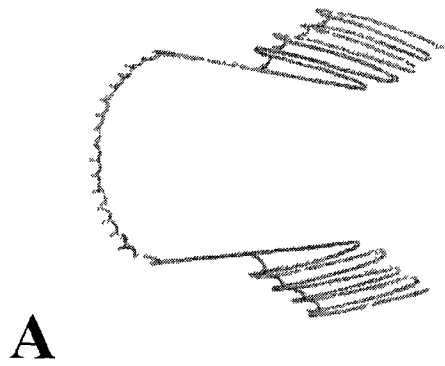
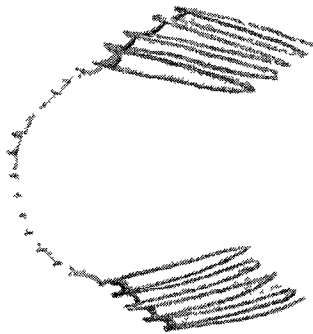


Figure 1.9. Graph depicting the ratio between the length of the posteriormost anal-fin ray and the length of the caudal fin among recognized species of *Zebrias* (diamonds) and *Pseudaesopia* (squares). Ratio was examined in a subset of 155 specimens.



**A**



**B**

Figure 1.10. Diagram illustrating the generalized attachment of the posteriormost vertical fin rays to the caudal fin as observed in A) *Pseudaesopia* and B) *Zebrias*.

*Zebrias altipinnis* (Alcock, 1890)

Figures 1.11-1.12, Table 1.7



Figure 1.11. Photographs of *Zebrias altipinnis*, USNM uncatalogued, 200 mm SL, India, showing the ocular (above) and blind (below) sides.

**Synonym(s):** *Synaptura altipinnis* Alcock, 1890

**Common name(s):** None.

**Material examined:** 11 specimens (148.13-234.89 mm TL)

**Type material:** Holotype, ZSI F12917: not examined.

**Non-type material:** USNM uncatalogued, 2(189.79-203.65 mm SL), India; USNM uncatalogued, 4(128.02-167.64 mm SL), Myanmar, Delta Fishing Area, D-9; USNM uncatalogued, Smithsonian Oceanographic Sorting Center Ref #334, 3(184.16-199.57 mm SL), USBCF India: Madras State; Porto Novo; CA.8 miles off mouth of Vellar Estuary (Bay of Bengal) (Bay of FHB:66-32); CAS205998, 2(126.48-169.04 mm SL), Indo-West Pacific, Thailand, Prachuap Khiri Khan, Gulf of Thailand, East Side of Goh Chuang, 40-81 miles offshore from Bangkok Fish Market.

**Diagnosis:** A species of *Zebrias* with the following combination of characters: Ocular-side maxilla nearly reaching posterior edge of ventral eye; ocular-side anterior nasal tube not reaching posterior nasal tube when flattened; 48-50 vertebrae; 5 pelvic-fin rays; 14-15 singular bands; 9-12 pectoral-fin rays; 100-113 lateral-line scales; eyes separated by scaly interorbital space; ocular-side caudal fin dark brown with two pale spots at its base; supracranial complex formula 1-1-(3-4).

**Description:** Meristic and morphometric characters are indicated in Table 1.7. Small sole, attaining a total length of 23 cm. Supracranial pterygiophores 5-6 ( $\bar{x} = 6$ ); formula 1-1-(3-4). Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes separated without tentacles. Scales in interorbital space. Ocular-side anterior nasal tube not reaching posterior nasal tube when flattened; base of nasal tube slightly wider than aperture.

Ocular-side posterior nasal tube approximately half length of anterior. Blind-side anterior nostril a short, uneven tube; anterior nasal tube inconspicuous, dorso-anterior to dorsalmost point of mouth. Blind-side posterior nasal tube short, slightly larger than ocular-side counterpart; dorso-posterior to anterior nasal tube, at vertical through posterior edge of mouth. Posterior nasal tube narrowing slightly toward distal end. Large mouth, posterior margin of ocular-side jaws nearly reaching vertical through posterior margin of ventral eye ( $\bar{x} = 37\%$  HL). Ocular-side lips smooth. Blind-side lower lip plicate. Teeth restricted to blind-side jaws. Ocular-side cirri restricted to short fringe along opercular margin. Cirri densely distributed at anterior end of blind-side head, extending along snout, chin and opercular margin. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line well developed on both sides. Supraorbital line present on ocular-side head. Blind-side lateral line not extending anterior to opercular margin. Lateral-line scales cycloid. Scales on body broad, rectangular; moderately ctenoid with 10-15 ctenii on ocular side and 10-17 ctenii on blind side. Anterior end of dorsal fin at, or slightly anterior to, vertical at anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Vertical-fin rays increasing in length toward posterior end, longest rays situated directly adjacent to caudal fin. Dorsal- and anal-fin rays branching at their distal ends. Caudal fin may be rounded or mildly trapezoidal; completely confluent with vertical fins. Scales extending onto median fins. Pectoral fins symmetrical, short (ocular-side fin 15-22% in HL, blind-side fin 16-22% in HL). Dorsalmost ray of pectoral fin longest; more ventral rays decreasing gradually in length. Pelvic fins of comparable length. Anus submedian on blind side. Genital papilla submedian on ocular side, not attached to ocular-side pelvic fin.

**Pigmentation of preserved specimens:** Ocular side light brown with series of 14-15 deeper brown, singular, broad bands (4 on head, 10-11 on body). Bands relatively uniform in width across body, those on head becoming narrower. Inter-band space slightly narrower than band width. Bands distinct, lightly demarcated. Blind side whitish, devoid of conspicuous pigmentation. Minute, dark spots frequently present around blind-side median-fin margins at posterior end of body. Interior of mouth grey to black, or white with minute, dark spots. Bands extending onto vertical fins where they become darker. Ocular-side caudal fin dark brown or black with two pale spots at its base; infrequently, smaller pale spots may be present toward distal end of fin. Ocular-side pectoral fin uniformly dark brown or black. Blind-side pectoral fin transparent or mostly transparent with minute, black spots; black spots may be present on skin beneath operculum.

Table 1.7. Meristic and morphometric characteristics of type and non-type specimens of *Zebrias altipinnis*. Means and standard deviations are shown in parentheses. Data for *Synaptura altipinnis* holotype were obtained from the original species description (Alcock, 1890). Measurements and abbreviations are described in Appendix B.

	<i>Synaptura altipinnis</i> holotype	<i>Z. altipinnis</i> non-type specimens (n=11)
<b>Standard length (mm)</b>	-	126.48-203.65 (166.8; 29.5)
<b>Total length (mm)</b>	-	148.13-234.89 (195.2; 32.4)
<b>Counts</b>		
Dorsal-fin rays	81	79-87 (83.6; 2.9)
Anal-fin rays	66	63-70 (67; 2.4)
Caudal-fin rays	18	18 (18; 0)
Precaudal vertebrae	-	9 (9; 0)
Caudal vertebrae	-	39-41 (39.6; 0.8)
Total vertebrae	-	48-50 (48.6; 0.8)
Haemopophyses	-	5 (5; 0)
Pterygiophores	-	5-6 (5.8; 0.4)
Pectoral-fin rays o.s.	9	7-12 (10.1; 1.4) <sup>2</sup>
Pectoral-fin rays b.s.	-	9-12 (10.8; 0.9)
Pelvic-fin rays o.s.	4	4-5 (4.9; 0.3)
Pelvic-fin rays b.s.	-	5 (5; 0)
Lateral-line scales	135 <sup>1</sup>	100-113 (104.9; 4.3)
Number of bands	-	14-15 (14.7; 0.5)
<b>Measurements</b>		
<b>%SL</b>		
Head length	-	0.18-0.21 (0.19; 0.009)
Head depth	-	0.17-0.23 (0.21; 0.02)
Body depth	-	0.35-0.42 (0.38; 0.02)
Caudal-fin length	-	0.14-0.19 (0.17; 0.02)
Width caudal peduncle	-	0.06-0.08 (0.07; 0.008)
<b>%HL</b>		
Length of pectoral fin o.s.	-	0.15-0.22 (0.18; 0.03)
Length of pectoral fin b.s.	-	0.16-0.22 (0.19; 0.02)
Length of pelvic fin o.s.	-	0.19-0.29 (0.24; 0.03)
Length of pelvic fin b.s.	-	0.19-0.33 (0.24; 0.04)
Pre-orbital head length	-	0.14-0.28 (0.18; 0.04)
Post-orbital head length	-	0.56-0.70 (0.61; 0.04)
Snout length	-	0.24-0.30 (0.26; 0.02)
Nostril to snouth distance	-	0.12-0.21 (0.17; 0.03)
Mouth length o.s.	-	0.34-0.40 (0.37; 0.02)
Mouth length b.s.	-	0.26-0.32 (0.29; 0.02)
Ventral eye diameter	-	0.18-0.23 (0.20; 0.02)
Width of orbits	-	0.26-0.37 (0.33; 0.03)
Longest dorsal ray	-	0.55-0.77 (0.66; 0.07)
Longest anal ray	-	0.61-0.71 (0.65; 0.03)
IOD/V	-	0.07-0.39 (0.24; 0.09)
BPC/OPc	-	0.87-1.34 (1.09; 0.2)
BPv/OPv	-	0.92-1.13 (0.99; 0.07)

<sup>1</sup>: count from origin on snout to base of caudal fin.

<sup>2</sup>: 1/11 specimens with 7, rest with 9-12.

**Geographic distribution:** *Zebrias altipinnis* has been reported from the Bay of Bengal, Eastern coast of India (Krishnan and Mishra, 1993; Mishra and Krishnan, 2003), the coast of Myanmar, the Gulf of Thailand, and Malaysia (Mohsin and Ambak, 1996) at depths of 22-40 m.

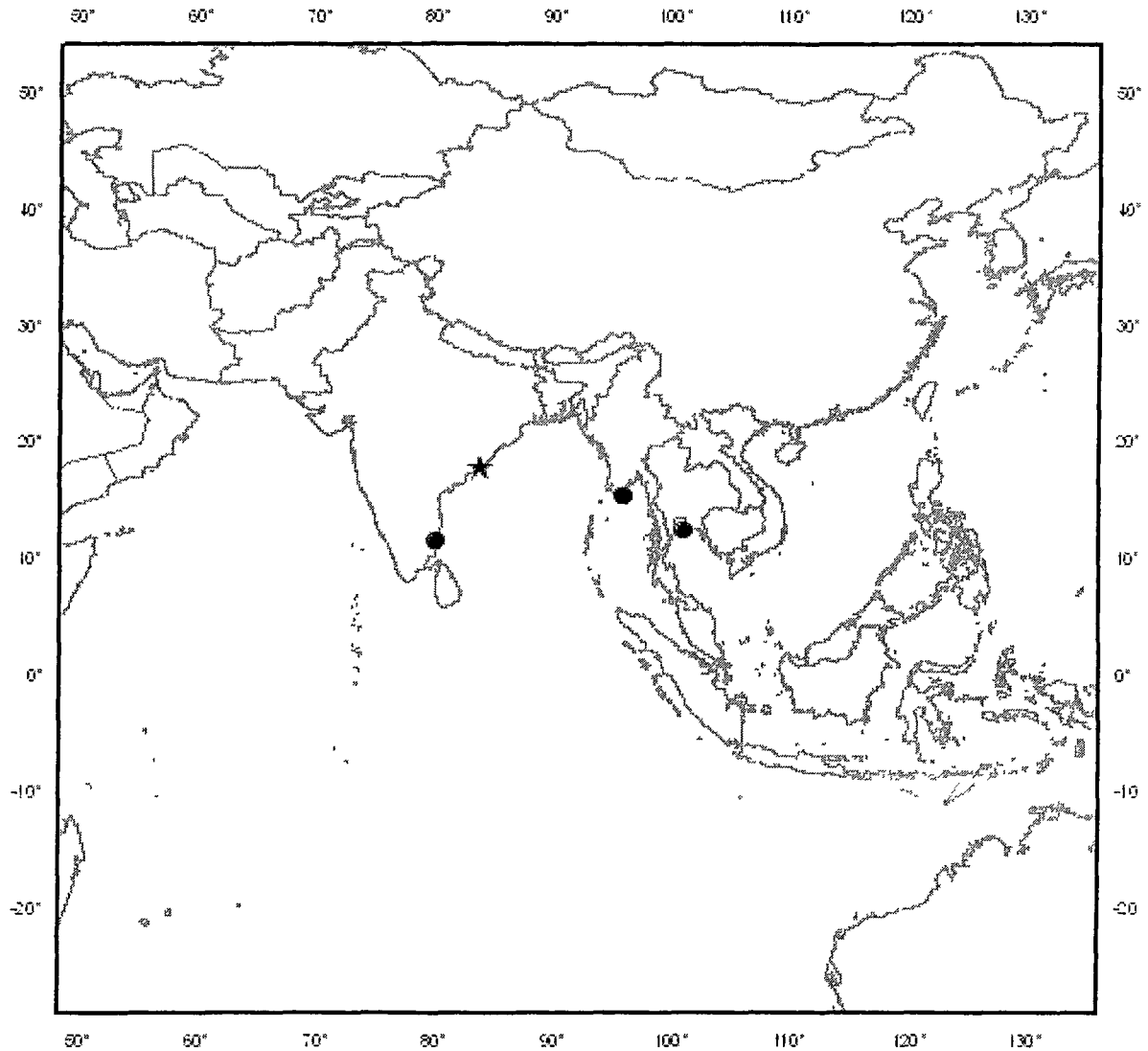


Figure 1.12. Geographic distribution of *Zebrias altipinnis*. Star denotes locality of type material according to Alcock (1890).

**Remarks:** In Alcock's (1890) original description, the band count of 28 refers to both the bands and the interband spaces (counted as light bands).

**Comparisons:** *Z. altipinnis* can be distinguished from all of its congeners by its large mouth (ocular side nearly reaching the posterior margin of the ventral eye), and short ocular-side anterior nasal tube (not reaching posterior nasal tube when flattened). With the exception of *Z. zebra* (Bloch, 1787) and *Z. cancellatus* (McCulloch, 1916), *Z. altipinnis* can be distinguished by its high meristic values: vertebral count (48-50), number of scales along the lateral line (100-113), and number of pectoral-fin rays (9-12). *Z. zebra* is distinguished by the presence of barbels on the blind-side chin and anterior end of the dorsal fin, in addition to 24 paired bands. *Z. cancellatus* differs in having a parabolic pigmentation pattern on its ocular side and contiguous eyes. *Z. craticula* (McCulloch, 1916) is easily distinguished in having more numerous, narrower bands that extend from the snout to the tip of the caudal fin (17-24). *Z. quagga* (Kaup, 1858) and *Z. captivus* Randall, 1995 differ in the presence of contiguous eyes with tentacles. *Z. maculosus* (Oommen, 1977) and *Z. annularis* (Fowler, 1934) are distinguished by the presence of irregular spots in lieu of bands. *Z. scalaris* Gomon, 1987 and *Z. penescalaris* Gomon, 1987 differ in having more numerous, indistinct bands (17-23) and uniformly dark median fins.

*Zebrias annularis* (Fowler, 1934)

Figures 1.13-1.15, Tables 1.8

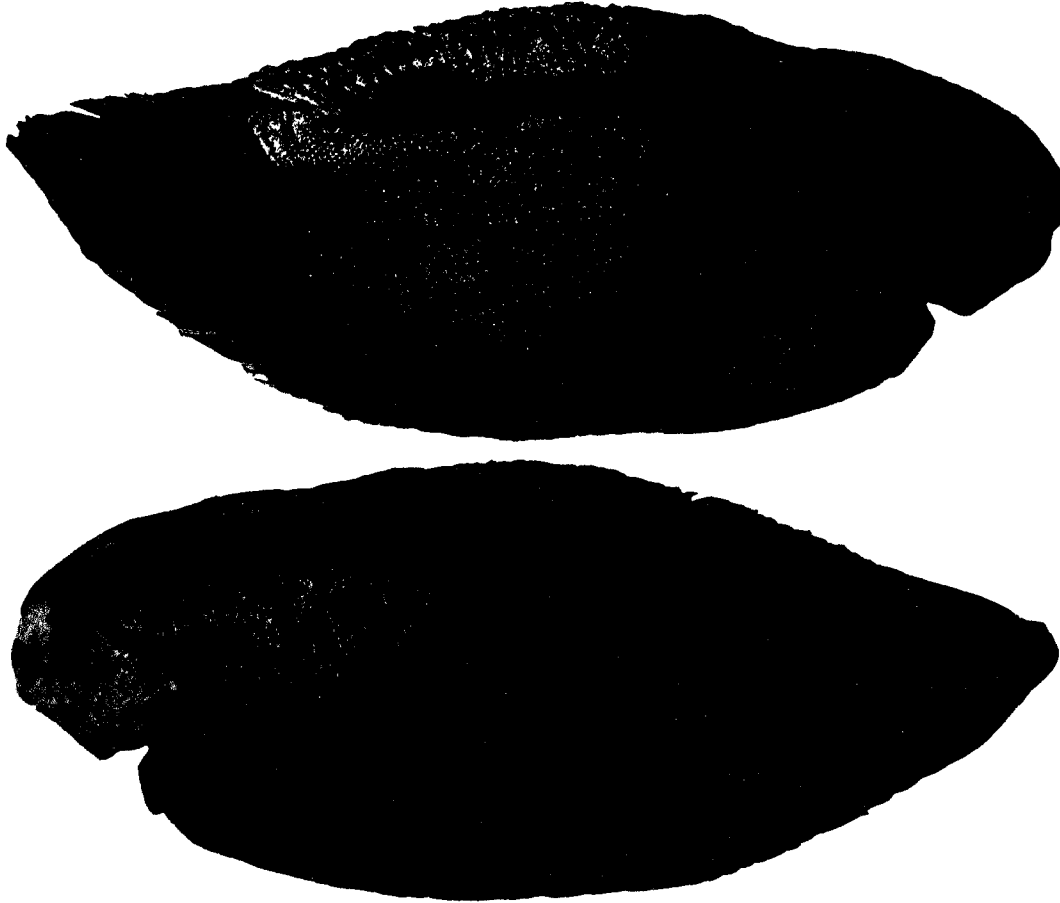


Figure 1.13. Photographs of *Zebrias annularis*, holotype, USNM93095, 129 mm SL, Taiwan (Pacific Taiwan), China Sea, vicinity of Formosa (=Taiwan), 21°40'N, 116°58'E, depicting the ocular (above) and blind (below) sides.

**Synonym(s):** *Brachirus annularis* Fowler, 1934; *Synaptura nebulosa* Chen and Weng, 1965.

**Common name(s):** Annular sole, Wamon-ushinoshita.

**Material Examined:** 3 specimens (131.3-143.4 mm TL)

**Type material:** Holotype, USNM93095, 1(129.12 mm SL), 21°40'N, 116°58'E, Taiwan (Pacific Taiwan), China Sea, vicinity of Formosa; Paratype, USNM93206, 1(116.84 mm SL), Pacific Taiwan.

**Non-type material:** AMSI.22828-015, 1(120.88 mm SL), NW Shelf, Australia.

**Diagnosis:** A species of *Zebrias* with the following combination of characters: darkly-demarcated, irregular spots; 71-74 dorsal-fin rays; 55-60 anal-fin rays; 93-100 lateral-line scales; head length 17-18% SL.

**Description:** Morphometrics are presented in Table 1.8. Small sole, attaining a total length of 14 cm. Supracranial pterygiophores 5; formula: 1-1-3. Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes separate, but nearly contiguous. Interorbital space not elevated, covered with scales. Ocular tentacles absent. Ocular-side anterior nasal tube just reaching or slightly surpassing anterior margin of ventral eye when flattened. Nasal tube narrowing slightly toward distal end. Ocular-side posterior nasal tube one third to one half length of anterior nasal tube; slightly tapered. Blind-side anterior nostril a short, thick tube, as in holotype, or a short, uneven tube with one side disproportionately higher than the other. Anterior nasal tube slightly dorso-anterior to dorsalmost point of mouth. Blind-side posterior nasal tube slightly longer than ocular-side counterpart; dorso-posterior to anterior nasal tube at vertical through posterior edge of mouth. Posterior nasal tube relatively wide and tapered. Posterior margin of ocular-side jaws reaching vertical through midpoint of ventral eye. Ocular-side lips smooth. Blind-side lower lip

plicate. Minute teeth restricted to blind-side jaws. Ocular-side cirri restricted to short fringe along opercular margin. Cirri densely distributed at anterior end of blind-side head, extending along snout, chin and opercular margin; cirri thicker and more densely distributed on chin. Short patches of cirri associated with blind-side lateral line, anterior to opercular margin. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Branchiostegal membrane quite prominent in type material. Lateral line well developed on both sides. Supraorbital line present on ocular-side head. Lateral-line scales cycloid. Scales on body relatively large, squoval; moderately ctenoid on both sides with 6-8 ctenii. Anterior end of dorsal fin at vertical slightly anterior to dorsal eye. Anterior end of anal fin just posterior to anus. Dorsal- and anal-fin rays shortest at anterior end of body, increasing gradually in length toward posterior end; longest fin rays directly adjacent to caudal fin. Caudal fin somewhat squarish. Scales extending along proximal half of median fins. Pectoral fins rudimentary, ocular-side pectoral fin slightly longer than blind-side counterpart (ocular-side fin 18-25% HL, blind-side fin 12-17% HL). Membrane connecting pectoral-fin rays very thin, transparent. Uppermost pectoral-fin rays the longest; fin rays decreasing in length ventrally. Pelvic fins of comparable length. Anus on ventral midline. Genital papilla submedian on ocular side. Genital papilla attached to ocular-side pelvic fin for non-type specimen, but detached among type specimens (possibly due to damage).

**Pigmentation of preserved specimens:** Ocular-side body light brown with deeper brown, irregular spots. Spots with a thick, dark brown outline. Blind side uniformly light-colored with no conspicuous pigmentation. Blind side of holotype with minute, dark brown spots around median fin margins, but otherwise devoid of pigmentation.

Blind side of paratype with brown-black and reddish-brown spots at posterior end of body around median fin margins. Mouth pale, whitish. Ocular-side vertical fins dark brown, almost black toward distal ends. Ocular-side caudal fin greyish at base and dark brown at distal end. Dorsalmost ray of ocular-side pectoral fin solid brown; rest of fin transparent with minute brown spots (pectoral fin of fresh specimens is likely solid brown). Blind-side pectoral fin transparent. Pelvic fins whitish.

Table 1.8. Meristic and morphometric characteristics of type and non-type specimens of *Zebrias annularis*. Measurements and abbreviations are described in Appendix B.

	<i>Brachirus annularis</i> holotype	<i>B. annularis</i> paratype (n=1)	<i>Zebrias annularis</i> non- type specimens (n=1)
<b>Standard length (mm)</b>	129.12	116.84	120.88
<b>Total length (mm)</b>	143.4	131.3	137.86
<b>Counts</b>			
Dorsal-fin rays	71	71	74
Anal-fin rays	55	57	60
Caudal-fin rays	18	18	18
Precaudal vertebrae	9	9	9
Caudal vertebrae	34	33	34
Vertebrae			
Haemopophyses	5	5	5
Pterygiophores	5	5	6
Pectoral-fin rays o.s.	4*	7	8
Pectoral-fin rays b.s.	8	8	6
Pelvic-fin rays o.s.	5	5	4
Pelvic-fin rays b.s.	5	5	5
Lateral-line scales	97	100	93
Number of bands	0	0	0
<b>Measurements</b>			
<b>%SL</b>			
Head length	0.18	0.17	0.18
Head depth	0.18	0.18	0.2
Body depth	0.36	0.34	0.33
Caudal fin length	0.11	0.12	0.14
Width caudal peduncle	0.075	0.071	0.074
<b>%HL</b>			
Length of pectoral fin OS	0.18	0.21	0.25
Length of pectoral fin BS	0.12	0.14	0.17
Length of pelvic fin OS	0.29	0.33	0.33
Length of pelvic fin BS	0.23	0.31	0.35
Pre-orbital head length	0.2	0.2	0.26
Post-orbital head length	0.69	0.65	0.56
Snout length	0.26	0.27	0.32
Nostril to snouth distance	0.16	0.2	0.28
Mouth length OS	0.33	0.33	0.35
Mouth length BS	0.23	0.25	0.3
Ventral eye diameter	0.18	0.21	0.2
Width of orbits	0.27	0.28	0.31
Longest dorsal ray	0.53	0.55	0.53
Longest anal ray	0.51	0.54	0.52
IOD/V	0.38	0.3	0
BPc/OPc	0.65	0.67	0.69
BPv/OPv	0.8	0.92	1.04

\*: Fin damaged.

**Geographic distribution:** The species has been recorded from Japan (Gonzales et al., 1994), the China Sea (Fowler, 1934), Taiwan (Shen and Lee, 1981), the Philippines (Nakabo, 2002), and the NW Shelf, Australia (Sainsbury et al. 1985). Also reported from southwest India, off Kochi (Nair, 2006); no representative specimens examined in this study. Reported from depths up to 200 m.

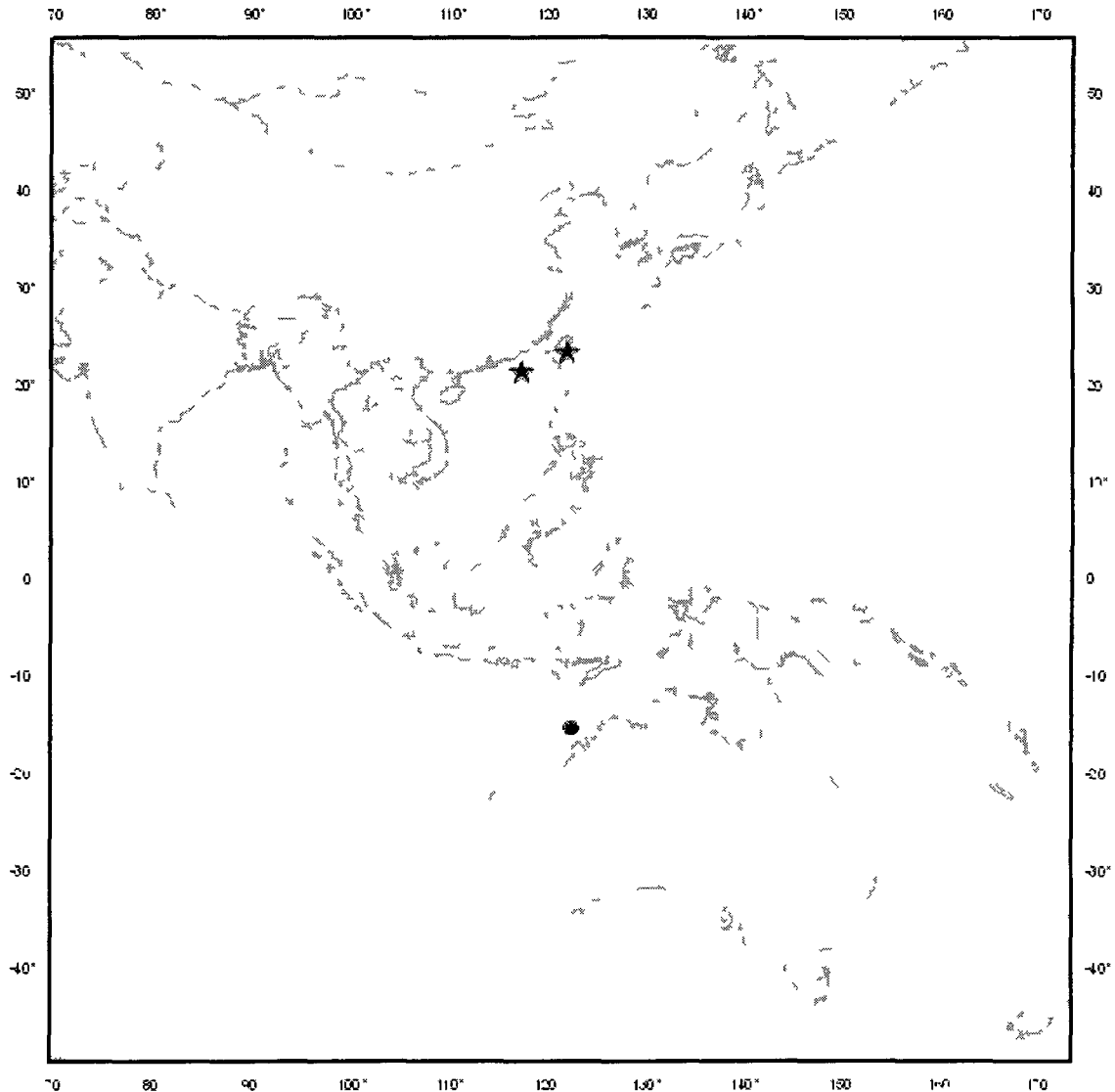


Figure 1.14. Geographic distribution of *Zebrias annularis*. Stars denote locality of type material.

**Remarks:** Chabanaud (1936) first associated *Z. annularis* with the genus *Zebrias*, due to the resemblance of its darkly-bordered spots to discontinuous transverse bands. At first glance, the species may not appear to belong in this genus, due to the absence of complete transverse bands; however, the supracranial complex (Figure 1.15) and confluent caudal fin suggest that this species is better-placed in *Zebrias*, rather than *Brachirus* or *Synaptura*. The large, irregular spots could represent modified bands, or alternatively, they may represent the precursor to transverse bands. The variation in banding pattern, in addition to the banding irregularities observed in this genus, suggest the potential for pigmentation to change or evolve. As Taki (1938) proposed, pigmentation, being restricted to the epidermal layer, is a variable character capable of alteration without affecting the underlying dermal structure of the fish. If the irregular spots are, in fact, a precursor to bands, then this would suggest that *Z. annularis* is the most plesiomorphic species within *Zebrias*.

*Zebrias annularis* is most closely allied to *Zebrias maculosus* Oommen, 1977 from the Arabian Sea. Based on the illustration in the original species description, *Z. maculosus* bears a striking superficial resemblance to *Z. annularis*; however, the reported range of dorsal- and anal-fin ray counts for *Z. annularis* are lower than those reported for *Z. maculosus*: 70-76 dorsal-fin rays, 56-59 anal-fin rays (Fowler, 1934; Chen and Weng, 1965; Shen and Lee, 1981; Gonzales et al., 1994; Nair, 2006). The corresponding counts reported in the original description of *Z. maculosus*, based on three specimens, are 58-66 dorsal-fin rays and 50-54 anal-fin rays. Moreover, the recorded lateral-line scale counts for *Z. annularis* have been consistently lower (85-106 for *Z. annularis*; 120-135 for *Z. maculosus*). The type material for *Z. maculosus* could not be obtained for examination, and non-type material could not be located. As a result, the validity of this species could

not be confirmed. An examination of this type material is necessary to determine whether *Z. maculosus* is synonymous with *Z. annularis*, or a distinct species. In the absence of this information, *Z. maculosus* is tentatively regarded as a distinct, valid species.

In Fowler's original description of *Z. annularis*, he noted the absence of the blind-side pectoral fin. Upon examination of both the holotype and paratype, a pectoral fin was found on the blind side of both specimens; however, the membrane connecting the fin rays is very thin and transparent, and it is only with careful manipulation that the fin can be lifted from the skin and observed. Previous authors have also noted the presence of the blind-side pectoral fin for this species (Gonzales et al., 1994; Nair, 2006; Chen and Weng, 1965; Shen and Lee, 1981). The ocular-side pectoral fin of the holotype appears to be damaged; 9 pectoral-fin rays were recorded in the original description, whereas only four rays were present when examined in the present study.

**Comparisons:** With the exception of *Z. maculosus*, *Z. annularis* can be easily distinguished from all of its congeners by the presence of irregular spots, as opposed to bands. *Z. maculosus* can be distinguished from *Z. annularis* by its lower dorsal-fin ray count (58-66), lower anal-fin ray count (50-54), higher lateral-line scale count (120-135), and larger head length (26-27% SL for *Z. maculosus*).

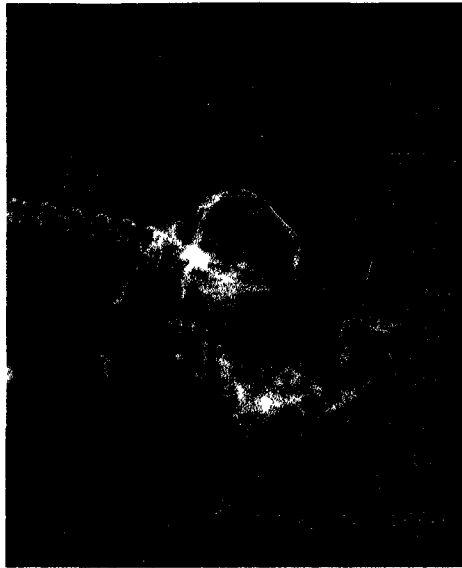


Figure 1.15. Digital x-ray showing the supracranial structure of *Zebrias annularis*, AMSI.22828-015, 121 mm SL, NW Shelf.

*Zebrias cancellatus* (McCulloch, 1916)

Figures 1.16-1.1.18, Tables 1.9

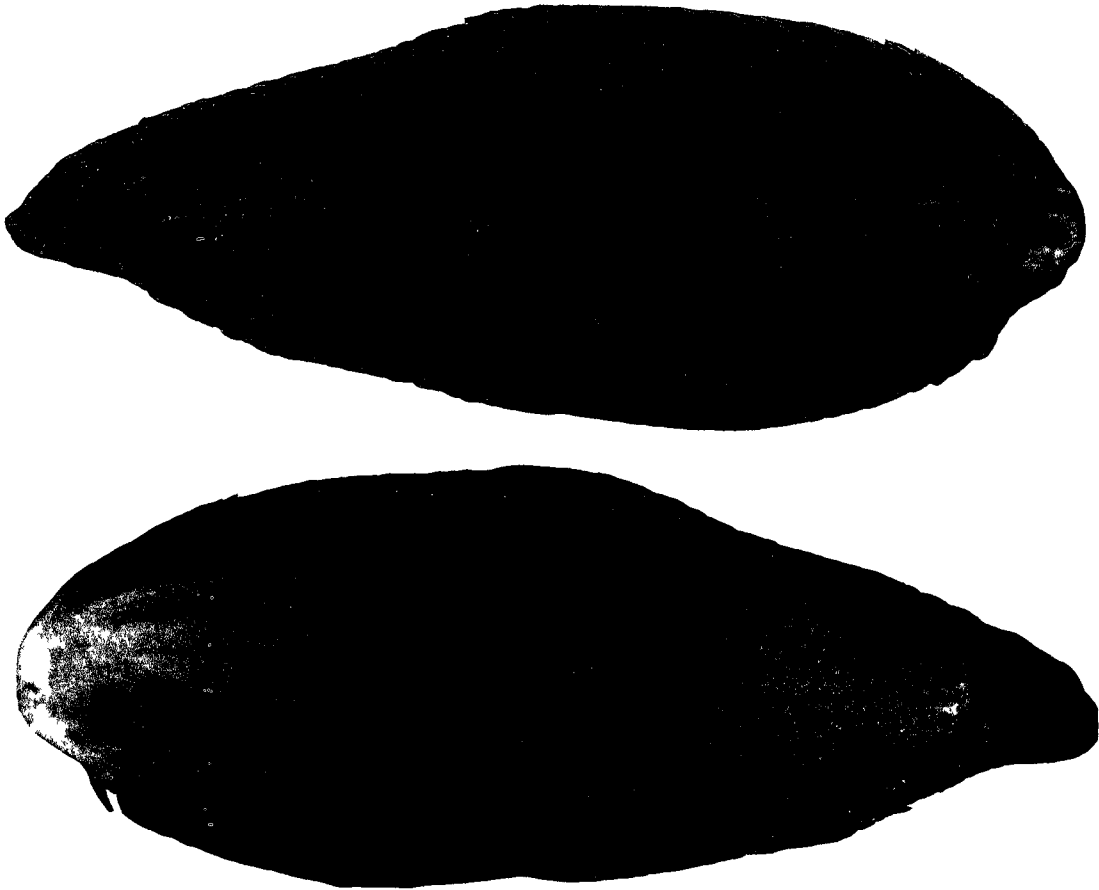


Figure 1.16. Photographs of *Zebrias cancellatus*, WAM P28613-006, 151 mm SL, Western Australia, King George Sound, 2 km SE of Emu Pt., 35°01'S, 117°57'E.

**Synonym(s):** *Synaptura cancellata*, McCulloch 1916

**Common name(s):** Harrowed Sole

**Material examined:** 35 specimens (86.4-325.85 mm TL)

**Type material:** Holotype, AMSI13199, 1(151.94 mm SL), near Fremantle, Rockingham Western Australia; Paratype, AMSE.2486, 1(163.39 mm SL), between Cape Naturaliste and Geraldton, Western Australia.

**Non-type material:** AMSI.20788-008, 1(108.68 mm SL), Western Australia, off Carnarvon; AMSI.33312008, 1(96.9 mm SL), 40 km south of Carnarvon; CSIRO CA1518, 1(164.94 mm SL), Western Australia, NE of Poissanier Point; CSIRO CA3409, 1(263.67 mm SL), Western Australia, Great Australian Bight; CSIRO CA3410, 1(290.93 mm SL), Western Australia, Great Australian Bight; CSIRO H569-2, 1(222.11 mm SL), Western Australia, off Albany; CSIRO H573-08, 1(224.21 mm SL), Western Australia, off Albany; CSIROCA1517, 1(212.05 mm SL), Western Australia, NE of Poissanier Point; SAMF11771, 1(197.19 mm SL), Australia, SA, West Coast Eyre Peninsula, 4.4 miles SE of Evans Is.; SAMF4747, 3(75.4-214.67 mm SL), Australia, SA, Ceduna, West Coast Eyre Peninsular, 4 km SE of Evans Is.; WAM13300, 1(95.8 mm SL), Shark Bay, Western Australia; WAMP.2861-001, 1(212.72 mm SL), Western Australia, Cheyne Beach; WAMP.32274.001, 1(108.45 mm SL), Western Australia, Shark Bay, Cape Peron North, 19.7 km ENE of Cape, Station SB-04-011; WAMP.32302.001, 1(117.82 mm SL), Western Australia, Shark Bay, Dirk Hartog Is., 10.83 km E of island, Station SB-15-043; WAMP.32578.002, 5(125.18-141.25 mm SL), Western Australia, Shark Bay, Cape Le Villain, 21.17 km east of Cape, Station SB-21-293; WAMP14726.001, 1(117.35 mm SL), Western Australia, Shark Bay; WAMP14740.001, 1(207.23 mm SL), Western Australia, Rottnest Island; WAMP22139, 2(178.42-235.67 mm SL), Rockburn Sd; WAMP23675-7, 2(116.56-144.69 mm SL), Carnarvon; WAMP28613-006, 1(151 mm SL), Western

Australia, King George Sound, 2 km SE of Emu Pt.; WAMP4693, 1(232.04 mm SL), near Michaelmas J., King George Sound; WAMP4747, 1(146.65 mm SL), Albany; WAMP5528.001, 1(126.52 mm SL), Western Australia, Exmouth Gulf; WAMP5866, 1(135.86 mm SL), Shark Bay, Western Australia; AMSI.7238, 1(207.25 mm SL).

**Diagnosis:** A species of *Zebrias* with the following combination of characters: a distinct pigmentation pattern consisting of darker blotches arranged along bands posterior to operculum to form 2-3 parabolic shapes (Figure 1.16); 11-20 singular transverse bands across body; 45-49 vertebrae; 105-129 lateral-line scales; eyes contiguous; 18 caudal-fin rays.

**Description:** Meristic and morphometric characters are indicated in Table 1.9. Small sole, attaining a total length of 33 cm. Supracranial pterygiophores 3-4 ( $\bar{T} = 3.4$ ); formula: 1-1-(1-2). Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes contiguous, scales absent in interorbital space. Ocular tentacles absent. When flattened, ocular-side anterior nasal tube extending as far as posterior nasal tube or anterior margin of ventral eye; aperture of anterior nasal tube slanted and considerably narrower than base. Ocular-side posterior nasal tube approximately half the length of anterior nasal tube. Blind-side anterior nostril a short, uneven tube with higher end covering aperture. Blind-side anterior nostril slightly dorso-anterior to dorsalmost point of mouth. Blind-side posterior nasal tube slightly shorter than ocular-side anterior nasal tube; located dorso-posteriorly to anterior nostril at vertical through posterior edge of mouth and at posterior margin of

dense patch of cirri on anterior region of head. Posterior nasal tube narrowing slightly toward distal end. Posterior margin of ocular-side jaws extending as far as vertical through midpoint of ventral eye. Ocular-side lips smooth. Blind-side lower lip plicate. Teeth minute, restricted to blind-side jaws. Ocular-side cirri restricted to short fringe along opercular margin. Cirri densely distributed at anterior end of blind-side head, extending along snout, chin and opercular margin. Long, single strands of cirri often found on mid-head region between scales posterior to dense patch of cirri on anterior region, cirri not extending posterior to opercular margin. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line well developed on both sides. Supraorbital line present on ocular-side head. Lateral-line scales cycloid on both sides. Scales on body moderately ctenoid with 4-9 ctenii. Anterior end of dorsal fin at, or slightly anterior to, vertical at anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Vertical-fin rays increasing gradually in length toward posterior end of body; longest fin rays directly adjacent to caudal fin. Caudal fin rounded, posteriormost anal-fin ray length 57-81% relative to caudal fin length. Scales extending onto ocular- and blind-side median fins. Pectoral fins symmetrical, rudimentary (ocular-side fin length 7-20% HL, blind-side fin length 8-22% HL). Dorsalmost pectoral-fin ray longest, more ventral rays decreasing gradually in length. Ocular-side pelvic fin slightly longer than blind-side fin; blind-side pelvic fin with cirri, absent from ocular-side fin. Anus submedian on blind side. Genital papilla at base of posteriormost ocular-side pelvic-fin ray. Genital papilla not attached to ocular-side pelvic fin.

**Pigmentation of preserved specimens:** Ocular side light brown with series of 11-20 deeper brown, singular transverse bands. Bands relatively uniform in width, those on head becoming narrower. Bands slightly narrower than inter-band spaces. Just posterior to ocular-side opercular margin, darker blotches of pigmentation arranged along bands to form 2-3 parabolic shapes. Blind side uniformly pale, typically whitish with no conspicuous pigmentation. Bands extending onto dorsal and anal fins, becoming darker. Ocular-side caudal fin with brown or grey base and thin black strip near distal end. Distal ends of ocular-side median fins bordered by white margin. Ocular-side pectoral fin grey, dark brown or black. Blind-side pectoral fin of most specimens transparent; others with mostly transparent fins with minute black spots. Pelvic fins whitish.

Table 1.9. Meristic and morphometric characteristics of type and non-type specimens of *Zebrias cancellatus*. Means and standard deviations are shown in parentheses. Measurements and abbreviations are described in Appendix B.

	<i>Synaptura cancellata</i> holotype	<i>Synaptura cancellata</i> paratype (n=1)	<i>Zebrias cancellatus</i> non- type specimens (n=33)
<b>Standard length (mm)</b>	151.94	163.39	75.4-290.93 (165.04; 54.1)
<b>Total length (mm)</b>	173.61	186.68	86.4-325.85 (187.27; 60.3)
<b>Counts</b>			
Dorsal-fin rays	81	75	68-81 (74.7; 3.1)
Anal-fin rays	70	67	61-70 (65.0; 2.5)
Caudal-fin rays	18	15	13-18 (17.5-1.1)
Precaudal vertebrae	9	9	8-10 (9.0; 0.3)
Caudal vertebrae	39	39	36-40 (38.0; 1.2)
Total vertebral count	48	48	45-49 (46.9; 1.2)
Haemopophyses	5	5	5 (5.0; 0)
Pterygiophores	6	7	5-7 (6.1; 0.7)
Pectoral-fin rays o.s.	7	7	5-11 (6.8; 1.1)
Pectoral-fin rays b.s.	8	8	6-10 (7.5; 1.1)
Pelvic-fin rays o.s.	4	4	3-5 (4.0; 0.3)
Pelvic-fin rays b.s.	4	4	3-4 (4.0; 0.2)
Lateral-line scales	120	109	105-129 (117.1; 5.4)
Number of bands	18	14	11-20 (15.0; 1.9)
<b>Measurements</b>			
<b>%SL</b>			
Head length	0.16	0.14	0.12-0.16 (0.15; 0.009)
Head depth	0.15	0.17	0.14-0.19 (0.17; 0.01)
Body depth	0.33	0.33	0.28-0.38 (0.34; 0.02)
Caudal fin length	0.14	0.14	0.10-0.18 (0.14; 0.02)
Width caudal peduncle	0.06	0.06	0.05-0.07 (0.06; 0.005)
<b>%HL</b>			
Length of pectoral fin o.s.	0.13	0.11	0.10-0.19 (0.15; 0.03)
Length of pectoral fin b.s.	0.14	0.12	0.08-0.22 (0.16; 0.03)
Length of pelvic fin o.s.	0.40	0.34	0.29-0.45 (0.37; 0.03)
Length of pelvic fin b.s.	0.32	0.25	0.23-0.35 (0.28; 0.03)
Pre-orbital head length	0.18	0.23	0.15-0.24 (0.19; 0.02)
Post-orbital head length	0.63	0.61	0.48-0.65 (0.59; 0.04)
Snout length	0.22	0.24	0.18-0.32 (0.25; 0.03)
Nostril to snouth distance	0.14	0.16	0.13-0.24 (0.17; 0.03)
Mouth length o.s.	0.28	0.29	0.27-0.33 (0.30; 0.02)
Mouth length b.s.	0.22	0.26	0.22-0.36 (0.27; 0.03)
Ventral eye diameter	0.23	0.27	0.22-0.36 (0.26; 0.03)
Width of orbits	0.29	0.37	0.22-0.48 (0.36; 0.05)
Longest dorsal ray	0.61	0.72	0.60-0.77 (0.69; 0.05)
Longest anal ray	0.71	0.75	0.61-0.78 (0.69; 0.05)
IOD/V	0	0	0-0.16 (0.02; 0.05)
BPc/OPc	1.08	1.08	0.55-1.63 (1.07; 0.3)
BPv/OPv	0.81	0.73	0.64-0.96 (0.76; 0.07)

**Geographic distribution:** *Zebrias cancellatus* has been reported from Australia, ranging from the southern coast to the north-western coast at depths of 14-182 m.

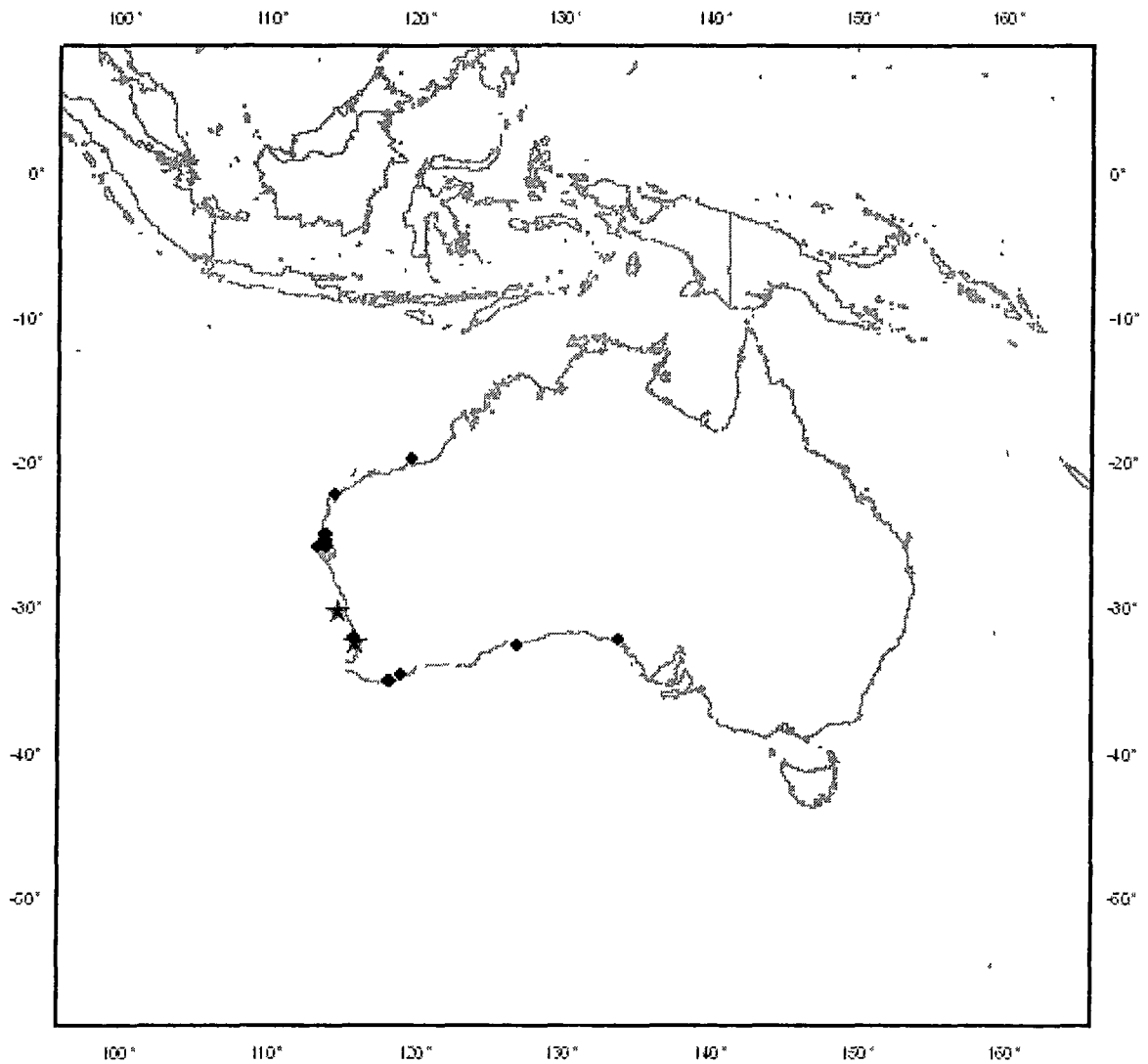


Figure 1.17. Geographical distribution of *Zebrias cancellatus*. Stars denote locality of type material.

**Remarks:** *Zebrias cancellatus*, originally placed in the genus *Synaptura*, was assigned to the genus *Strabozebias* by Chabanaud (1943a), due to the presence of “perfectly” contiguous, stalked eyes, having a common ocular membrane. Despite the acknowledgement that the eyes of *Zebrias quagga* (Kaup, 1858) are also contiguous, Chabanaud deemed the latter to be “*imperfectly contiguous*” in addition to not being protruded when at rest. It is of the opinion of the present author that these characters alone do not warrant placing *Z. cancellatus* in its own genus, and that it is well-placed in *Zebrias*, with which it shares the diagnostic characters that define this genus.

**Comparisons:** *Zebrias cancellatus* can be easily distinguished from all of its congeners by its unique parabolic pigmentation pattern on the ocular side. It is most closely allied to *Z. craticula* (McCulloch, 1916), the latter species being distinguished by having fewer vertebrae (41-43), fewer scales along the lateral line (77-94), and transverse bands extending the length of the caudal fin. In addition, *Z. annularis* (Fowler, 1934) and *Z. maculosus* (Oommen, 1977) can be distinguished by the presence of irregular spots, in lieu of bands. *Z. quagga* (Kaup, 1858) and *Z. captivus* Randall, 1995 can be distinguished by the presence of ocular tentacles. *Z. zebra* (Bloch, 1787) differs in having modified cirri, or barbels, on the blind-side chin and anterior end of the dorsal fin. *Z. altipinnis* (Alcock, 1890) is distinguished by its large mouth (extending as far as the posterior margin of the ventral eye), short ocular-side anterior nasal tube (not reaching the posterior nasal tube when flattened), eyes separated by a scaly interorbital space, and more numerous pelvic-fin rays (5). *Z. penescalaris* Gomon, 1987 and *Z. scalaris* Gomon,

1987 can be distinguished by their narrow, indistinct transverse bands (17-23), fewer lateral-line scales (67-93), and eyes separated by a scaly interorbital space.

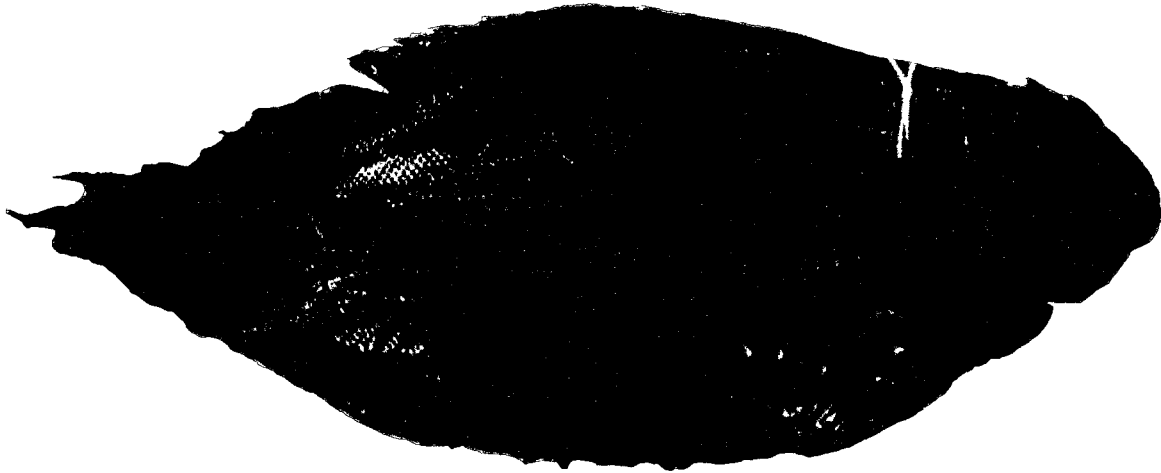


Figure 1.18. Photograph of *Synaptura cancellata* (= *Zebrias cancellatus*), holotype, AMSI.13199, 152 mm SL, near Fremantle, Rockingham Western Australia.

***Zebrias captivus*, Randall 1995**

Figures 1.19-1.22, Tables 1.10

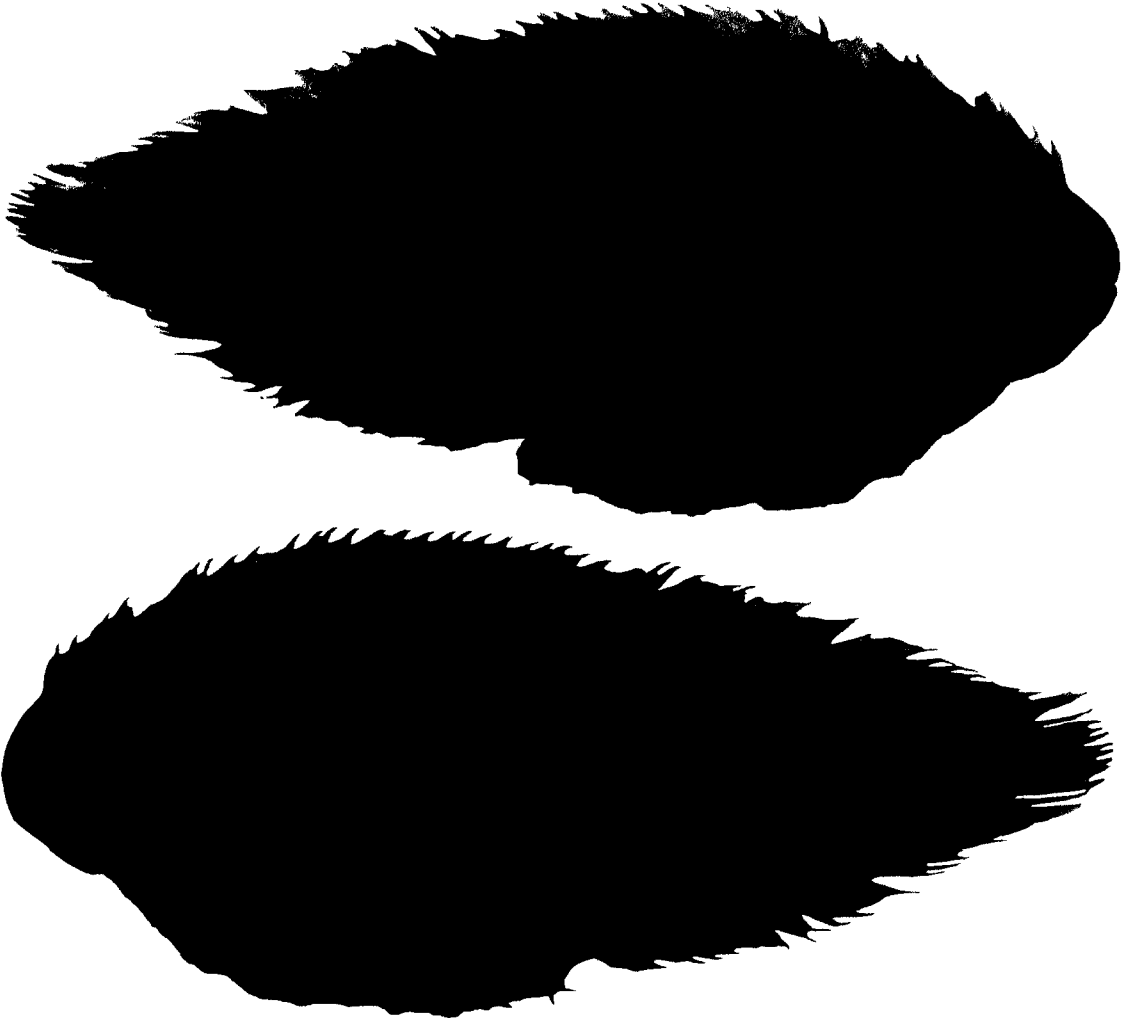


Figure 1.19. Photographs of *Zebrias captivus*, BPBM29478, holotype, 81 mm SL, Persian Gulf, off Bahrain, depicting the ocular (above) and blind (below) sides.

**Synonym(s):** None.

**Common name(s):** Convict zebra sole

**Material examined:** 2 specimens (68.83-93.73 mm total length)

**Type material:** BPBM29478, Holotype, 80.55 mm SL, Persian Gulf, off Bahrain;  
USNM334423, Paratype, 58.02 mm SL, Persian Gulf, off Bahrain, from trawler.

**Non-type material:** None.

**Diagnosis:** A species of *Zebrias* with the following combination of characters: A tentacle on one or both eyes (Figure 1.21); 13 singular bands, each one of comparable width to the adjacent inter-band space; 38-39 vertebrae; 63-66 dorsal-fin rays; 51-54 anal-fin rays; 74-75 lateral-line scales; upper two rays of ocular-side pectoral fin tightly joined by a thin membrane, second ray the most elongate; caudal fin dark with light “V” or “M” shape at its base and at least two light spots around dorsal and ventral margins of fin toward its distal end.

**Description:** Meristic and morphometric characters are presented in Table 1.10. Small sole, attaining a total length of 10 cm. Supracranial pterygiophores 3-4; formula: 1-1-(1-2). Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes contiguous, ocular tentacle present on one or both eyes. Scales absent in interorbital space. When flattened, ocular-side anterior nasal tube reaching posterior nasal tube in paratype, and anterior margin of ventral eye in holotype. Ocular-side posterior nasal tube approximately half the length of anterior tube. Blind-side anterior nasal tube dorso-anterior to dorsalmost point of mouth; anterior nostril a simple aperture as in the holotype, or a short, uneven tube as in the paratype. Blind-side posterior nasal tube postero-dorsal to anterior tube at a vertical

through posterior edge of mouth. Posterior margin of ocular-side jaws reaching vertical through midpoint of ventral eye. Ocular-side lips smooth; lower lip partially conceals upper lip. Blind-side lower lip plicate. Teeth minute, restricted to blind-side jaws. Cirri absent on ocular side. Cirri densely distributed at anterior end of blind-side head, extending along snout, chin and opercular margin. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line well developed on both sides. Blind-side lateral line not extending anterior to opercular margin. Supraorbital line present on ocular-side head. Lateral-line scales cycloid. Scales on body moderately ctenoid with 12-15 ctenii. Anterior end of dorsal fin at vertical through anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Caudal fin rounded. Scales extending onto base of median fins. Upper two rays of ocular-side pectoral fin tightly joined by thin membrane; second ray most elongate, rays decreasing in length toward ventral end. Dorsalmost ray of blind-side pectoral fin longest; rays decreasing gradually in length toward ventral end. Pelvic fins of comparable length. Anus submedian on blind side. Genital papilla submedian on ocular side at posterior edge of anus. Genital papilla not attached to ocular-side pelvic fin.

**Pigmentation of preserved specimens:** Ocular side beige with series of thirteen darkly-demarcated brown bands (nine on body, four on head). Bands relatively uniform in width across body, those on head becoming narrower; posteriormost band widest. Bands and inter-band spaces of comparable width. Blind side pale, devoid of conspicuous pigmentation; minute, dark spots found along blind-side median fin margins at posterior end of body in paratype. Interior of mouth pale with minute, dark spots. Bands

extending onto dorsal and anal fins, becoming darker. Bands visible through distal ends of blind-side vertical fins. Ocular-side caudal fin dark brown with pale “V” or “M” shape at its base; light spots present toward distal end of caudal fin in paratype. Distal end of ocular-side pectoral fin brown in holotype, proximal end devoid of pigmentation (likely due to preservation); paratype with rust-coloured spots at proximal end of ocular-side pectoral fin. Blind-side pectoral fin transparent. Pelvic fins whitish.

Table 1.10. Meristic and morphometric characteristics of type and non-type specimens of *Zebrias captivus*. Means and standard deviations are shown in parentheses. Measurements and abbreviations are described in Appendix B.

	<i>Z. captivus</i> holotype	<i>Z. captivus</i> paratype (n=1)
<b>Standard length (mm)</b>	80.55	58.02
<b>Total length (mm)</b>	93.73	68.83
<b>Counts</b>		
Dorsal-fin rays	63	66
Anal-fin rays	51	54
Caudal-fin rays	18	18
Precaudal vertebrae	8	9
Caudal vertebrae	30	30
Total vertebrae	38	39
Haemopophyses	5	5
Pterygiophores	6	6
Pectoral-fin rays o.s.	6	6
Pectoral-fin rays b.s.	6	5
Pelvic-fin rays o.s.	4	4 <sup>1</sup>
Pelvic-fin rays b.s.	4	4
Lateral-line scales	74	75 <sup>2</sup>
Number of bands	13	13
<b>Measurements</b>		
<b>%SL</b>		
Head length	0.19	0.22
Head depth	0.18	0.22
Body depth	0.37	0.34
Caudal fin length	0.16	0.19
Width caudal peduncle	0.08	0.07
<b>%HL</b>		
Length of pectoral fin o.s.	0.27	0.27
Length of pectoral fin b.s.	0.19	0.18
Length of pelvic fin o.s.	0.34	0.28
Length of pelvic fin b.s.	0.33	0.27
Pre-orbital head length	0.19	0.18
Post-orbital head length	0.56	0.52
Snout length	0.23	0.23
Nostril to snouth distance	0.17	0.18
Mouth length o.s.	0.26	0.3
Mouth length b.s.	0.24	0.23
Ventral eye diameter	0.24	0.30
Width of orbits	0.30	0.44
Longest dorsal ray	0.67	0.59
Longest anal ray	0.66	0.59
IOD/V	0	0
BPc/OPc	0.72	0.65
BPv/OPv	0.97	1

<sup>1</sup>: pelvic fins damaged.

<sup>2</sup>: approximation as a few scales are missing.

**Geographic distribution:** *Zebrias captivus* has been reported from the Persian Gulf.

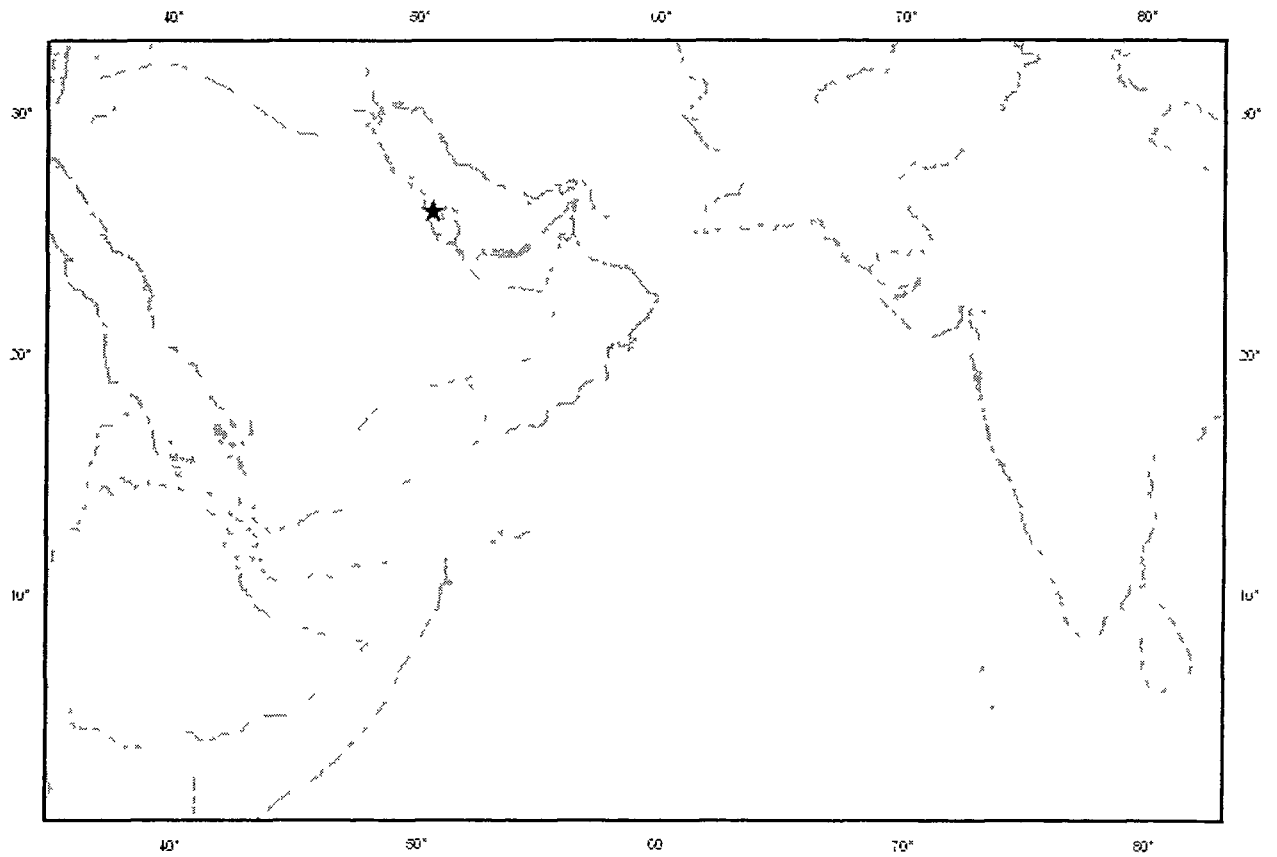


Figure 1.20. Geographic distribution of *Zebrias captivus*. Stars denote locality of type material.

**Remarks:** Randall (1995) distinguishes *Zebrias captivus* from its most closely allied congener, *Z. quagga* (Kaup, 1858) by its caudal fin pattern and number of pectoral-fin rays, among other characters. The present authors did not find these characters to be of assistance in distinguishing the two species. The caudal fin pattern of the *Z. captivus* paratype closely resembles the pattern observed among many specimens of *Z. quagga*. Moreover, while Randall was correct in pointing out that the holotype of *Z. quagga* has considerably more pectoral-fin rays than *Z. captivus* (12 ocular, 10 blind), this high meristic value is restricted to the holotype, which may be an anomaly. All other specimens examined have 4-9 pectoral fin rays (Table 1.4), which is consistent with *Z. captivus*.

**Comparisons:** With the exception of *Z. quagga* (Kaup, 1858), *Z. captivus* can be distinguished from all of its congeners by the presence of ocular tentacles. *Z. quagga*, found in the waters surrounding India and eastward to southeast Asia and northern Australia, differs from *Z. captivus* by its band morphology. The bands of this species are broader than the inter-band spaces. In addition, *Z. quagga* can be distinguished by its higher meristic values, having more scales along the lateral line (76-104), generally more vertebrae (38-44), generally more dorsal-fin rays (64-88), and generally more anal-fin rays (52-64).

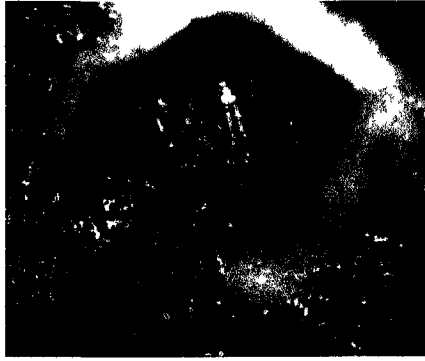


Figure 1.21. Photograph depicting an ocular tentacle, diagnostic of *Zebrias captivus*, BPBM29478, holotype, 81 mm SL, Persian Gulf, off Bahrain.

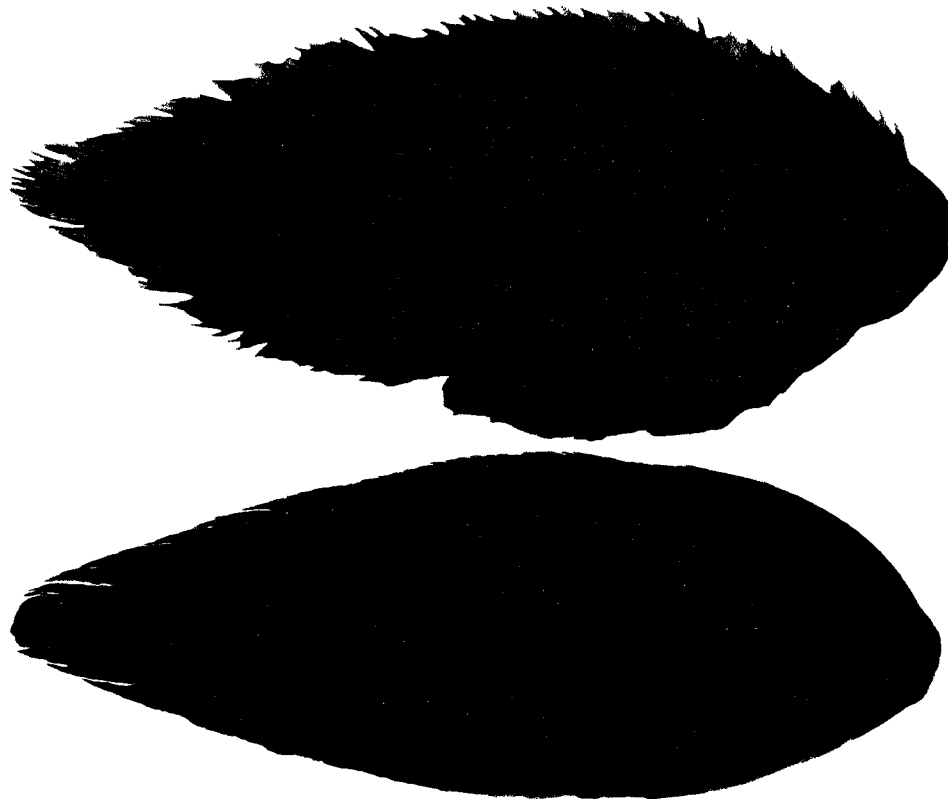


Figure 1.22. Photographs depicting the difference in band morphology between *Z. captivus* (above: BPBM29478, holotype, Persian Gulf, off Bahrain) and *Z. quagga* (below: MNHN1965-487, 110 mm SL, 10.35°S, 104.3°E).

*Zebrias craticula* (McCulloch, 1916)

Figures 1.23–1.24, Table 1.11

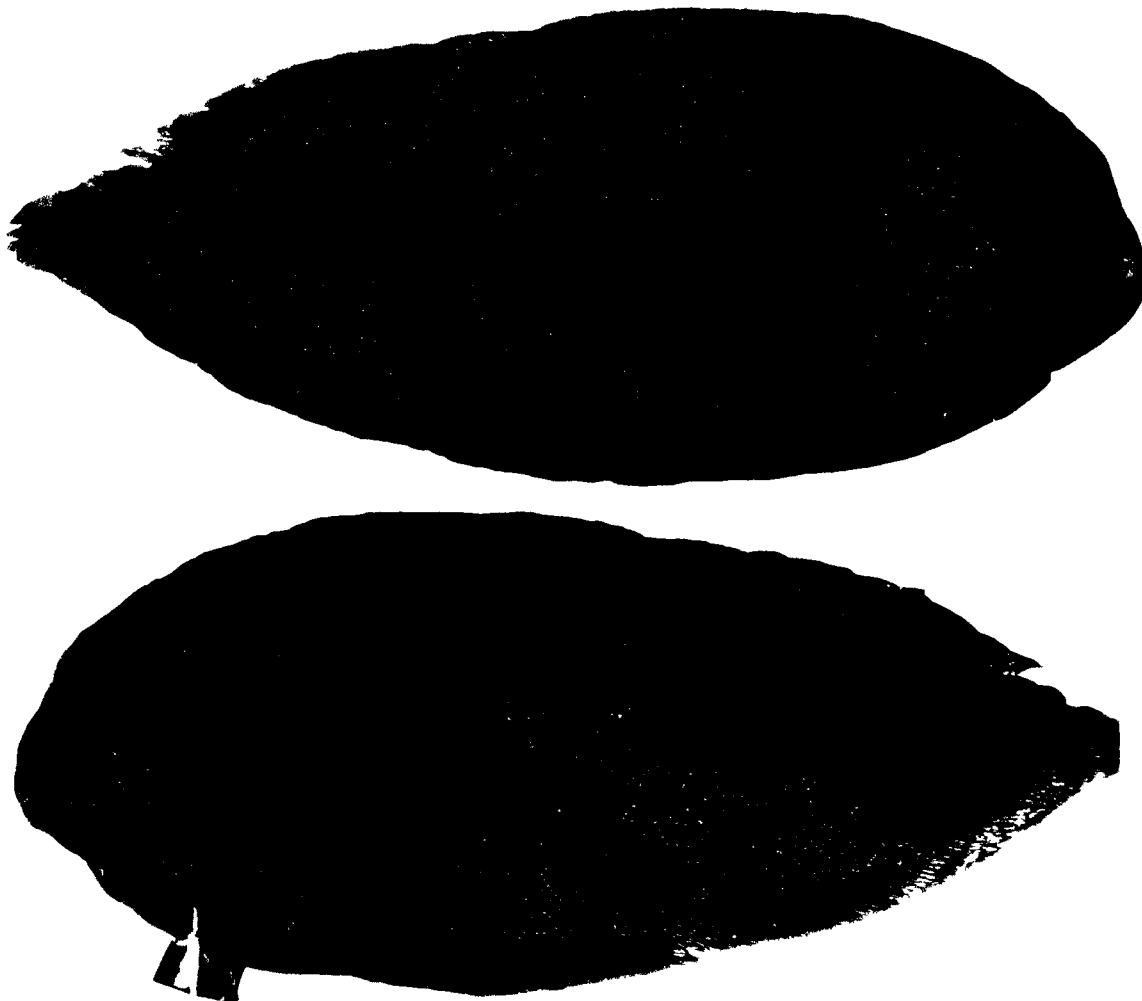


Figure 1.23. Photographs of *Synaptura craticula* (= *Zebrias craticula*), holotype, AMSE.2700, 124 mm SL, 19 km NE Bowen, depicting the ocular (above) and blind (below) sides.

**Synonym(s):** *Synaptura craticula* McCulloch, 1916

**Common name(s):** Wickerwork sole

**Etymology:** The Latin word “*craticula*” means gridiron, or grill, and refers to the numerous, narrow bands across the body of this species. It is derived from the Latin word “*cratis*”, which means wickerwork.

**Material examined:** 46 specimens (38.07-183.61 mm TL)

**Type material:** Holotype, AMSE.2700, 124.43 mm SL, 19 km NE Bowen, Queensland, 19°50'S, 148°25'E; Paratype, AMSI.13616, 135.45 mm SL, near Bowen, Queensland, 20°01'S, 148°15'E.

**Non-type material:** AMSI.15557064, 2(90.22-118.68 mm SL), Gulf of Carpentaria, Queensland, 17°29'S, 140°45'E; AMSI.20771-037, 4(100.58-117.93 mm SL), 1-9 miles east of Captain Billy Creek, Cape York, Queensland; AMSI.21639-005, 1(133.09 mm SL), NW Shelf Western Australia; AMSI.22832-005, 1(130.09 mm SL), NW Shelf; AMSI.A3745, 1(34.48 mm SL), Albany Passage, Queensland, Australia; CSIROCA1533, 1(132.42 mm SL), NT, west of Darwin, 12°18'S, 129°20'E; CSIROCA2904, 1(109.25 mm SL), Western Australia, north of Nickol Bay, 20°19'S, 116°47'E; CSIROH4201-02, 1(131.56 mm SL), Western Australia, north of Nickol Bay, 20°01'S, 116°57'E; CSIROH4205-01, 1(133.56 mm SL), Western Australia, NNE of Port Hedland, 19°30'S, 118°52'E; CSIROH6382-05, 1(110.69 mm SL), Western Australia, NW of Shark Bay, 24°37'S, 112°40'E; CSIROH6530-01, 1(117.97 mm SL), Queensland, north of Gladstone, 22°52'S, 151°04'E; CSIROH6531-01, 2(94.16-117.21 mm SL), Queensland, north of Gladstone, 23°21'S, 151°11'E; CSIROH6532-01, 1(110.35 mm SL), Queensland, NE of Shelburne Bay, 11°09'S, 143°18'E; CSIROH6533-01, 1(124.04 mm SL), Queensland, north of Bundaberg, 24°04'S, 152°28'E; CSIROH6534-01, 1(145.89 mm SL), Queensland, Capricorn Group (NE of Gladstone), 23°15'S, 151°41'E;

CSIROMA2262, 1(107.09 mm SL), Queensland, Gulf of Carpentaria, 16°32'S, 140°47'E; NTMS.13311-010, 1(113.23 mm SL), Timor Sea, N.T., Station No. Shot136, 12°58'S, 129°54'E; NTMS.14231-001, 1(123.56 mm SL), north of Port Hedland, NW Shelf, Western Australia, 19°26'S, 118°28'E; NTMS.14363-003, 1(93.79 mm SL), NW of Basset Smith Shoal, Western Australia, Station RW 96-13, 13°13.11'S, 125°14.86'E; QMI140004, 1(145.61 mm SL), SE Queensland, Australia, 24°23.1'S, 152°35.7'E; QMI.17414, 1(93.1 mm SL), Torres Straights, 10°23'S, 141°53'E; QMI.20886, 1(104.5 mm SL), Gulf of Carpentaria, 16°51'S, 139°2.5'E; QMI.21470, 2(90.2-112.86 mm SL), 22°14'S, 152°27'E; QMI.23584, 1(113.12 mm SL), east of Hinchinbrook Is., 18°31'S, 146°33'E; QMI.23591, 1(107.62 mm SL), east of Palm Islands, 18°33.4'S, 146°37.6'E; QMI.36084, 2(61.98-76.37 mm SL), ME. Queensland, Australia, 21°35.7'S, 149°44.1'E; QMI.36934, 2(108.42-111.5 mm SL), East of Ussher Point, Cape York, N. Queensland, Australia, 11°11'S, 142°55'E; QMI.36959, 1(92.34 mm SL), north of Booby Island, N. Queensland, Australia, 10°17'S, 141°53'E; QMI.37927, 1(123.03 mm SL), SE Queensland, Australia, 21°49.5'S, 152°31.5'E; WAMP.14238-39, 2(103.81-110.9 mm SL), Australia, NT, Darwin area; WAMP.32429.002, 1(96.12 mm SL), Western Australia, Shark Bay, Cape Bellefin, 21.41 km NNW of Station SB-18-126, 25°49.939'S to 25°50.189'S, 113°14.272'E to 113°14.274'E; WAMP.32493.001, 1(120.36 mm SL), Western Australia, Shark Bay, Herald Bay, 12.52 km east of Bay, Station SB-16-220, 25°54.479'S to 25°55.037'S, 113°13.989'E to 113°13.999'E; WAMP.32563.001, 1(162.21 mm SL), Western Australia, Shark Bay, Red Cliff Point, 11.85 km east of Station: SB-23-268, 24°56.211'S to 24°55.674'S, 113°16.048'E to 113°16.021'E; WAMP.32578.001, 1(125.48 mm SL), Western Australia, Shark Bay, Cape Levillain, 21.17 km east of Cape

Station SB 21-293, 25°32.904'S to 25°33.448'S, 113°13.247'E to 113°13.335'E;

WAMP5515.001, 1(120.04 mm SL), Western Australia, Shark Bay, 25°21'S, 113°44'E.

**Diagnosis:** A species of *Zebrias* with the following combination of characters: 17-24 narrow, singular bands extending from snout to tip of caudal fin; lighter, indistinct bands present between darker bands; eyes contiguous; interorbital scales absent; 41-43 vertebrae; 77-94 lateral-line scales.

**Description:** Meristic and morphometric characters are indicated in Table 1.11. Small sole, attaining a total length of 19 cm. Supracranial pterygiophores 3-4; formula: 1-1-2, infrequently 1-1-1. Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes contiguous; scales absent in interorbital space. Ocular tentacles absent. Ocular-side anterior nasal tube reaching posterior nasal tube or anterior margin of ventral eye when flattened. Ocular-side posterior nasal tube approximately half the length of anterior nasal tube. Blind-side anterior nostril dorso-anterior to dorsalmost point of mouth; anterior nostril an uneven tube with higher end folding over to cover nasal aperture. Blind-side posterior nasal tube dorso-posterior to anterior nasal tube, at vertical through posterior edge of mouth; posterior nasal tube slightly larger than ocular-side counterpart. Posterior margin of ocular-side jaws just surpassing vertical through anterior margin of ventral eye. Ocular-side lips smooth. Blind-side lower lip plicate. Teeth minute, restricted to blind-side jaws. Short fringe of cirri present along ocular-side opercular margin; cirri otherwise absent from ocular side. Cirri densely distributed at anterior end of blind-side head, covering snout and extending along chin and opercular margin. Long, individual cirri

frequently present on mid-head region between scales posterior to dense patch of cirri on anterior region, cirri extending posteriorly to opercular margin and along small portion of lateral line. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line well developed on both sides. Supraorbital line present on ocular-side head. Blind-side lateral line not extending anterior to opercular margin. Lateral-line scales cycloid. Scales on body strongly ctenoid on both sides with 5-13 ctenii. Anterior end of dorsal fin at, or slightly anterior to, vertical at anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Vertical-fin rays increasing in length toward posterior end of body; longest rays directly adjacent to caudal fin. Caudal fin short, squarish. Posteriormost anal-fin ray length 59-73% relative to caudal fin length. Scales extending onto proximal half of median fins. Pectoral fins short, symmetrical, dorsalmost ray longest; more ventral rays decreasing gradually in length (ocular-side fin length 17-38% HL, blind-side fin length 14-38% HL). Pelvic fins of comparable length; ocular-side fin frequently slightly longer. Anus submedian on blind side. Genital papilla submedian on ocular side. Genital papilla free from ocular-side pelvic fin.

**Pigmentation of preserved specimens:** Ocular side light to dark grey with series of 17-24 dark grey or grey-brown bands. Very thin, lighter gray lines present in inter-band spaces. Bands singular, narrow, darkly demarcated, and relatively uniform in width; bands becoming slightly narrower on head. Inter-band width comparable to band width. Bifurcating and incomplete bands frequently observed. Blind side uniformly white, without conspicuous pigmentation. Infrequently, minute black spots present along blind-side median fin margins at posterior end of body; spots infrequently extending onto head and body, giving them a dusky appearance. Black spots infrequently observed on skin

beneath operculum. Interior of mouth white, dark grey, black, or white with minute dark spots. Bands extending onto dorsal and anal fins. Bands continue to distal end of ocular-side caudal fin. Ocular-side pectoral fin grey to dark brown or black. Blind-side pectoral fin of most specimens mostly transparent with minute black spots; others with transparent fins. Pelvic fins whitish.

Table 1.11. Meristic and morphometric characteristics of type and non-type specimens of *Zebrias craticula*. Means and standard deviations are shown in parentheses. Measurements and abbreviations are described in Appendix B.

	<i>Synaptura craticula</i> holotype	<i>Synaptura craticula</i> paratype (n=1)	<i>Zebrias craticula</i> non-type specimens (n=44)
<b>Standard length (mm)</b>	124.43	135.45	34.48-162.21 (111.12; 21.8)
<b>Total length (mm)</b>	143.3	153.61	38.07-183.61 (125.17; 24.1)
<b>Counts</b>			
Dorsal-fin rays	73	79	71-80 (75.1; 2.3) <sup>2</sup>
Anal-fin rays	62	68	61-69 (64.3; 2.1) <sup>2</sup>
Caudal-fin rays	18	18	16-19 (17.9; 0.4) <sup>2</sup>
Precaudal vertebrae	9	9	5-9 (8.9; 0.6) <sup>2</sup>
Caudal vertebrae	34	33	32-34 (33.2; 0.6) <sup>2</sup>
Total vertebrae	43	42	38-43 (42.1; 0.9) <sup>2</sup>
Haemopophyses	5	5	4-6 (5; 0.2) <sup>2</sup>
Pterygiophores	6	6	4-7 (6.2; 0.6) <sup>2</sup>
Pectoral-fin rays o.s.	6	7	5-8 (6.8; 0.6)
Pectoral-fin rays b.s.	8	8	7-9 (7.6; 0.7)
Pelvic-fin rays o.s.	4	4	3-4 (4; 0.2)
Pelvic-fin rays b.s.	4	4	3-4 (4; 0.2)
Lateral-line scales	87	85	77-94 (86.3; 3.9) <sup>1</sup>
Number of bands	21	18	17-24 (19; 1.6) <sup>1</sup>
<b>Measurements</b>			
<b>%SL</b>			
Head length	0.16	0.17	0.14-0.21 (0.17; 0.01)
Head depth	0.21	0.22	0.18-0.24 (0.20; 0.01)
Body depth	0.41	0.40	0.30-0.42 (0.38; 0.02)
Caudal fin length	0.15	0.13	0.07-0.17 (0.13; 0.02)
Width caudal peduncle	0.08	0.07	0.05-0.09 (0.07; 0.008)
<b>%HL</b>			
Length of pectoral fin o.s.	0.31	0.24	0.17-0.38 (0.24; 0.04)
Length of pectoral fin b.s.	0.25	0.22	0.14-0.38 (0.22; 0.04)
Length of pelvic fin o.s.	0.48	0.36	0.31-0.58 (0.45; 0.06)
Length of pelvic fin b.s.	0.33	0.30	0.16-0.45 (0.32; 0.05)
Pre-orbital head length	0.21	0.20	0.14-0.28 (0.21; 0.03)
Post-orbital head length	0.58	0.58	0.47-0.63 (0.56; 0.04)
Snout length	0.26	0.25	0.22-0.34 (0.27; 0.03)
Nostril to snouth distance	0.22	0.17	0.15-0.24 (0.19; 0.02)
Mouth length o.s.	0.29	0.28	0.26-0.40 (0.32; 0.03)
Mouth length b.s.	0.24	0.25	0.17-0.32 (0.27; 0.03)
Ventral eye diameter	0.31	0.31	0.26-0.40 (0.31; 0.03)
Width of orbits	0.37	0.39	0.31-0.49 (0.39; 0.04)
Longest dorsal ray	0.58	0.55	0.48-0.73 (0.60; 0.05)
Longest anal ray	0.58	0.54	0.53-0.70 (0.60; 0.04)
IOD/V	0	0	0
BPc/OPc	0.80	0.92	0.61-1.76 (0.92; 0.20)
BPv/OPv	1.4	1.2	1.0-1.9 (1.4; 0.2)

<sup>1</sup>: n=43.

<sup>2</sup>: n=41.

**Geographic distribution:** *Zebrias craticula* has been reported from north-western Australia to north-eastern Australia at depths of 7–100 m.

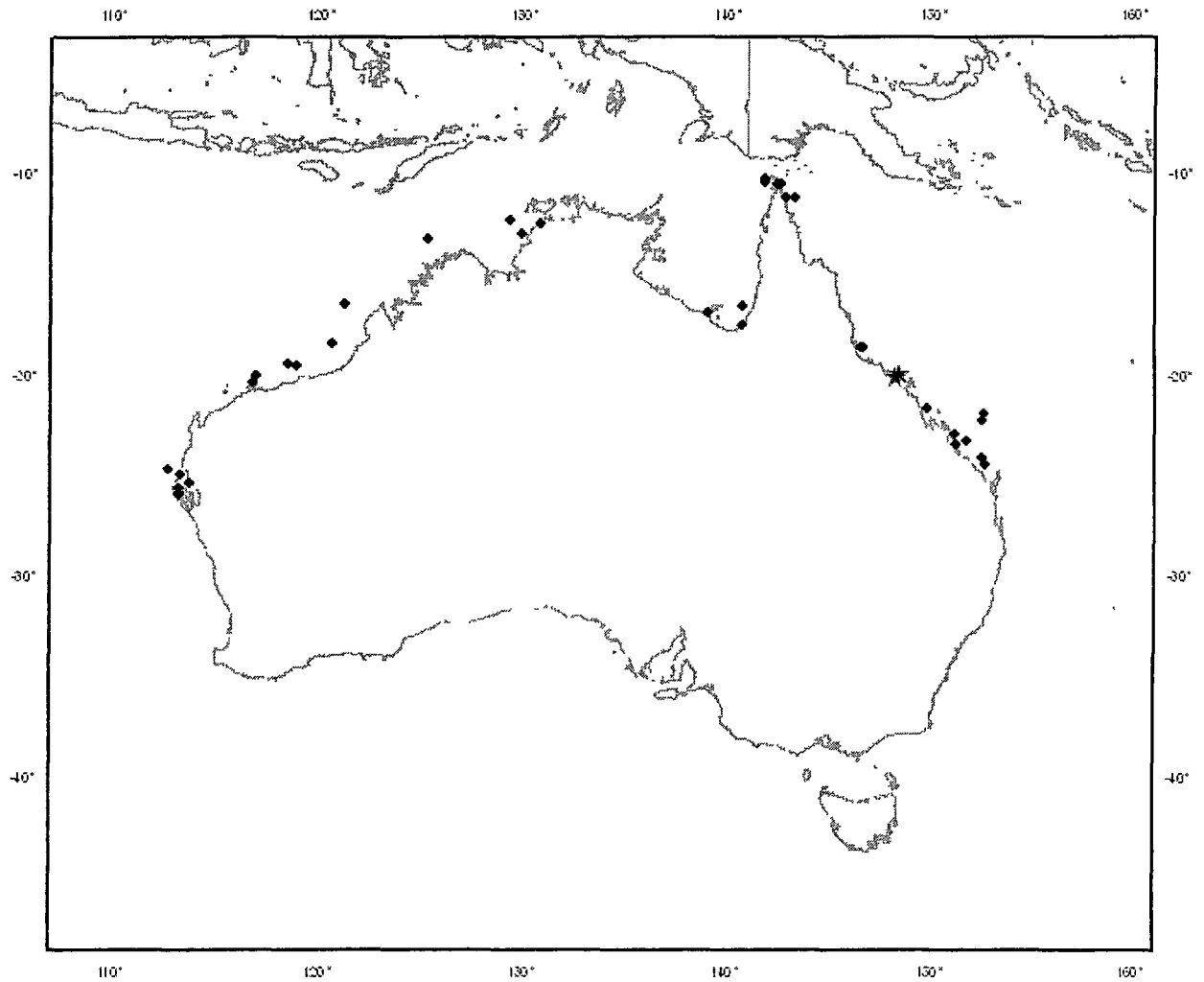


Figure 1.24. Geographic distribution of *Zebrias craticula*. Stars denote locality of type material.

**Remarks:** Eschmeyer (2010) remarked that the name *craticula* might be a noun and that the correct name of this species might be *Zebrias craticula*, whereas it has also been referred to as *Zebrias craticulus*. The latin word, *craticula*, is a feminine noun meaning gridiron or grill. According to the International Code of Zoological Nomenclature (1999), the specific name can be a noun, in which case it does not have to agree in case and gender with the genus; therefore, the original species name, *craticula*, is the correct name for this species.

**Comparisons:** *Z. craticula* is easily distinguished from all of its congeners by its unique pigmentation and caudal fin pattern (transverse bands extending to tip of caudal fin). *Z. craticula* appears to be most closely allied to *Z. cancellatus* (McCulloch, 1916), which can be distinguished by its unique pigmentation, consisting of dark blotches arranged to form 2-3 parabolic shapes posterior to the opercular margin on the ocular side. In addition, *Z. cancellatus* has more vertebrae (45-49), and more scales along the lateral line (105-129). *Z. quagga* (Kaup, 1858) and *Z. captivus* Randall, 1995 are easily distinguished by the presence of ocular tentacles. *Z. maculosus* (Oommen, 1977) and *Z. annularis* (Fowler, 1934) differ in having irregular spots in place of transverse bands. *Z. penescalaris* Gomon, 1987 and *Z. scalaris* Gomon, 1987 are distinguished by the presence of numerous, indistinct bands (17-23) and separate eyes with a scaly interorbital space. *Z. altipinnis* (Alcock, 1890), having similarly high meristic values, is distinguished by its separate eyes with a scaly interorbital space, a shorter ocular-side anterior nasal tube (does not reach posterior nasal tube when flattened) and a larger mouth (commissure reaching posterior margin of ventral eye). *Z. zebra* (Bloch, 1787)

differs in having 2-3 modified cirri, or barbels, on the blind-side chin and anterior end of the dorsal fin.

*Zebrias maculosus* Oommen, 1977

Figures 1.25-1.26, Tables 1.12

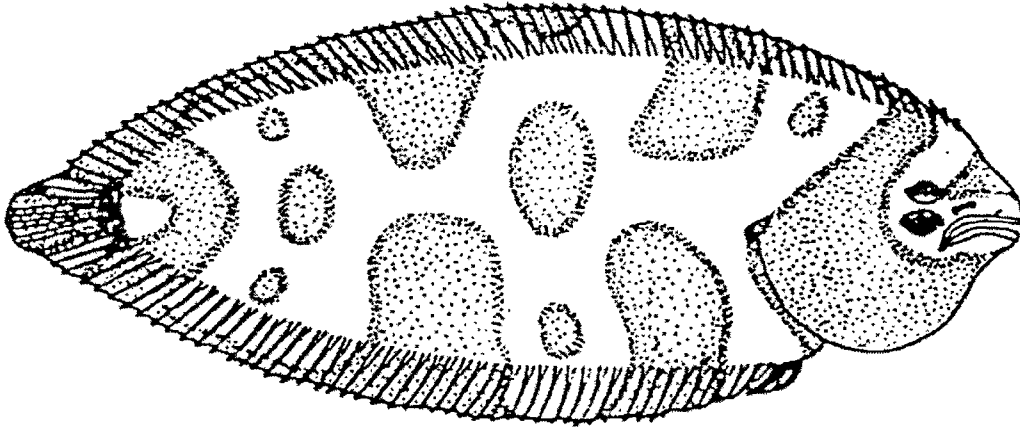


Figure 1.25. *Zebrias maculosus*, as depicted in the original type description (Oommen, 1977), IFP F55a, holotype, 128 mm SL, Arabian Sea, 9°30'N, 75°50'E, depth 150 fathoms.

**Synonym(s):** None known, although species is of questionable validity and may actually be a synonym of *Zebrias annularis* (Fowler, 1934).

**Common name(s):** None known.

**Material examined:** The holotype for this species could not be obtained. No representative specimens could be located in museum collections.

**Diagnosis:** A species of *Zebrias* with the following combination of characters: darkly-demarcated, irregular spots; 58-66 dorsal-fin rays; 50-54 anal-fin rays; 120-135 lateral-line scales; head length 26-27% SL.

**Description:** Description summarized from original text (Oommen, 1977).

Morphometrics are presented in Table 1.12. Dextral flatfish with separate but nearly contiguous eyes without tentacles. Eyes in alignment, ventral eye somewhat larger than dorsal. Scales present in interorbital space. Ocular-side anterior nasal tube short. Membranous flap concealing blind-side anterior nostril. Snout tapering to a point overhanging mouth. Posterior margin of ocular-side jaws reaching vertical through anterior third of ventral eye. Lips fringed on blind side. Cirri covering anterior part of head on blind side with row of cirri extending along preopercular border. Preopercle edge covered by skin. Lateral line straight on both sides. Scales on body ctenoid on both sides and of comparable size on head and body. Anterior end of dorsal fin slightly anterior to vertical at anterior margin of dorsal eye. Anterior vertical-fin rays not enlarged, shorter than subsequent rays. Scales extending onto vertical-fin rays. Dorsal and anal fins continuous with caudal fin, which is scarcely distinct and rounded. Pectoral fins broad-based and small, upper pectoral-fin rays attached to branchiostegal membrane. Pelvic fins short and free from both each other and anal fin. Ocular-side pelvic fin attached to genital papilla. Ocular side brownish with dark patches and spots.

Table 1.12. Meristic and morphometric characteristics of type and non-type specimens of *Zebrias maculosus*, as reported in the original species description (Oommen, 1977).

NT=Length of ocular anterior nasal tube. Measurements and abbreviations are described in Appendix B.

	<i>Zebrias maculosus</i> holotype	<i>Zebrias maculosus</i> paratypes (n=2)
<b>Standard length (mm)</b>	128	110-122
<b>Total length (mm)</b>	134	120-130
<b>Counts</b>		
Dorsal fin rays		58-66 <sup>1</sup>
Anal fin rays		50-54 <sup>1</sup>
Lateral line scales		120-135 <sup>1</sup>
<b>Measurements</b>		
BD in TL	3.5	3.2
BD in SL	3.4	2.8
Moc in HL	2.7	2.6-2.8
V in HL	6	5.1-5.6
V in IOD	0.6	0.6-0.7
NT in HL	15	14-15.5
HL in TL	-	4.2-4.3
HL in SL	-	3.7-3.8

<sup>1</sup>: Corresponding values for holotype and paratype were not indicated, only range provided.

**Geographic distribution:** *Zebrias maculosus* has been reported from the Arabian Sea, south-east coast of India.

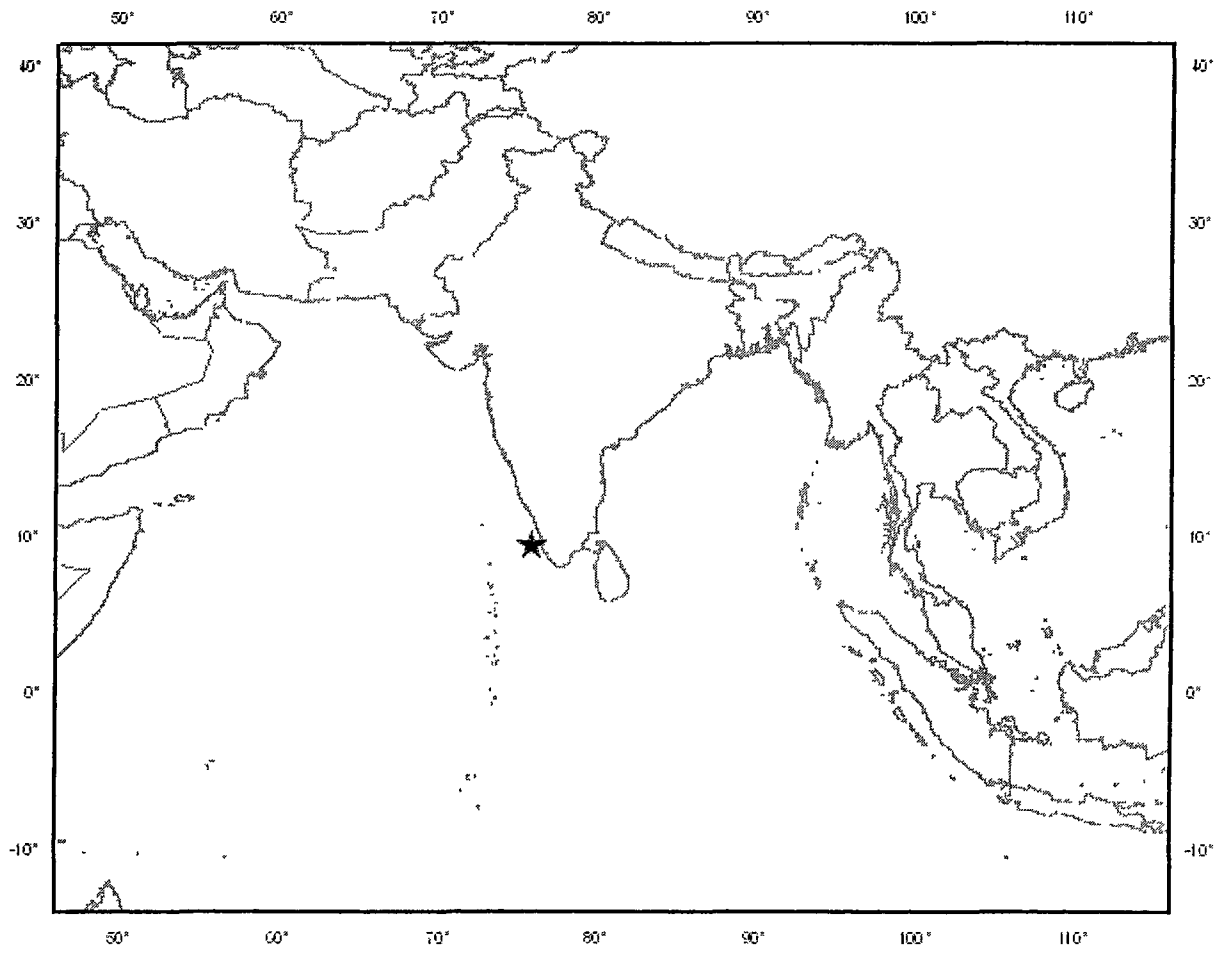


Figure 1.26. Geographic distribution of *Zebrias maculosus*. Star denotes locality of type material, according to Oommen (1977).

**Remarks:** When *Z. maculosus* was described, it was compared to other Indian species of *Zebrias*, but not to its most closely-allied congener, *Z. annularis* (Fowler, 1934). This is most likely due to the fact that *Z. annularis* was then associated with the genera, *Brachirus* Swainson, 1838 and *Synaptura* Cantor, 1849. Moreover, *Z. annularis* was not reported from India until many years later (Nair, 2006).

The type material for *Z. maculosus* could not be obtained and needs to be examined before a firm designation of this species' placement can be made. The museum holdings examined did not include representatives of this species, and the original description is lacking; valuable information such as a description of the supracranial complex and counts, including vertebrae, caudal-fin rays, pelvic-fin rays and pectoral-fin rays are absent. This information is crucial to assessing the validity of the species and determining its best generic placement.

**Comparisons:** With the exception of *Z. annularis*, *Z. maculosus* can be distinguished from all of its congeners by the presence of irregular spots in lieu of bands. *Z. annularis* differs from *Z. maculosus* in having a higher dorsal-fin ray count (71-74), higher anal-fin ray count (55-60), lower lateral-line scale count (93-100), and smaller head length (17-18% SL for *Z. annularis*; 26-27% SL for *Z. maculosus*).

*Zebrias penescalaris*, Gomon 1987

Figures 1.27-1.30, Tables 1.13

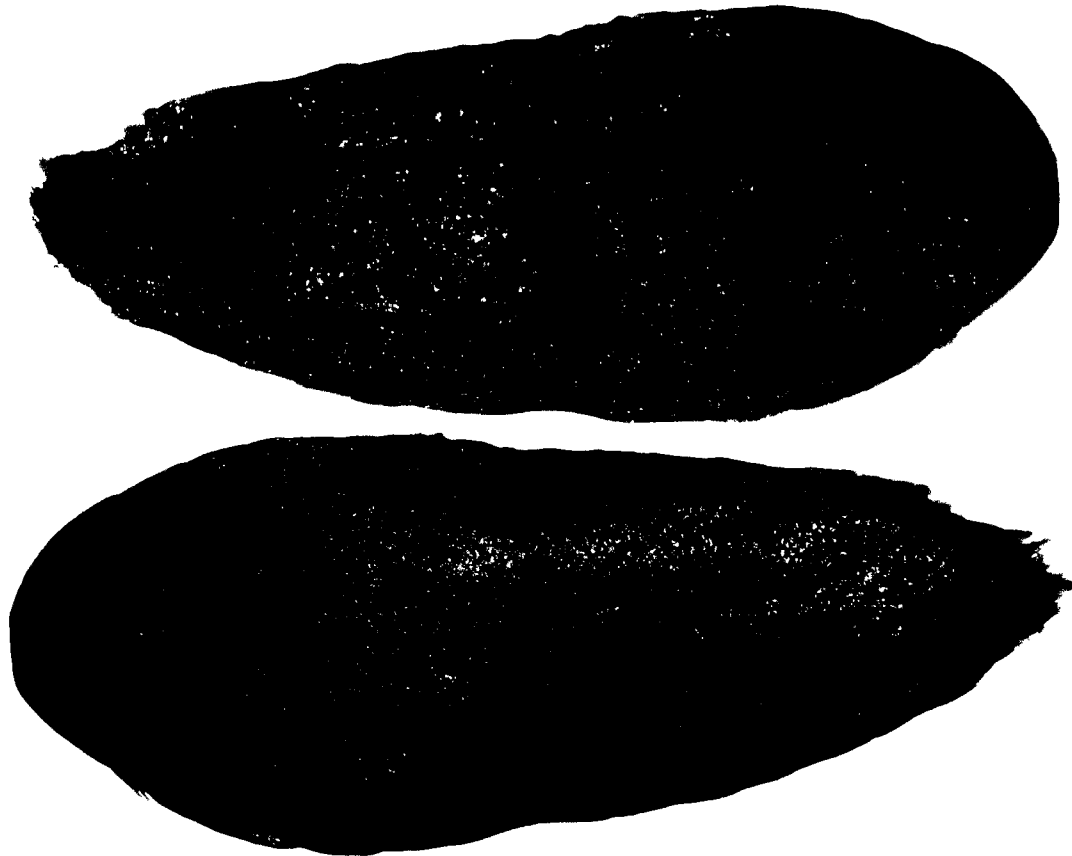


Figure 1.27. Photographs of *Zebrias penescalaris*, paratype, AMS I.20194-029, 119 mm SL, South Australia, Investigator Strait, showing the ocular (above) and blind (below) sides.

**Synonym(s):** None.

**Common name(s):** Duskybanded sole.

**Material examined:** 21 specimens (107.69-152.38 mm total length)

**Type material:** Paratype, CSIROH572-3, 1(112.84 mm SL), Western Australia, off Albany; Paratypes, AMSI.20194-029, 7(104.89-122.16 mm SL), South Australia, Investigator Strait.

**Non-type material:** MVA29225-006, 1(95.02 mm SL), South Australia, Spencer Gulf, off Plank Point (Site 2, Night 2); SAMF11777, 1(107.3 mm SL), South Australia, West Coast Eyre Peninsula, off Venus Bay; NMVA29215-007, 1(110.41 mm SL), South Australia, Spencer Gulf, off Plank Point (Site 2, Night 4); NMVA29333-002, 1(112.22 mm SL), South Australia, Spencer Gulf, off Wallaroo (Site 4, Night 4); SAMF10607, 1(115.5 mm SL), South Australia, St. Vincent Gulf; QM I.26630, 4(119.8- 128.58 mm SL), St. Vincent Gulf, South Australia; NMVA21358, 1(120.57 mm SL), South Australia, Investigator Strait; NMVA29333-001, 1(121.23 mm SL), South Australia, Spencer Gulf, off Wallaroo (Site 4, Night 4); SAMF10589, 1(127.27 mm SL), label reads: “data to come”; SAMF11779, 1(137.7 mm SL), South Australia, outer harbour, St. Vincent Gulf, 25 km WSW.

**Diagnosis:** A species of *Zebrias* with the following combination of characters: 17-22 narrow, indistinct, singular bands; ocular side light brown; genital papilla situated at base of posteriormost ocular-side pelvic-fin ray; 16 caudal-fin rays; 67-77 lateral-line scales; median fins uniformly pigmented.

**Description:** Meristic and morphometric characters are indicated in Table 1.13. Small sole, attaining a total length of 15 cm. Supracranial pterygiophores 4-6 ( $\bar{x} = 4.4$ ); formula: 1-1-(1-3). Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes close-set but clearly separated by narrow, scaly interorbital space. Ocular tentacles absent. Ocular-side anterior nasal tube reaching or slightly surpassing anterior margin of ventral eye when flattened. Ocular-side posterior nasal tube approximately half the length of anterior tube. Blind-side anterior nostril slightly dorso-anterior to dorsalmost point of mouth; anterior nostril a short, uneven tube, higher end covering nasal aperture. Blind-side posterior nasal tube dorso-posterior to anterior nostril at vertical through posterior edge of mouth and at posterior border of dense patch of cirri on anterior head region. Posterior margin of ocular-side jaws just surpassing vertical through anterior margin of ventral eye. Ocular-side lips smooth. Blind-side lower lip plicate. Teeth minute, restricted to blind-side jaws. Cirri absent from ocular side except for short fringe along opercular margin. Cirri densely distributed at anterior end of blind-side head, extending along snout, chin and opercular margin. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line well developed on both sides. Supraorbital line present on ocular-side head. Blind-side lateral line extending horizontally along body to opercular margin but not extending anterior to it. Lateral-line scales cycloid. Scales on body strongly ctenoid on both sides of body with 6-9 ctenii. Anterior end of dorsal fin at, or slightly anterior to, vertical at anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Dorsal- and anal-fin rays increasing in length toward posterior end; longest rays directly adjacent to caudal fin. Caudal fin rounded or squarish. Pectoral fins

symmetrical, rudimentary (ocular-side fin length 4-11% HL, blind-side fin length 4-12% HL); dorsalmost ray longest, more ventral rays decreasing gradually in length. Ocular-side pelvic fin typically slightly longer than blind-side fin. Anus submedian on blind side. Genital papilla located at base of posteriormost ocular-side pelvic-fin ray. Genital papilla free from ocular-side pelvic fin in type specimens, but attached by thin membrane in all non-type material examined (detachment observed in type material possibly resulting from damage).

**Pigmentation of preserved specimens:** Ocular side pale brown with scarcely distinct deeper brown bands. Bands narrow, unpaired: 17-22 across body. Bands relatively uniform in width across body, those on head becoming narrower. Blind side whitish with no conspicuous pigmentation. Interior of mouth white with or without minute, dark spots. Individual bands not discernible on dorsal and anal fins, which appear uniformly grey or brown. Ocular-side caudal fin uniformly grey or brown with no distinct pattern. Ocular-side pectoral fin grey or dark brown. Blind-side pectoral fin transparent or mostly transparent with minute black spots; spots typically found in conjunction with black spots on skin beneath operculum. Pelvic fins whitish.

Table 1.13. Meristic and morphometric characteristics of type and non-type specimens of *Zebrias penescalaris*. Means and standard deviations are shown in parentheses. Measurements and abbreviations are described in Appendix B.

	<i>Zebrias penescalaris</i> paratypes (n=8)	<i>Z. penescalaris</i> non-type specimens (n=13)
<b>Standard length (mm)</b>	104.89-122.16 (113.38; 6.17)	95.02-137.70 (118.90; 10.9)
<b>Total length (mm)</b>	119.38-134.41 (125.66; 5.66)	107.69-152.38 (133.68; 12.0)
<b>Counts</b>		
Dorsal-fin rays	71-80 (75.3; 2.9)	71-79 (74.3; 2.4)
Anal-fin rays	60-67 (64; 2.3)	61-69 (64.2; 2.1)
Caudal-fin rays	15-16 (15.9; 0.4)	16-18 (16.2; 0.6)
Precaudal vertebrae	8-9 (8.9; 0.4)	9 (9; 0)
Caudal vertebrae	34-35 (34.9; 0.4)	34-36 (34.9; 0.8)
Total vertebrae	43-44 (43.8; 0.5)	43-45 (43.9; 0.8)
Haemopophyses	5-6 (5.1; 0.4)	5-6 (5.1; 0.3)
Pterygiophores	5-6 (5.6; 0.5)	4-6 (5.6; 0.7)
Pectoral-fin rays o.s.	5-7 (5.4; 0.8)	5-7 (5.8; 0.8) <sup>1</sup>
Pectoral-fin rays b.s.	5-6 (5.3; 0.5)	5-7 (5.8; 0.6) <sup>1</sup>
Pelvic-fin rays o.s.	4 (4; 0)	4 (4; 0)
Pelvic-fin rays b.s.	4 (4; 0)	4 (4; 0)
Lateral-line scales	67-77 (71.2; 3.9)	68-77 (73.1; 2.9) <sup>3</sup>
Number of bands	17-20 (19.0; 1.5) <sup>1</sup>	17-22 (20.2; 1.5) <sup>1</sup>
<b>Measurements</b>		
<b>%SL</b>		
Head length	0.17-0.19 (0.18; 0.2)	0.15-0.18 (0.17; 0.01)
Head depth	0.20-0.22 (0.21; 0.007)	0.14-0.24 (0.21; 0.02)
Body depth	0.31-0.36 (0.34; 0.02)	0.34-0.39 (0.36; 0.02)
Caudal fin length	0.09-0.15 (0.11; 0.02)	0.11-0.15 (0.12; 0.01)
Width caudal peduncle	0.06-0.09 (0.07; 0.01)	0.06-0.09 (0.07; 0.007)
<b>%HL</b>		
Length of pectoral fin o.s.	0.05-0.10 (0.07; 0.02)	0.04-0.11(0.08; 0.02) <sup>1</sup>
Length of pectoral fin b.s.	0.06-0.08 (0.07; 0.01)	0.04-0.12 (0.08; 0.02)
Length of pelvic fin o.s.	0.31-0.44 (0.39; 0.04)	0.31-0.42 (0.37; 0.03)
Length of pelvic fin b.s.	0.24-0.42 (0.32; 0.06)	0.28-0.42 (0.34; 0.04)
Pre-orbital head length	0.15-0.30 (0.20; 0.05)	0.12-0.25 (0.21; 0.04)
Post-orbital head length	0.54-0.63 (0.58; 0.03)	0.53-0.66 (0.58; 0.04)
Snout length	0.22-0.28 (0.25; 0.02)	0.20-0.37 (0.28; 0.05)
Nostril to snouth distance	0.15-0.21 (0.17; 0.02)	0.13-0.26 (0.20; 0.03)
Mouth length o.s.	0.25-0.34 (0.31; 0.03)	0.26-0.39 (0.33; 0.03)
Mouth length b.s.	0.22-0.35 (0.30; 0.04)	0.20-0.33 (0.29; 0.03)
Ventral eye diameter	0.23-0.29 (0.27; 0.02)	0.19-0.28 (0.25; 0.03)
Width of orbits	0.32-0.41 (0.37; 0.03)	0.28-0.43 (0.37; 0.04)
Longest dorsal ray	0.55-0.63 (0.59; 0.03)	0.47-0.75 (0.60; 0.08)
Longest anal ray	0.56-0.65 (0.59; 0.03)	0.49-0.74 (0.60; 0.08)
IOD/V	0.15-0.21 (0.18; 0.02)	0.10-0.43 (0.23; 0.1)
BPc/OPc	0.83-1.17 (0.98; 0.1)	0.61-1.45 (1.05; 0.3)
BPv/OPv	0.62-1.01 (0.83; 0.1)	0.76-1.2 (0.94; 0.1)

<sup>1</sup>: n=12.

<sup>2</sup>: n=6.

<sup>3</sup>: n=11.

**Geographic distribution:** *Zebrias penescalaris* is endemic to Australia and has been reported from the southern coast (South Australia) to the southwest coast (Western Australia) at depths of 20-45 m.

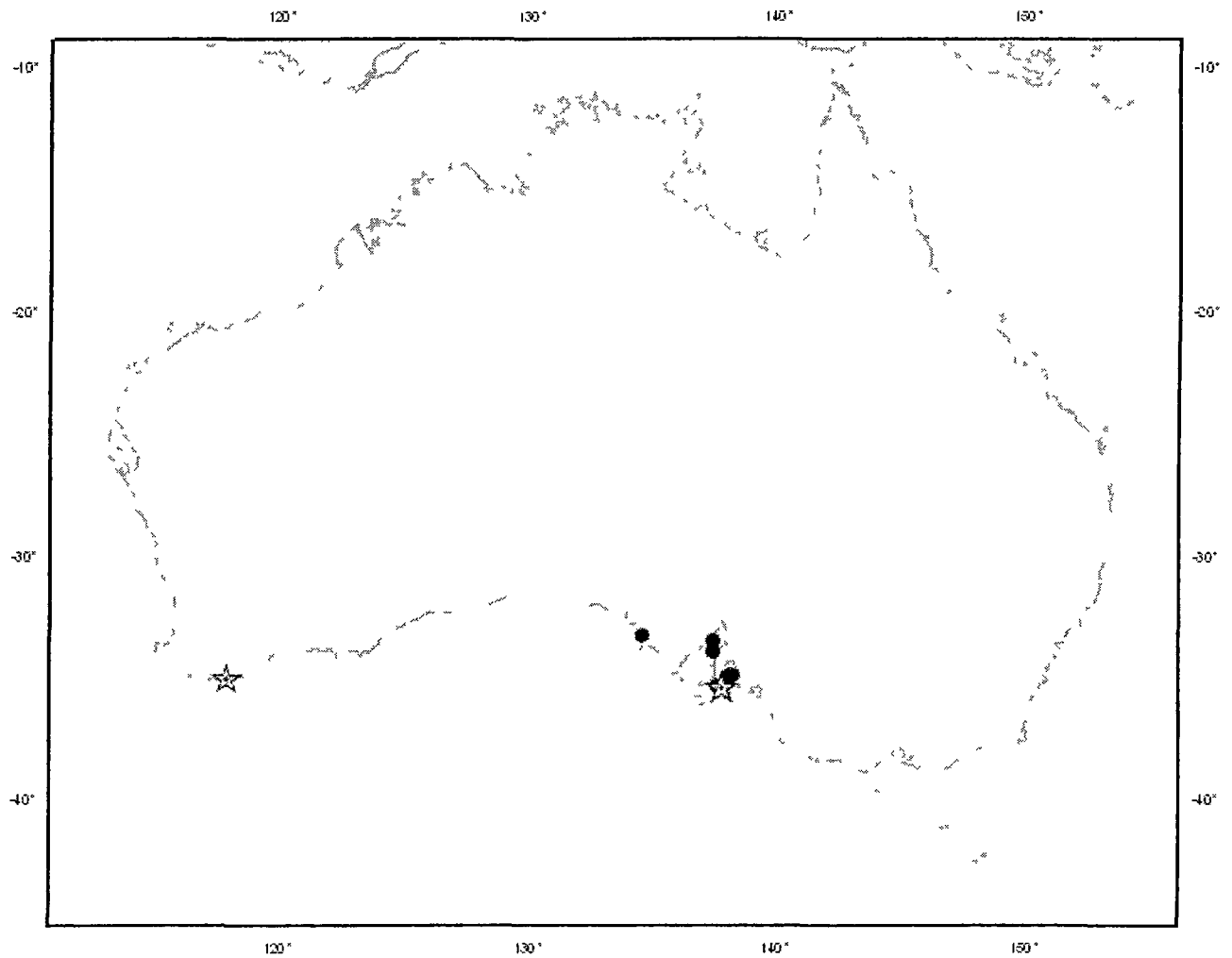


Figure 1.28. Geographic distribution of *Zebrias penescalaris*. Stars denote locality of type material.

**Remarks:** *Zebrias penescalaris* is most closely allied to *Zebrias scalaris* Gomon, 1987, from which it is scarcely distinguishable. The two species exhibit distinct geographical partitioning into eastern and western populations along the southern Australian coast (Figure 1.29). The range of *Z. penescalaris* is restricted to the South-west Marine Region, a 1.2 million km<sup>2</sup> region of ocean that extends from offshore Cape Inscription in Western Australia to the eastern end of Kangaroo Island in South Australia. In contrast to the east coast, the ecology and biodiversity of the South-west Marine Region are strongly influenced by the Leeuwin Current (Figure 1.30), which originates in the tropical waters of the Indian Ocean. The region is known to be nutrient-poor and is characterised by high species diversity as well as a high level of endemism (Australian Government, 2007). This endemism can, in part, be attributed to the unidirectional flow of the Leeuwin Current, which effectively acts as a geographic barrier resulting in the isolation of the region from other land masses. The distribution of *Z. scalaris* is found east of the South-west Marine Region in a region influenced by the south-flowing East Australian Current (Waters and Roy, 2003) (Figure 1.30). This species has been reported from south-eastern Australia ranging from Three-Hummock Island, Tasmania and Cape Woolamai, Victoria to the Sunshine Coast, Queensland.

The east-west distribution of *Z. scalaris* and *Z. penescalaris* can be seen in other southern Australian marine species. Cool temperatures and the emergence of the Bassian Isthmus (a land bridge that connects Tasmania to mainland Australia during glacial periods when the sea level drops) during glacial periods are thought to have promoted allopatric divergence between eastern and western populations of several southern Australian marine species, including fishes (Burrige, 2000; references therein),

jellyfishes (Dawson, 2005), barnacles (York et al., 2008), sea stars (Waters and Roy, 2003), starfishes (Waters et al., 2004), kelp (Fraser et al., 2009), and sea snails (Waters et al., 2005). Additional species are referenced by Dawson (2005). It is likely that geographic isolation and exposure to dissimilar selective pressures were the driving factors that resulted in the speciation of *Z. scalaris* and *Z. penescalaris*. Given the striking resemblance between these species, an examination of additional material from further southwest and in any region where the two species overlap (if such a region exists) would be useful in further supporting the distinction between *Z. scalaris* and *Z. penescalaris*.

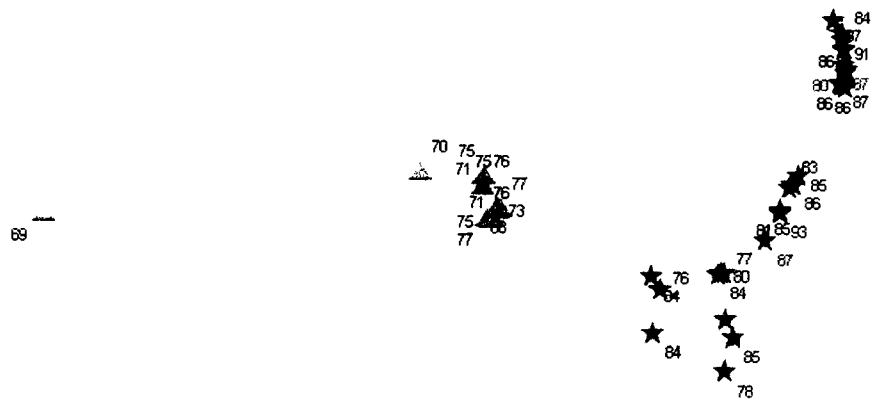


Figure 1.29. Geographic distribution of *Zebrias scalaris* (stars) and *Zebrias penescalaris* (triangles). The number of lateral line scales is indicated for each specimen. It should be noted that the two *Z. scalaris* specimens indicated as having lateral line scale counts of 76 and 78 are missing many scales and therefore, these values are likely underestimates.

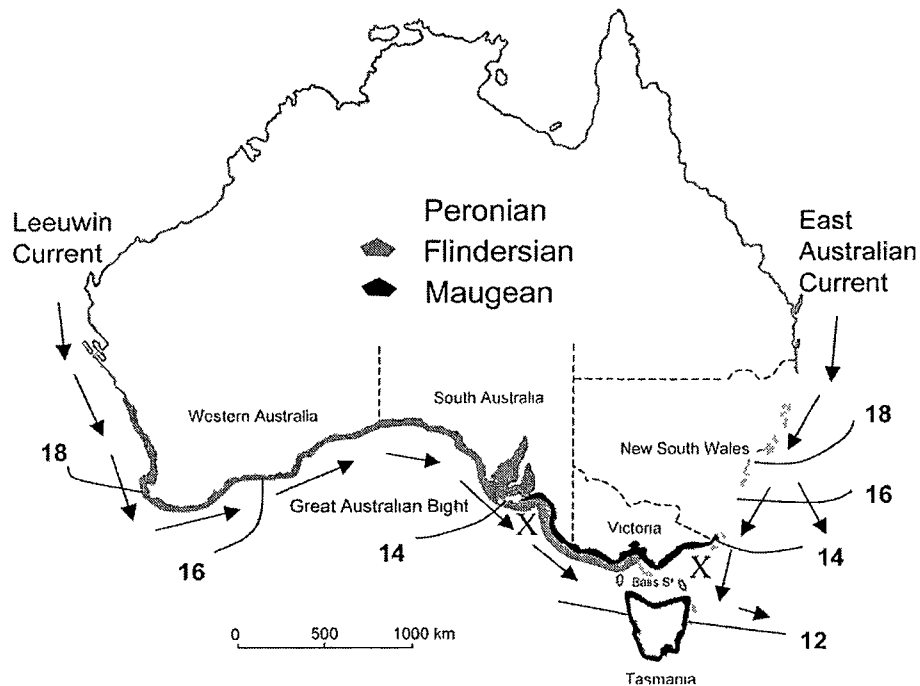


Figure 1.30. Diagram depicting the direction of flow of the Leeuwin Current, as illustrated by Waters et al. (2004).

**Comparisons:** With the exception of its most closely allied congener, *Zebrias scalaris* Gomon, 1987, *Z. penescalaris* can be distinguished from all species of *Zebrias* by its numerous, indistinct bands (17-22) and uniformly dark median fins. It can also be distinguished by the position of the genital papilla, located at the base of the posteriormost ocular-side pelvic fin ray, although this character is shared by *Z. cancellatus* (McCulloch, 1916). *Z. scalaris* differs from *Z. penescalaris* in having more scales along the lateral line (76-93) and in general, a deeper brown pigmentation with slightly more defined bands (the banding pattern of *Z. penescalaris* being somewhat less discernible). *Z. cancellatus* can be distinguished by its contiguous eyes and parabolic pigmentation pattern (Figure 1.16). *Z. quagga* (Kaup, 1858) and *Z. captivus* Randall, 1995 are easily distinguished by the presence of contiguous eyes bearing ocular tentacles.

*Z. maculosus* Oommen, 1977 and *Z. annularis* (Fowler, 1934) differ in having irregular spots in place of bands. *Z. zebra* (Bloch, 1787) is distinguished by the presence of 24 broad, paired bands and 2-3 barbels on the blind-side chin and anterior end of the dorsal fin. *Z. altipinnis* (Alcock, 1890) differs in having 14-15 broad, singular bands, more pelvic-fin rays (5), more caudal-fin rays (18), more scales along the lateral line (100-113) and more pectoral-fin rays (9-12 ocular). *Z. craticula* (McCulloch, 1916) can be distinguished by the presence of 17-24 broad bands extending from the tip of the snout to the tip of the caudal fin.

***Zebrias quagga* (Kaup, 1858)**

Figures 1.31-1.33, Tables 1.14-1.15



Figure 1.31. Photographs of *Zebrias quagga*, MNHN1998-1307, holotype, 150 mm SL, Maharashtra, Bombay, India, 18°933'N, 72°85'E, depicting the ocular (above) and blind (below) sides.

**Synonym(s):** *Aesopia quagga* Kaup, 1858; *Synaptura zebra* (Day, 1888)

**Common name(s):** Quagga sole (English), Jerree-potoo (Telugu), Varri-amler (Tamil), Lep (Marathi), Fringefin zebra sole

**Material examined:** 115 specimens (58.01-175.2 mm TL)

**Type material:** Holotype, MNHN1998-1307, 1(149.9 mm SL), Maharashtra, Bombay, India, Sector 5114, 18°933'N, 72°85'E.

**Non-type material:** USNM Uncatalogued, 1(74.06 mm SL), Java Sea, Station 66; AMSI.15421-032, 7(102.87-118.7 mm SL), Townsville, Queensland, 19°16'S, 146°48'E; AMSI.113, 1(80.31 mm SL), Bombay, India; AMSI.15557-065, 1(109.15 mm SL), Gulf of Carpentaria, Queensland, 17°00'S 140°16'E; AMSI.26248-002, 2(77.02-99.21 mm SL), Queensland, Gulf of Carpentaria, midway between Sweers Is. And Little Bountiful Island, 16°45'S 139°50'E; AMSI.33311-007, 1(110.29 mm SL), Western Australia, Exmouth Gulf, 21°53'S-22°05'S 114°15'E-114°22'E; AMSIB3305, 1(115.19 mm SL), Repulse Bay, Queensland; ANSP123153, 3(93.37-109.89 mm SL), Indian Ocean, India, Bandia: Bombay Harbor; ANSP145357, 11(87.57-109.54 mm SL), Indian Ocean; ASIZP0062406, 1(77.33 mm SL), open sea, Xingda Harbor, Kaohsiung, 22°87'S 120°1'E; ASIZP0064112, 1(102.21 mm SL), 3-3-1, SW Taiwan, 23°21'S 119°97'E; BPBM18589, 1(81.3 mm SL), Indonesia, obtained from fish market in Jakarta, Java; BPBM20633, 2(93.21-107.31 mm SL), India, Gulf of Mannar Clanding at Mandapam Camp, Mandapam Camp; CAS130708, 3(58.45-109.26 mm SL), Indo-West Pacific, Singapore; CAS201665, 1(69.21 mm SL), Indo-West Pacific, Thailand, Gulf of Thailand, 20.5 miles from Laem Pahkbia, green water; CAS201673, 1(116.72 mm SL), Indo-West Pacific, Vietnam, Khanh Hoa Province, open water from NE side of Hon Con I., south to Pte. De Camranh, via fish market at Nhatrang; CAS205993, 1(105.25 mm SL), Indo-West Pacific, Thailand, Gulf of Thailand, 20.5 miles from Laem Phakbia, green water; CSIROH6529-01, 1(109.04 mm SL), Queensland, Abbot Bay, 19°48'S 147°53'E;

CSIROA2270, 1(100.51 mm SL), Queensland, Gulf of Carpentaria, 16°47'S 140°50'E;  
CSIROA2322, 1(91.31 mm SL), Queensland, Gulf of Carpentaria, 16°55'S 140°23'E;  
CSIROA2398, 1(99.77 mm SL), Queensland, Gulf of Carpentaria, 16°35'S 140°56'E;  
CSIROA2842, 1(94.62 mm SL), Queensland, Gulf of Carpentaria, 17°02'S 140°38'E;  
CSIROA2845, 1(93.26 mm SL), Queensland, Gulf of Carpentaria, 16°49'S 140°51'E;  
CSIROA2878, 1(95.76 mm SL), Queensland, Gulf of Carpentaria, 16°35'S 140°41'E;  
CSIROC3985, 1(120.53 mm SL), NT, 17 miles NE of Robinson River, 15°55'S  
137°30'E; CSIROC4197, 1(98.63 mm SL), Queensland, halfway between Sweers and  
Bountiful Islands, 16°52'S 139°45'E; CSIROH3605-01, 1(93.24 mm SL), Queensland,  
Gulf of Carpentaria, WNW of Wepa, 12°26'S 141°32'E; CSIROH6525-01, 1(107.92 mm  
SL), Queensland, SE of Cairns, 17°16'S 146°03'E; CSIROH6526-01, 1(102.21 mm SL),  
Queensland, south of Cape Direction, 13°07'S 143°35'E; CSIROH6527-01, 1(76.34 mm  
SL), Queensland, north of Townsville, 19°07'S 146°56'E; CSIROH6528-01, 1(90.55 mm  
SL), Queensland, Princess Charlotte Bay, 14°16'S 144°01'E; CSIROH6529-01; 1(95.15  
mm SL), Queensland, Abbot Bay, 19°48'S 147°53'E; FMNH47517, 2(68.4-83.56 mm  
SL), East Indies, Singapore; FMNH51921, 1(67.94 mm SL), East Indies, Malaysia,  
Sabah, East Coast Residency, Sandakan Dist., Sandakan Fish Market; MNHN1965-487,  
2(110.1-116.9 mm SL), Cambodge, kep, Pacific, sector: 7111, 10.35°S 104.3°E; NSMT-  
P55942, 6(69.07-109.18 mm SL), Thailand, Malay Peninsula, off Songkhla (fish market),  
Western Pacific; NSMT-P55943, 1(118.73 mm SL), Thailand, Gulf of Thailand, off  
Rayong; NSMT-P60760, 1(75.68 mm SL), Western Pacific, China, south coast of Hainan  
Is., Sanya Bay; NTM S.10400-003, 1(47.77 mm SL), Lee Point, Shoal Bay, N.T., Stn:  
D11416, 12°19'S 130°54'E; NTMS.10284-002, 1(100.53 mm SL), Shoal Bay, Darwin,

N.T., 12°18'S 130°58'E; NTMS.12434-012, 1(94.13 mm SL), west of Orontes Reef, Cobourg Peninsula, N.T., Stn: RW86-3, 11°06'S 132°06'E; NTMS.12445-011, 1(97.93 mm SL), south of Orontes Reef, Cobourg Peninsula, NT, Station RW 86-4, 11°06'S 132°04'E; NTMS.13145-002, 1(93.03 mm SL), north of Bickerton Is., N.T., Station: SHOT 3-D6, 13°35'S 136°20'E; QMI.11811, 1(85.75 mm SL), off Round Hill Head, 24°09'S 151°53'E; QMI.14231, 2(92.84-107.8 mm SL), off Dampier, Western Australia, 20°39'S, 116°43'E; SIO 66-525-64D, 1(80.86 mm SL), Queensland Australia, on shelf of west coast of Stanley Is., Flinders Group inside Great Barrier Reef; SIO73-177, 1(109.91 mm SL), Indonesia, McCluer Gulf, 1°13.1'S 130°34'E; SMF22264, 1(128.91 mm SL), IAA. Gulf of Thailand; SMF25322, 1(68.31 mm SL), Sudchin, Meer, Hainan (China), Qinglan; SMF27449, 1(109.56 mm SL), Indian Ocean, Madras, India; SOS334, 3(81.99-107.42 mm SL), India; UMMZ191496, 3(104.39-112.52 mm SL), Asia, Thailand, Prachuab Khiri Khan, Ban Khlong Wan Fish Market, Gulf of Thailand; UMMZ219962, 1(110.84 mm SL), Asia, Vietnam, South China Sea, Paknam St. P-111-12 (Station 13); UMMZ223066, 3(108.85-111.88 mm SL), Asia, Thailand, Bangkok Fish Market, Gulf of Thailand; UMMZ227069, 7(98.01-142.03 mm SL), Asia, Vietnam, South China Sea, Paknam Station 3, 23 km ESE Kien Hoa Province, Mekong River Plume, 10°0'48"N 107°1'0"E; WAMP11779.001, 1(64.6 mm SL), Western Australia, Dampier Archipelago, Lewis Island, 20°35'S 116°38'E; WAMP11787, 1(81.7 mm SL), Western Australia, Exmouth Gulf; WAMP11788.001, 1(105.8 mm SL), Western Australia, Exmouth Gulf, 22°05'S 114°15'E; WAMP25396.007, 5(84.35-119.29 mm SL), Indian Ocean, 17°26'S 121°54'E; WAMP32643.009, 1(109.23 mm SL), Western Australia, Exmouth Gulf, Sunday Island, 9.7 km east of island, Station: EG-18-025,

21°43.648'S to 21°43.133'S 114°30.351'E to 114°30.613'E; WAMP4508-001, 1(117.2 mm SL), Western Australia, Shark Bay, 25°21'S 113°44'E; WAMP5738, 1(100.16 mm SL), Exmouth Gulf; ZRC39244, 1(88.95 mm SL), Singapore, Sungei Punggoi; USNM Uncatalogued, 5(x-ray only), India.

**Diagnosis:** A species of *Zebrias* with the following combination of characters: Presence of an ocular tentacle on one or both eyes (Figure 1.21); bands wider than inter-band spaces; 76-104 lateral-line scales; upper two rays of ocular-side pectoral fin tightly joined by a thin membrane, second ray the most elongate; 38-44 vertebrae; 64-88 dorsal-fin rays; 52-64 anal-fin rays; caudal fin dark with light “V” or “M” shape at its base and at least two light spots around dorsal and ventral margins of fin toward its distal end.

**Description:** Morphometrics are presented in Table 1.14. Small sole, attaining a total length of 18 cm. Supracranial pterygiophores 3-5; formula: 1-1-(1-2). Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes contiguous, or nearly so, with tentacle on one or both eyes. Dorsal eye slightly in advance of ventral eye. Scales absent in interorbital space. Ocular-side anterior nasal tube reaching posterior nasal tube when flattened, infrequently reaching anterior margin of ventral eye (12/110 specimens); base of anterior nasal tube wider than aperture. Ocular-side posterior nasal tube approximately half length of anterior tube or slightly longer. Blind-side anterior nostril dorso-anterior to dorsalmost point of mouth; anterior nostril a short, uneven tube. Blind-side posterior nasal tube dorso-posterior to anterior nasal tube, at vertical through posterior edge of mouth and at

posterior border of dense patch of cirri on anterior region of head. Posterior margin of ocular-side jaws just surpassing vertical through anterior margin of ventral eye, extending as far as vertical through anterior third of ventral eye. Ocular-side lips smooth. Blind-side lower lip plicate with series of cirri on inside border of lip. Teeth minute, restricted to blind-side jaws. Cirri absent from ocular side apart from short fringe along opercular margin. Cirri densely distributed at anterior end of blind-side head, extending along snout, chin and opercular margin. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line well developed on both sides. Supraorbital line present on ocular-side head. Blind-side lateral line may be associated with patches of cirri on head. Lateral-line scales cycloid. Scales on body moderately ctenoid; number of ctenii variable, ranging from 10-20. Anterior end of dorsal fin at, or slightly anterior to, vertical at anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Caudal fin rounded with slight peak in center. Scales on proximal half of median fins. Ocular-side pectoral fin relatively short ( $\bar{x} = 37\%$  HL); two dorsalmost fin rays tightly joined by thin membrane. Second dorsalmost ocular-side pectoral-fin ray longest; more ventral rays decreasing gradually in length. Blind-side pectoral fin relatively short ( $\bar{x} = 23\%$  HL); dorsalmost ray longest, more ventral rays decreasing gradually in length. Ocular-side pelvic fin typically slightly longer than blind-side fin. Anus submedian on blind side. Genital papilla submedian on ocular side. Genital papilla attached to ocular-side pelvic fin by thin membrane.

**Pigmentation of preserved specimens:** Ocular side light to deep brown or grey with series of 11-23 thinly-demarcated, deeper brown or grey bands; bands may be singular,

paired, or a combination of the two. Bands wider than inter-band spaces; posteriormost band widest. Bands on head becoming narrower. Blind side typically pale, whitish, devoid of conspicuous pigmentation. Minute, dark spots may be present on blind side from middle to posterior end of body, concentrated along median fin margins, and on skin beneath pectoral fin. Infrequently, dark spots extending onto blind-side head with median fin margins appearing dusky (4/108 specimens). Interior of mouth pale with few scattered, minute, dark spots; alternatively, dark grey to black. Bands extending onto dorsal and anal fins, becoming darker. Blind-side median fins uniformly dark. Ocular-side caudal fin pigmentation variable; typical pattern consisting of a “V” or “M” shape at base of fin and at least two or more light spots along ventral and dorsal margins of fin toward distal end. Ocular-side pectoral fin light to dark brown or grey. Blind-side pectoral fin of most specimens transparent; others mostly transparent with minute, dark spots. Pelvic fins whitish.

Table 1.14. Meristic and morphometric characteristics of type and non-type specimens of *Zebrias quagga*. Means and standard deviations are shown in parentheses. Measurements and abbreviations are described in Appendix B.

	<i>Aesopia quagga</i> holotype	<i>Zebrias quagga</i> non-type specimens (n=109)
<b>Standard length (mm)</b>	149.9	68.40-142.03 (98.83; 16.6)
<b>Total length (mm)</b>	175.2	58.01-166.33 (116.4; 19.1)
<b>Counts</b>		
Dorsal-fin rays	75	64-88 (69.8; 2.7) <sup>1</sup>
Anal-fin rays	61	52-64 (57.8; 2.4) <sup>1</sup>
Caudal-fin rays	18	16-19 (17.9; 0.3) <sup>2</sup>
Precaudal vertebrae	9	8-10 (9.0; 0.2) <sup>1</sup>
Caudal vertebrae	35	30-34 (31.3; 0.9) <sup>1</sup>
Total vertebrae	44	38-43 (40.3; 1.0) <sup>1</sup>
Haemopophyses	5	5-6 (5.1; 0.2) <sup>3</sup>
Pterygiophores	7	6-8 (6.9; 0.5) <sup>1</sup>
Pectoral-fin rays o.s.	12	4-8 (6.5; 0.8)
Pectoral-fin rays b.s.	10	4-9 (7.2; 0.7)
Pelvic-fin rays o.s.	4	3-5 (4.0; 0.2) <sup>4</sup>
Pelvic-fin rays b.s.	4	3-5 (4.0; 0.2) <sup>5</sup>
Lateral-line scales	77	76-104 (89.0; 6.1) <sup>4</sup>
Number of bands	13	11-23 (13.3; 2.4) <sup>6</sup>
<b>Measurements</b>		
<b>%SL</b>		
Head length	0.24	0.17-0.20 (0.18; 0.009)
Head depth	0.25	0.17-0.23 (0.20; 0.01)
Body depth	0.41	0.31-0.40 (0.36; 0.02)
Caudal fin length	0.17	0.09-0.23 (0.18; 0.02) <sup>4</sup>
Width caudal peduncle	0.06	0.06-0.12 (0.084; 0.009)
<b>%HL</b>		
Length of pectoral fin o.s.	0.24	0.15-0.77 (0.37; 0.1)
Length of pectoral fin b.s.	0.14	0.14-0.36 (0.23; 0.03)
Length of pelvic fin o.s.	0.30	0.20-0.37 (0.29; 0.03) <sup>4</sup>
Length of pelvic fin b.s.	0.27	0.18-0.36 (0.28; 0.04) <sup>4</sup>
Pre-orbital head length	0.11	0.13-0.30 (0.22; 0.03)
Post-orbital head length	0.59	0.49-0.69 (0.59; 0.03)
Snout length	0.16	0.20-0.38 (0.27; 0.03)
Nostril to snouth distance	0.07	0.12-0.58 (0.20; 0.05)
Mouth length o.s.	0.23	0.24-0.36 (0.31; 0.02)
Mouth length b.s.	0.15	0.17-0.32 (0.26; 0.03)
Ventral eye diameter	0.15	0.21-0.35 (0.26; 0.02)
Width of orbits	0.23	0.27-0.45 (0.35; 0.04)
Longest dorsal ray	0.47	0.47-0.92 (0.66; 0.08)
Longest anal ray	0.49	0.48-0.87 (0.66; 0.08)
IOD/V	0.19	0-0.14 (0.002; 0.02)
BPc/OPc	0.57	0.26-1.95 (0.70; 0.3)
BPv/OPv	0.90	0.59-1.30 (0.95; 0.1) <sup>4</sup>

<sup>1</sup>: n=111; <sup>2</sup>: n=112; <sup>3</sup>: n=113; <sup>4</sup>: n=108; <sup>5</sup>: n=107; <sup>6</sup>: n=106.

**Geographic distribution:** *Zebrias quagga* has been reported from the coasts of India, the Bay of Bengal, the South China Sea, Indonesia, and the northern coast of Australia. Fowler (1956) and Krishnan and Mishra (1994) report this species from the Red Sea but examined fish from China and Little Andaman, respectively. Reported from depths of 9-30 m.

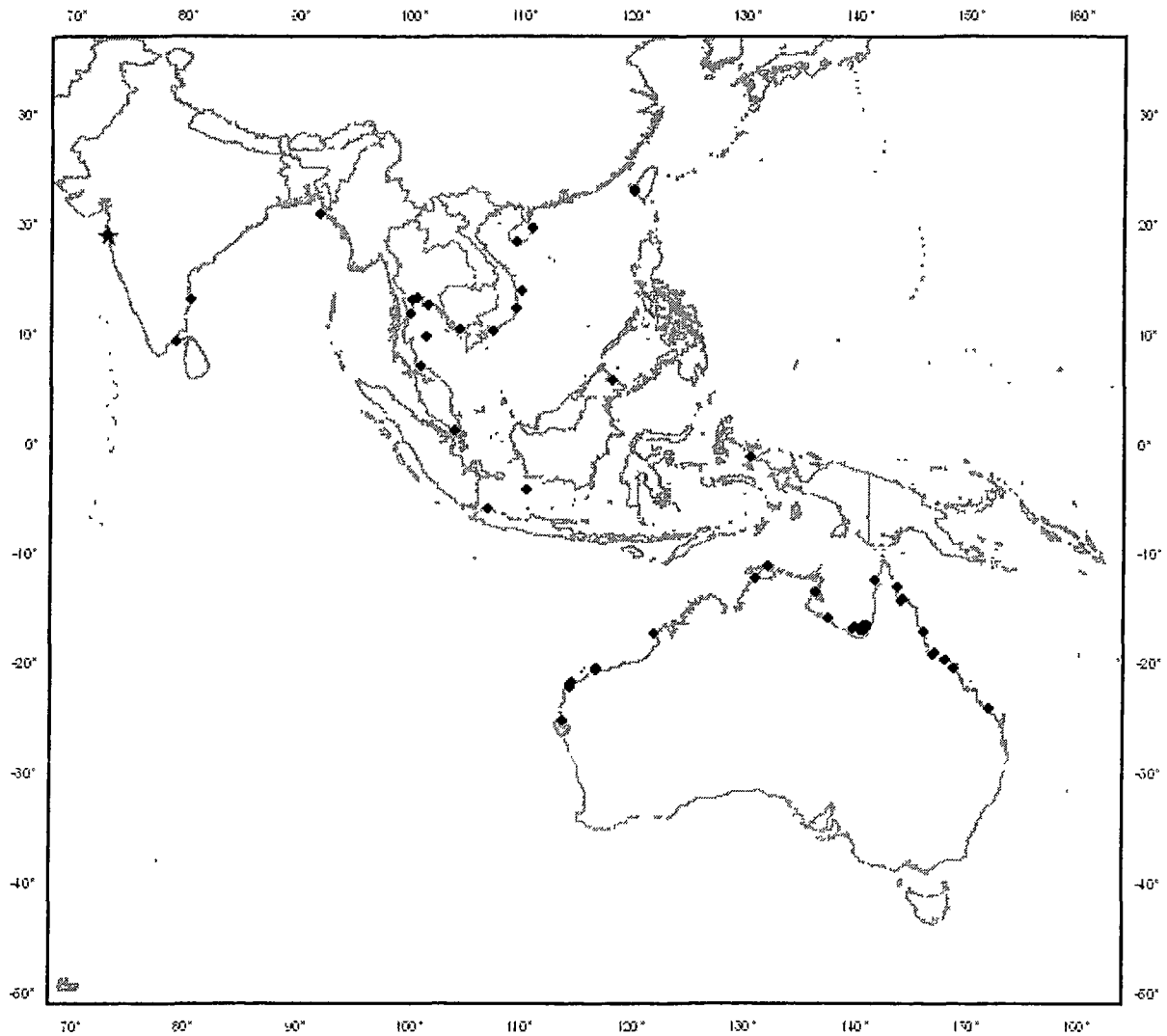


Figure 1.32. Geographic distribution of *Zebrias quagga*. Star denotes locality of type material.

**Remarks:** There are 12 ocular-side and 10 blind-side pectoral-fin rays on the holotype of *Z. quagga*. This specimen appears to be an anomaly, as the remainder of representative specimens examined were found to have only 4-8 ocular-side and 4-9 blind-side pectoral fin rays (Table 1.4). Krishnan and Mishra (1994) report 11 pectoral fin rays for this species based on a collection of fish from Little Andaman, India.

Day (1888) described a species having ocular tentacles, which he referred to as “*Synaptura zebra*”. It is highly probable this fish actually represents a specimen of *Z. quagga*.

Norman (1928) briefly discusses specimens in the British Museum from the Persian Gulf. He describes them as being nearly identical to *Z. quagga*, but having a different band arrangement and lacking the ocular tentacles diagnostic of the species. Norman suggests these specimens could represent an undescribed species. The British Museum’s online database does not list the Persian Gulf as the locality of any of its three *Z. quagga* lots and Norman does not identify the specimens to which he refers; therefore, the specimens in question could not be examined. Yazdani (1976) suggested that the identity of Norman’s fish may be *Zebrias zebra* (Bloch, 1787); however, the distribution of specimens examined in the present study suggests that *Z. zebra* does not inhabit Indian waters.

In the present study, three specimens of *Z. quagga* from the west coast of Australia were found to have an abnormal caudal fin pattern (WAMP32643.009, WAMP4508-001, QMI14231). Among the majority of specimens examined, the caudal fin is typically dark with a “V” or “M” shape at its base and at least two light spots at the dorsal and ventral fin margins toward the distal end (Figure 1.33). The abnormal pattern

consists of a black center and white outline with oblong black spots (Figure 1.33). These specimens were not found to differ in morphometrics or any other qualitative character from the other specimens examined; therefore, there is currently insufficient data to differentiate them as a distinct species. These specimens may require further examination.

**Comparisons:** With the exception of its most closely allied congener, *Zebrias captivus* Randall, 1995, *Zebrias quagga* can be distinguished from all of its congeners by the presence of ocular tentacles. *Z. captivus*, native to the Persian Gulf, differs from *Z. quagga* by its band morphology which consists of darkly-demarcated, uniform bands of comparable width to the inter-band spaces. In addition, *Z. captivus* can be distinguished by its lower meristic values, including fewer scales along the lateral line (74-75), generally fewer vertebrae (38-39), generally fewer dorsal-fin rays (63-66), and generally fewer anal-fin rays (51-54).



Figure 1.33. Photographs of *Z. quagga* depicting abnormal (left, center) and typical (right) caudal fin patterns. Left - QMI.14231, off Dampier, Western Australia, 20°39'S 116°43'E; Center – WAMP4508-001, Western Australia, Shark Bay, 25°21'S 113°44'E; Right - NTMS.10284-002, Shoal Bay, Darwin, N.T., 12°18'S 130°58'E.

Table 1.15. Frequency distribution of transverse band number and arrangement among specimens of *Zebrias quagga*. Asterisk denotes value of holotype; n = sample size.

Total Number of Transverse Bands											
11	12	13	14	15	17	18	20	21	22	23	n
3	53	17*	22	2	1	2	3	2	1	1	107
Transverse Band Arrangement											
Singular	Some Paired		Paired								
58*	11		33								103

*Zebrias scalaris*, Gomon 1987

Figures 1.34-1.36, Tables 1.16

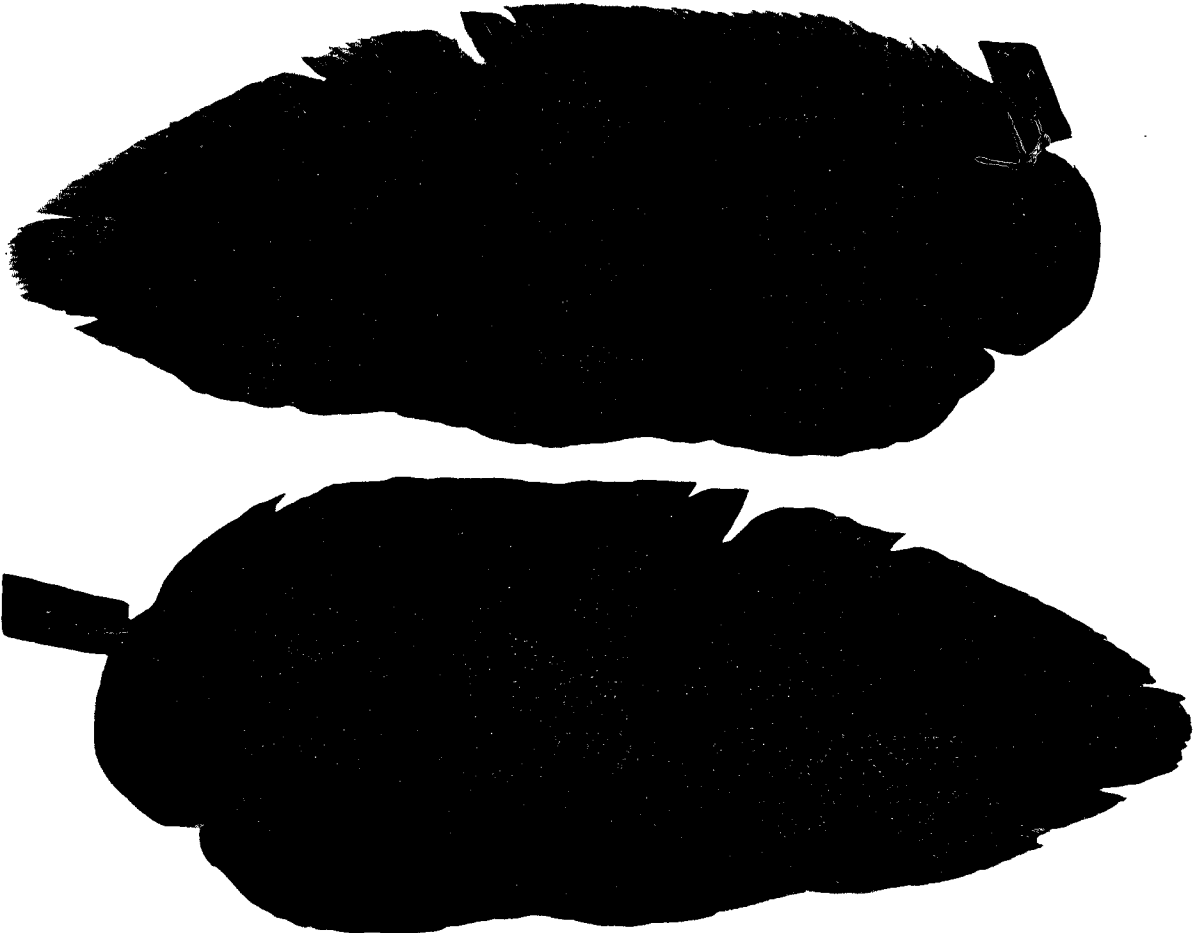


Figure 1.34. Photographs of *Zebrias scalaris*, AMS E1792, 155 mm SL, NSW, 18 km ESE Clarence River, depicting the ocular (above) and blind (below) sides.

**Synonym(s):** *Synaptura fasciata* Macleay, 1882

**Common name(s):** Many-banded sole; Many-band sole

**Material examined:** 34 specimens (55.05-208.52 mm TL)

**Type material:** Holotype, AMS I.16281-001, 1(151.98 mm SL), Port Jackson, New South Wales, Australia, 33°50'S, 151°15'E.

**Non-type material:** NMVA3244, 1(47.15 mm SL), Australia, Victoria, Eastern Bass Strait, 19 km east of Lake Tyers entrance, Victoria; CSIROMT1414-02, 1(95.57 mm SL), Tasmania, Great Oyster Bay; AMSI.25665-027, 3(98.8-120.63 mm SL), New South Wales, NE Yamba; QMI.29697, 1(108.25 mm SL), Point Lookout, Stradbroke Island, SE Queensland, Australia; NMVA2787, 1(112.05 mm SL), Australia, Queensland, off Moreton Is.; NMVA3751, 1(112.49 mm SL), Australia, Victoria, Bass Strait, southeast of Cape Woolamai; QMI.34246, 1(113.74 mm SL), Cape Moreton, SE Queensland, Australia; NMVA3750, 1(127.91 mm SL), Australia, Victoria, Bass Strait, off lake entrance, Victoria; NMVA1564, 1(130.82 mm SL), Australia, Tasmania, Eastern Bass Strait, 39 km NNE of Eddystone Point, Tasmania; CSIROH679-1, 1(138.31 mm SL), Tasmania, between Gutton Point (Robbins Island) and Three Hummocks; AMS I.123455-001, 1(138.98 mm SL), New South Wales, Botany Bay; AMSI.38420-004, 1(141.95 mm SL), New South Wales, Clarence River; AMSI.19392-005, 1(145.61 mm SL), New South Wales, Jervis Bay; AMSI.25894003, 2(147.38 mm - 151.11 mm SL), north of Yamba, New South Wales; AMSI.28514-001, 1(151.06 mm SL), ACT, Darling Rd., Jervis Bay; QMI.37459, 1(151.8 mm SL), East of South Strabroke Is., SE Queensland, Australia; QMI.9976, 1(152.33 mm SL), 4-5 miles east of Point Cartwright, SE Queensland, Australia; CSIROH3540-11, 1(153.12 mm SL), New South Wales, east of Bermagui; NMV A3203, 1(155.3 mm SL), Australia, Victoria, Bass Strait, 2 km south of Lake Tyers; AMSE1792, 1(155.36 mm SL), New South Wales, 18 km ESE Clarence

River; AMSI.16892-001, 1(157.62 mm SL), ACT, Jervis Bay, off Centre Bay;  
NMV54296, 1(161.17 mm SL), Australia, New South Wales, Port Jackson; AMSI.11244,  
1(162.2 mm SL), New South Wales, Richmond River: North Head N.10; AMSE2076,  
1(162.28 mm SL), New South Wales, 12 km from North Head, Richmond River;  
AMSE2075, 1(164.04 mm SL), New South Wales, 18 km north Cape Byron;  
CSIROT1910-1, 1(177.09 mm SL), Tasmania, off Babel Island (Furneaux Group);  
AMSI.3995, 1(182.62 mm SL), New South Wales, off Broken Head; CSIROCA467,  
1(185.85 mm SL), Victoria, SW of Cape Woolamai; CSIROT1711, 1(x-ray only),  
Tasmania, NE coast Flinders Island, 40°S 148°E; CSIROT1712, 1(x-ray only), Tasmania,  
NE coast Flinders Island, 40°S 148°E.

**Diagnosis:** A species of *Zebrias* with the following combination of characters: 17-23 narrow, indistinct, singular bands; ocular side deep brown; genital papilla situated at base of posteriormost ocular-side pelvic-fin ray; 16 caudal-fin rays; 76-93 lateral-line scales; median fins uniformly pigmented.

**Description:** Meristic and morphometric characters are indicated in Table 1.16. Small sole, attaining total length of 21 cm. Supracranial pterygiophores 4-5; formula: 1-1-(2-3). Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes separate, but close-set. Scales present in interorbital space. Ocular tentacles absent. Ocular-side anterior nasal tube reaching or slightly surpassing anterior margin of ventral eye when flattened. Base of anterior nasal tube considerably wider and more bulbous than aperture. Ocular-side

posterior nasal tube approximately half the length of anterior nasal tube. Blind-side anterior nostril a short, uneven tube; higher end of tube covering nasal aperture. Anterior nostril slightly dorso-anterior to dorsalmost point of mouth. Blind-side posterior nasal tube dorso-posterior to anterior tube at vertical through posterior margin of mouth; posterior nasal tube slightly larger than ocular-side counterpart. Posterior margin of ocular-side jaws extending as far as vertical through midpoint of ventral eye. Ocular-side lips smooth. Blind-side lower lip plicate. Teeth minute, restricted to blind-side jaws. Cirri restricted to opercular margin on ocular side. Cirri densely distributed at anterior end of blind-side head, extending along snout, chin and opercular margin.

Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line well developed on both sides. Supraorbital line present on ocular-side head. Lateral line not extending anterior to opercular margin on blind side. Lateral-line scales cycloid. Scales on body strongly ctenoid on both sides with 6-10 ctenii. Anterior end of dorsal fin at, or slightly anterior to, vertical at anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Dorsal- and anal-fin rays increasing in length toward posterior end of body; longest rays directly adjacent to caudal fin. Caudal fin rounded. Scales extending onto bases of median fins. Pectoral fins symmetrical, rudimentary (ocular-side fin length 4-14% HL, blind-side fin length 5-16% HL); dorsalmost ray longest, more ventral rays decreasing gradually in length. Pelvic fins of comparable length. Anus submedian on blind side. Genital papilla located at base of posteriormost ocular-side pelvic-fin ray; detached from ocular-side pelvic fin.

**Pigmentation of preserved specimens:** Ocular side deep brown with scarcely distinguishable transverse bands of a slightly darker hue. Bands narrow and unpaired: 17-23 across body. Bands relatively uniform in width across body, becoming narrower on head. Blind side uniformly whitish or beige; infrequently, minute, black spots present toward posterior end of body along median-fin margins. Interior of mouth white; minute, dark spots may be present on tongue or floor of mouth. Individual bands not discernible on dorsal and anal fins, which appear uniformly dark brown or black. Ocular-side caudal fin grey or brown. Ocular-side pectoral fin grey or dark brown. Blind-side pectoral fin transparent or mostly transparent with minute, black spots. Pelvic fins whitish.

Table 1.16. Meristic and morphometric characteristics of type and non-type specimens of *Zebrias scalaris*. Means and standard deviations are shown in parentheses. Measurements and abbreviations are described in Appendix B.

	<i>Zebrias scalaris</i> holotype	<i>Zebrias scalaris</i> non-type specimens (n=33)
<b>Standard length (mm)</b>	151.98	47.2-185.9 (139.1; 29.4) <sup>1</sup>
<b>Total length (mm)</b>	172.77	55.1-208.5 (158.1; 32.3) <sup>1</sup>
<b>Counts</b>		
Dorsal-fin rays	77	73-85 (79.2; 3.3)
Anal-fin rays	65	60-73 (65.9; 2.8)
Caudal-fin rays	16	14-18 (16; 0.6) <sup>1</sup>
Precaudal vertebrae	-	8-10 (9.0; 0.3)
Caudal vertebrae	-	34-37 (35.8; 0.7)
Total vertebrae	-	43-46 (44.9; 0.7)
Haemopophyses	-	5-6(5.2; 0.4)
Pterygiophores	-	4-6 (5.3; 0.6)
Pectoral-fin rays o.s.	-	4-8 (6.1; 0.9) <sup>2</sup>
Pectoral-fin rays b.s.	-	4-7 (6; 0.9) <sup>1</sup>
Pelvic-fin rays o.s.	4	4 (4;0) <sup>1</sup>
Pelvic-fin rays b.s.	4	4 (4;0) <sup>1</sup>
Lateral-line scales	86	76-93 (83.9; 3.8) <sup>1</sup>
Number of bands	-	17-23 (20.1; 1.8) <sup>2</sup>
<b>Measurements</b>		
<b>%SL</b>		
Head length	0.15	0.14-0.22 (0.16; 0.01) <sup>1</sup>
Head depth	0.22	0.16-0.25 (0.20; 0.02) <sup>1</sup>
Body depth	0.36	0.32-0.44 (0.37; 0.03) <sup>1</sup>
Caudal fin length	0.14	0.10-0.17 (0.13; 0.02) <sup>2</sup>
Width caudal peduncle	0.06	0.06-0.09 (0.070; 0.009) <sup>1</sup>
<b>%HL</b>		
Length of pectoral fin o.s.	-	0.04-0.14 (0.072; 0.02) <sup>1</sup>
Length of pectoral fin b.s.	-	0.05-0.16 (0.088; 0.03) <sup>1</sup>
Length of pelvic fin o.s.	0.37	0.28-0.46 (0.37; 0.04) <sup>1</sup>
Length of pelvic fin b.s.	0.32	0.27-0.44 (0.36; 0.04) <sup>1</sup>
Pre-orbital head length	0.17	0.16-0.28 (0.20; 0.03) <sup>1</sup>
Post-orbital head length	0.67	0.49-0.71 (0.59; 0.05) <sup>1</sup>
Snout length	0.22	0.20-0.33 (0.27; 0.03) <sup>1</sup>
Nostril to snouth distance	0.13	0.12-0.25 (0.19; 0.03) <sup>1</sup>
Mouth length o.s.	0.31	0.29-0.41 (0.33; 0.03) <sup>1</sup>
Mouth length b.s.	0.22	0.22-0.36 (0.29; 0.03) <sup>1</sup>
Ventral eye diameter	0.23	0.22-0.28 (0.24; 0.02) <sup>1</sup>
Width of orbits	0.28	0.28-0.45 (0.36; 0.04) <sup>1</sup>
Longest dorsal ray	0.68	0.48-0.81 (0.64; 0.08) <sup>1</sup>
Longest anal ray	0.75	0.46-0.76 (0.63; 0.07) <sup>1</sup>
IOD/V	0.29	0.13-0.60 (0.27; 0.1) <sup>1</sup>
BPc/OPc	-	0.83-2.70 (1.27; 0.4) <sup>1</sup>
BPv/OPv	0.87	0.82-1.13 (0.97; 0.07) <sup>1</sup>

<sup>1</sup>: n=31.

<sup>2</sup>: n=30.

<sup>3</sup>: Holotype devoid of pigmentation, pectoral fins absent, specimen in poor condition.

**Geographic distribution:** *Zebrias scalaris* is endemic to Australia and has been reported from the southeast coast (Victoria) up to the northeast coast (Queensland) at depths of 5-86 m.

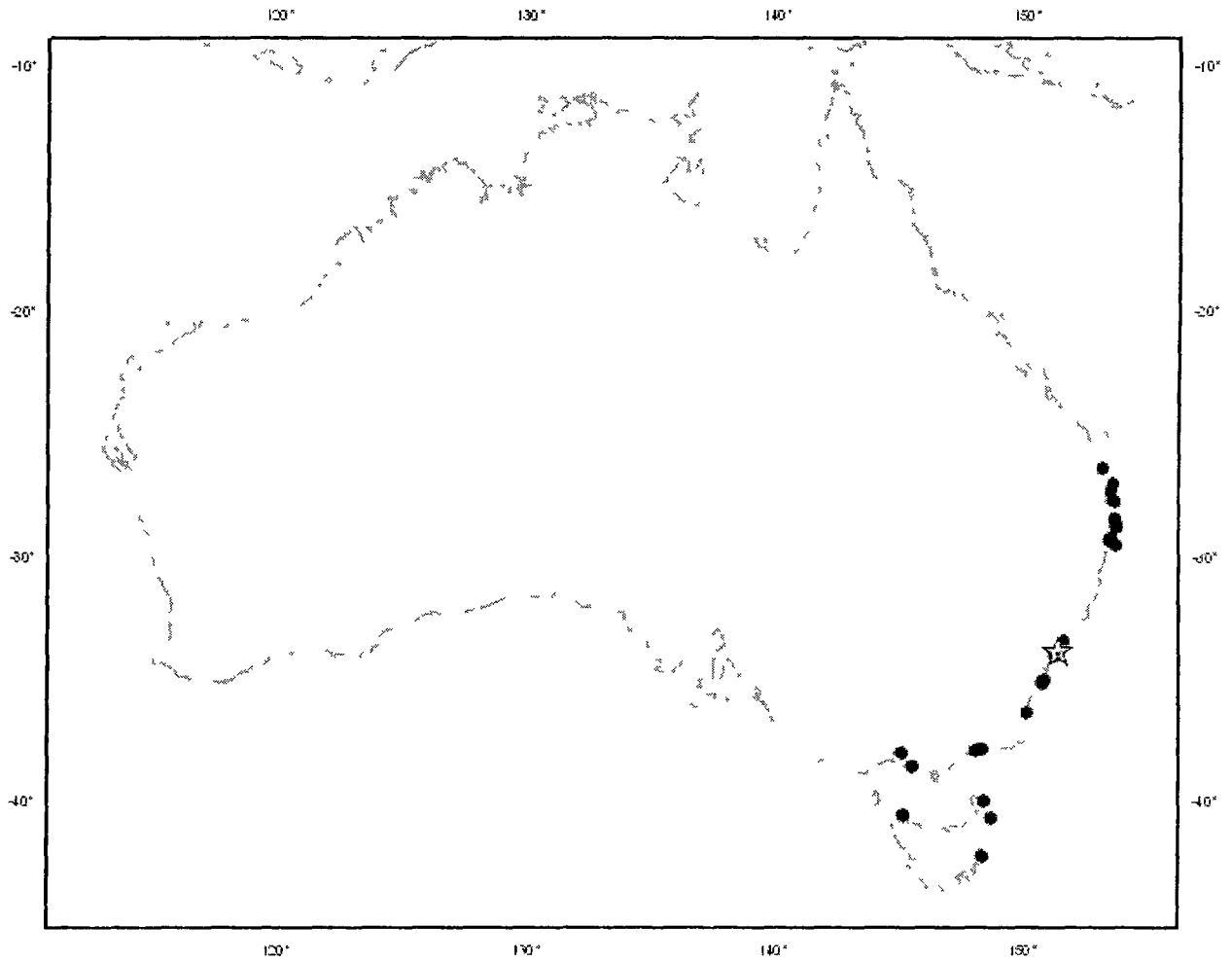


Figure 1.35. Geographic distribution of *Zebrias scalaris*. Star denotes locality of type material.

**Remarks:** *Z. scalaris* is a replacement name for *Synaptura fasciata* Macleay, 1882, which is secondarily preoccupied in *Zebrias* by *Solea fasciata* Basilewsky, 1855 (= *Z. zebra* Bloch, 1787).

**Comparisons:** With the exception of its most closely allied congener, *Zebrias penescalaris* Gomon, 1987, *Z. scalaris* can be distinguished from all species of *Zebrias* by its numerous, indistinct bands (17-23) and uniformly dark median fins. It can also be distinguished by the position of the genital papilla, located at the base of the posteriormost ocular-side pelvic-fin ray, although this character is shared by *Z. cancellatus* (McCulloch, 1916). *Z. penescalaris* differs from *Z. scalaris* in having fewer scales along the lateral line (67-77) and in general, a lighter brown pigmentation with less definition in the banding pattern. *Z. cancellatus* can be distinguished by its contiguous eyes and parabolic pigmentation pattern. *Z. quagga* (Kaup, 1858) and *Z. captivus* Randall, 1995 are easily distinguished by the presence of contiguous eyes bearing ocular tentacles. *Z. maculosus* Oommen, 1977 and *Z. annularis* (Fowler, 1934) differ in having irregular spots in place of bands. *Z. zebra* (Bloch, 1787) is distinguished by the presence of 24 broad, paired bands and 2-3 barbels on the blind-side chin and anterior end of the dorsal fin. *Z. altipinnis* (Alcock, 1890) differs in having 14-15 broad, singular bands, more pelvic-fin rays (5), more caudal-fin rays (18), more scales along the lateral line (100-113) and more pectoral-fin rays (9-12 ocular-side). *Z. craticula* (McCulloch, 1916) can be distinguished by the presence of 17-24 broad bands extending from the tip of the snout to the tip of the caudal fin.

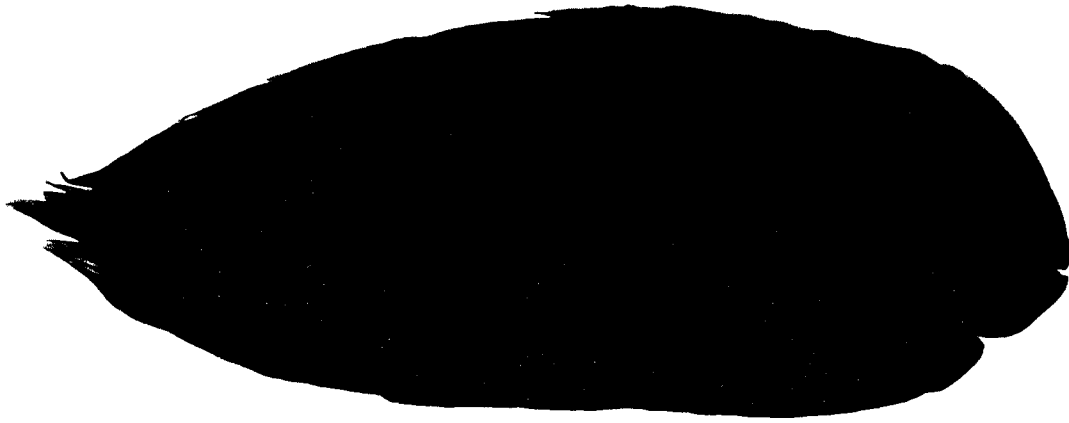


Figure 1.36. Photograph of *Zebrias scalaris*, holotype, AMS I.16281-001, 152 mm SL, Port Jackson, New South Wales, Australia, 33°50'S, 151°15'E.

*Zebrias zebra* (Bloch, 1787)

Figures 1.37-1.41, Tables 1.17-1.18

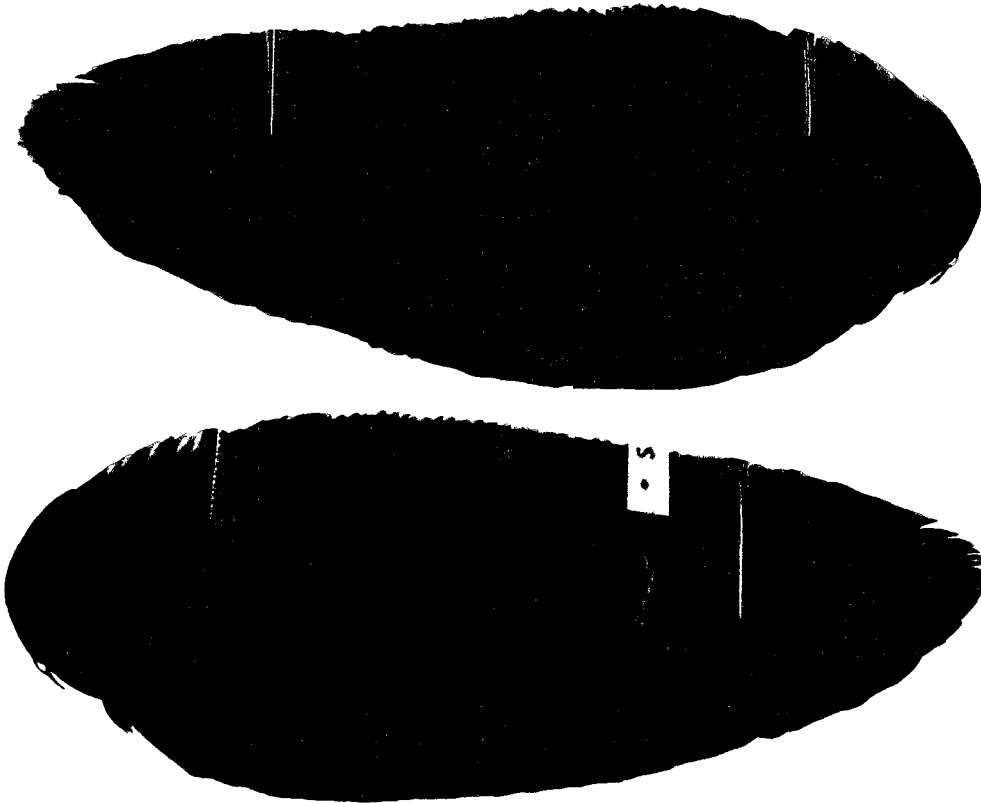


Figure 1.37. Photographs of *Zebrias zebra*, SU61077, 109 mm SL, Hong Kong, China, depicting the ocular (above) and blind (below) sides.

**Synonym(s):** *Pleuronectes zebra* Bloch, 1787; *Solea ommatura* Richardson, 1846; *Solea zebrina* Temminck and Schlegel, 1846; *Pleuronectes fasciatus* Gronow, 1854?; *Solea fasciata* Basilewsky, 1855.

**Common name(s):** Sea zebra (Bloch, 1787); Shima-ushinoshita (striped cow-tongue), Shimagarei (striped flounder) (Jordan and Starks, 1906); Tsurumaki, Tsurushita, Shimashita, Shimasetta (Jordan and Snyder, 1913); Lida, Lemper belang (Weber and Beaufort, 1929).

**Material examined:** 132 specimens (68.12-304.2 mm TL)

**Type material:** *Pleuronectes zebra*, lectotype, ZMB2423, 1(85.7 mm SL), Indian Ocean; *Pleuronectes zebra*, paralectotype, ZMB7406 1(dry, missing), unable to examine; *Solea zebrina*, lectotype, RMNH1308, 1(276.5 mm SL), Japan; *Solea zebrina*, paralectotype, RMNH1306, 1(166.1 mm SL), Japan; *Solea zebrina*, paralectotype, RMNH 1307, 1(245 mm SL), Japan; *Solea zebrina*, paralectotype, RMNH3580, 3(201.3 mm SL), Japan, note that two of these paralectotypes actually represent *Pseudaesopia japonica* (Bleeker, 1860); *Solea fasciata*, no type material is known; *Solea ommatura*, syntypes, Cambridge Philosophical Society, 2(whereabouts unknown), unable to examine.

**Non-type material:** AMNH15884, 1(91.36 mm SL), Java, Indonesia; AMNH89832, 2(87.07-158.57 mm SL), Taiwan; AMS B67, 1(161.59 mm SL), Tokyo; ANSP123573, 1(81.76 mm SL), Western Pacific, Kwangtung, China, Swabue; ANSP136725, 1(139.27 mm SL), China, Shangtung Province, Tsingtao; ANSP61637, 1(117.51 mm SL), Thailand, Bangkok, Siam; ANSP61638, 1(123.44 mm SL), Thailand; ANSP76702, 1(169.18 mm SL), China, Tai Po; ANSP87490, 1(162.47 mm SL), China, Aberdeen, Victoria; ANSP87491, 3(80.57-109.6 mm SL), China, Cheung Chan; ANSP89453, 1(133.63 mm SL), Thailand, Paknam, Siam; ASIZP0059577, 1(175.33 mm SL), Keelung Fish Market, Taiwan; CAS128192, 1(x-ray only, recorded as SU28192 on CAS website), Guangdong Province, China; CAS130709, 1(x-ray only, recorded as SU30709 on CAS website), Singapore; CAS130710, 1(x-ray only, recorded as SU30710 on CAS website), Indonesia, coast of Sumatra; CAS133912, 1(x-ray only, recorded as SU33912 on CAS website), Zhejiang, China; CAS201675, 10(x-ray only), Thailand, Chon Buri Province, CAS224632, 1(169.62 mm SL), Japan, off Heiza Ura, Awa Co., Chiba; CAS224633, 1(150.33 mm SL), Suruga Bay, Japan; CAS41710, 2(x-ray only), Indo-West Pacific, East China

Sea, CAS41711, 1(x-ray only), Sagami Bay, Japan, off Hayakawa; CAS879, 1(140.13 mm SL), Chefoo, China, NW and Central Pacific; FMNH55409, 1(266.57 mm SL), no location info available; FMNH76742, 1(119.29 mm SL), Sarawak, Telok Arang, Malaysia; FMNH89109, 1(193.09 mm SL), Sagami Sea, FMNH89253, 1(122.37 mm SL), Nagasaki, Japan, HUMZ135420, 1(264.01 mm SL), HUMZ101187, 1(179.57 mm SL), Hokkaido, Japan; HUMZ101822, 1(171.54 mm SL), Japan, Shizuoka Pref., Honshu; HUMZ107738, 1(107.61 mm SL), Taiwan; HUMZ107770, 1(126.64 mm SL), Taiwan; HUMZ108649, 1(186.63 mm SL), Pacific; HUMZ108905, 1(182.56 mm SL), Pacific; HUMZ108907, 1(166.33 mm SL), Pacific; HUMZ108909, 1(150.54 mm SL), Pacific; HUMZ108911, 1(170.56 mm SL), Pacific; HUMZ108912, 1(171.62 mm SL), Pacific; HUMZ108927, 1(148.88 mm SL), Pacific; HUMZ109652, 1(221.52 mm SL), Japan, Shizuoka Pref., Honshu; HUMZ109767, 1(165.23 mm SL), Japan, Niigata Pref., Honshu; HUMZ110403, 1(161.2 mm SL), Japan, Miyazaki Pref., Kyushu; HUMZ111044, 1(266.68 mm SL), Honshu, Shizuoka Pref., Japan; HUMZ111127, 1(62.41 mm SL), Shikoku, Kochi Pref., Japan; HUMZ135909, 1(144.87 mm SL), Japan, Yamagata Pref., Honshu; HUMZ33744, 1(206.44 mm SL), Japan; HUMZ43969, 1(164.57 mm SL), Japan, Yamagata Pref., Honshu; HUMZ44007, 1(191.35 mm SL), Japan, Yamagata Pref., Honshu; HUMZ53575, 1(153.18 mm SL), Japan, Ishikawa Pref., Honshu; HUMZ69552, 1(162.26 mm SL), Japan, Nagasaki Pref., Kyushu; HUMZ94849, 1(176.54 mm SL), Pacific; LACM43802-1, 1(173.06 mm SL), Sea of Japan, off Ishikawa, Kaga, Hashidate Harbor; LACM43803-1, 1(115.19 mm SL), Niigata, Japan, off Murakami; MNHN1941-212, 1(120.28 mm SL), China, Chantung, Tche-Fou; MNHN1941-213, 1(112.42 mm SL), China, Chantung, Tche-Fou; MNHN1941-214, 1(59.36 mm SL), China, Chantung, Tche-Fou; MNHN1976-387, 1(129.84 mm SL), Yokohama, Kanagawa, Japan; NMV46010, 1(147.19 mm SL), Indonesia, as

"East Indian Archipelago"; NMVA29628-001, 2(66.25-73.8 mm SL), No data, old collection; NSMT-P54001, 1(185.18 mm SL), Southern Japan, Honshu, Chiba Pref., Southern part of Boso Peninsula, Suno-Saki Point; NSMT-P54002, 1(211.62 mm SL), Southern Japan, Honshu, Chiba Pref., southern part of Boso Peninsula, Suno-Saki Point; NSMT-P54966, 2(194.78-198.41 mm SL), Southern Japan, Kyushu, Nagasaki Pref., Shimabara Peninsula, Tachibana Bay; NSMT-P54967, 1(237.29 mm SL), Kyushu, Nagasaki Pref., Japan; NSMT-P54968, 4(166.7-198.8 mm SL), Southern Japan, Honshu, Chiba Pref., southern part of Boso Peninsula, Suno-Saki Point; NSMT-P54969, 1(167.89 mm SL), East China Sea, Sector; NSMT-P63808, 1(147.23 mm SL), Japan, Kyushu, Nagasaki Pref., Tachibana Bay, Chijiwa, Southern Japan; SU30332, 1(79.18 mm SL), China, Kwangtung, Hainan Island, Hoihow (Hai-k'ou); SU32495, 3(169.9-197.18 mm SL), China, Zhejiang, Zhoushan Dao I., Dinhai; SU4615, 3(99.65-175.41 mm SL), Sea of Japan, Nazaki, off Sand Coast of Japan; SU61036, 1(139.56 mm SL), China, Hong Kong Spec Admin Reg., Shing Shi Mun, SU61077, 1(109.14 mm SL), China, Hong Kong, Urmston Roads; SU9972, 4(167.51-207.62 mm SL), Japan, Tokyo Wan (Tokyo Bay), Tokyo; UMMZ159650, 4(129.94-181.95 mm SL), Sea of Japan, close to Niigata (Niigata Market), Japan; UMMZ159652, 12(101.99-196.44 mm SL), Korea, near "Fusan" (=Pusan), at Pusan Market (no fishes shipped in from far away); UMMZ167371, 1(134.69 mm SL), China, Shantung, Chefoo (=Yantai); UMMZ225613, 3(132.93-160.01 mm SL), Thailand, Songkhla (probably Songkhla Lake); UMMZ243067, 1(177.11 mm SL), Java Sea, Indonesia; USNM0069092, 1(x-ray only), China, Hong Kong; USNM057485, 1(174.87 mm SL), Pacific Japan; USNM059762, 1(x-ray only), Japan; USNM072064, 1(x-ray only), Pacific Japan, Kagoshima Prefecture; USNM072082, 1(x-ray only), Pacific Japan, Tokyo Prefecture; USNM077141, 1(x-ray only), Japan; USNM077142, 1(x-ray only), Japan; USNM191154, 3(x-ray only), Pacific Taiwan.

**Diagnosis:** A species of *Zebrias* with the following combination of characters: Two to three barbels on blind-side chin and at anterior end of dorsal fin (Figure 1.39); completely confluent caudal fin, outline of dorsal, caudal and anal fins continuous; eyes separated by scaly interorbital space; 22-24 paired bands across body; 16 caudal-fin rays; 4 pelvic-fin rays; caudal fin with irregular spots arranged more or less in a circular pattern, or a U shape at base with irregular spots at distal end.

**Description:** Meristic and morphometric characters are presented in Table 1.17. Small sole, attaining a total length of 30 cm. Supracranial pterygiophores 3-5; formula: typically 1-1-2 (less frequently, 1-1-1 or 1-1-3). Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes separated; scales in interorbital space. Ocular tentacles absent. Ocular-side anterior nasal tube rarely extending beyond posterior nasal tube when flattened. Ocular-side posterior nasal tube approximately half the length of anterior tube. Blind-side anterior nostril a short, uneven tube; higher end covering nasal aperture. Anterior nostril slightly dorso-anterior to dorsalmost point of mouth. Blind-side posterior nasal tube dorso-posterior to anterior nasal tube at vertical through posterior edge of mouth and at posterior edge of dense patch of cirri on anterior region of head. Posterior nasal tube very short, of comparable length to ocular-side counterpart. Posterior margin of ocular-side jaws reaching vertical through anterior quarter to middle of ventral eye. Ocular-side lips smooth. Blind-side lower lip plicate. Teeth minute, restricted to blind-side jaws. Ocular-side cirri restricted to short fringe along opercular margin. Cirri densely distributed at anterior end of blind-side head, extending along snout, chin and opercular margin. Two to three elongate, thickened cirri, or barbels, on blind-side chin and near anterior end of dorsal fin. More sparsely

distributed cirri may be present on mid-head region between scales posterior to dense patch of cirri on anterior region, not extending posterior to opercular margin. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line extending horizontally from opercular margin to caudal peduncle on both sides. Supraorbital line present on ocular-side head. Patches of cirri may be associated with lateral line on blind side. Lateral-line scales cycloid. Scales on body strongly ctenoid on blind and ocular sides with 6-14 ctenii. Anterior end of dorsal fin at, or slightly anterior to, vertical at anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Vertical-fin rays increasing in length toward posterior end of body; longest rays directly adjacent to caudal fin. Caudal fin rounded. Length of posteriormost anal-fin ray 71-95% ( $\bar{x} = 83\%$ ,  $SD = 0.07$ ) relative to length of caudal fin. Caudal-fin rays typically 16 (100/123 specimens). Scales extending onto median fins. Ocular-side pectoral fin with upper 2-4 rays elongate, more ventral rays decreasing gradually in length; pectoral-fin length somewhat variable. Blind-side pectoral fin rudimentary, dorsalmost ray longest; more ventral rays decreasing gradually in length. Scales on base of ocular-side pectoral fin; absent from blind-side counterpart. Ocular-side pelvic fin typically slightly longer than blind-side fin. Anus submedian on blind side. Genital papilla submedian on ocular side; attached to ocular-side pelvic fin by thin membrane.

**Pigmentation of preserved specimens:** Ocular side light to deep brown with series of 22-24 darker brown bands in pairs. Bands relatively uniform in width across body, narrowing considerably on head. Blind side uniformly pale, whitish; minute, dark spots may be present toward posterior end of body along median-fin margins. Interior of mouth uniformly whitish, or pale with minute, dark spots. Bands extending onto dorsal and anal fins, becoming darker.

Ocular-side caudal fin dark brown or black with light spots arranged more or less in a circular pattern; alternative pattern consists of a “U” shape at base of caudal fin with light spots toward distal end. Ocular-side pectoral fin dark brown or black. Blind-side pectoral fin transparent or mostly transparent with minute, dark spots. Pelvic fins whitish.

Table 1.17. Meristic and morphometric characteristics of type and non-type specimens of *Zebrias zebra*. Means and standard deviations are shown in parentheses. Data for *Solea ommatura* were obtained from the original species description (Richardson, 1846). Measurements and abbreviations are described in Appendix B.

	<i>Pleuronectes zebra</i> lectotype (n=1)	<i>Solea ommatura</i> syntypes (n=2)	<i>Solea zebrina</i> lectotype and paralectotypes (n=4)	<i>Zebrias zebra</i> non-type specimens (n=123)
<b>Standard length (mm)</b>	85.7	-	166.1-276.5(222.2; 48.5)	59.36-266.68 (152.8; 42.6) <sup>4</sup>
<b>Total length (mm)</b>	95.4	-	183.7-304.2(249.9; 52.9)	68.12-303.72 (175.2; 48.7) <sup>4</sup>
<b>Counts</b>				
Dorsal-fin rays	80	70	75-78 (77; 1.7) <sup>1</sup>	67-97 (81.4; 7.3)
Anal-fin rays	-	60	63-71 (66.7; 4.0) <sup>1</sup>	57-86 (68.8; 6.9)
Caudal-fin rays	16	-	16 (16; 0) <sup>1</sup>	14-18 (16.0; 0.7) <sup>7</sup>
Precaudal vertebrae	9	-	9 <sup>2</sup>	7-10 (9.0; 0.4)
Caudal vertebrae	40	-	-	32-44 (39.0; 2.9)
Total vertebrae	49	-	-	41-53 (47.9; 2.9)
Haemopophyses	5	-	5 <sup>2</sup>	4-6 (5.1; 0.3)
Pterygiophores	6	-	5 <sup>2</sup>	4-8 (5.5; 0.7)
Pectoral-fin rays o.s.	8	11	9 <sup>2</sup>	5-10 (8.2; 1.1) <sup>6</sup>
Pectoral-fin rays b.s.	8	11	9 (9; 0) <sup>3</sup>	5-11 (8.8; 1.0) <sup>6</sup>
Pelvic-fin rays o.s.	-	3	4 (4; 0) <sup>3</sup>	3-5 (4.0; 0.2) <sup>5</sup>
Pelvic-fin rays b.s.	-	4	4 (4; 0) <sup>1</sup>	3-5 (4.0; 0.2) <sup>6</sup>
Lateral-line scales	108	-	96-104 (101; 3.8)	90-133 (107.4; 9.5) <sup>5</sup>
Number of bands	-	23	21-22 <sup>3</sup>	19-25 (23.2; 0.8) <sup>5</sup>
<b>Measurements</b>				
<b>%SL</b>				
Head length	0.18	-	0.15-0.17 (0.15; 0.01)	0.14-0.22 (0.17; 0.01) <sup>4</sup>
Head depth	0.17	-	0.14-0.18 (0.16; 0.02)	0.16-0.24 (0.19; 0.01) <sup>6</sup>
Body depth	0.26	-	0.30-0.38 (0.34; 0.04)	0.29-0.43 (0.36; 0.03) <sup>6</sup>
Caudal fin length	0.11	-	0.10-0.16 (0.13; 0.03)	0.10-0.20 (0.15; 0.02) <sup>6</sup>
Width caudal peduncle	0.07	-	0.05-0.06 (0.06; 0.007)	0.04-0.12 (0.06; 0.01) <sup>6</sup>
<b>%HL</b>				
Length of pectoral fin o.s.	0.55	-	0.55-0.71 (0.65; 0.08)	0.14-0.82 (0.52; 0.1) <sup>5</sup>
Length of pectoral fin b.s.	0.16	-	0.15-0.16 (0.16; 0.008) <sup>3</sup>	0.09-0.29 (0.19; 0.03) <sup>6</sup>
Length of pelvic fin o.s.	-	-	0.23-0.29 (0.26; 0.04) <sup>3</sup>	0.18-0.40 (0.30; 0.04) <sup>5</sup>
Length of pelvic fin b.s.	-	-	0.20-0.24 (0.22; 0.03) <sup>3</sup>	0.18-0.41 (0.28; 0.04) <sup>6</sup>
Pre-orbital head length	-	-	0.13-0.25 (0.19; 0.06) <sup>1</sup>	0.10-0.29 (0.21; 0.03) <sup>6</sup>
Post-orbital head length	0.68	-	0.61-0.68 (0.63; 0.03)	0.43-0.74 (0.63; 0.05) <sup>6</sup>
Snout length	0.25	-	0.22-0.27 (0.23; 0.02)	0.17-0.48 (0.27; 0.04) <sup>6</sup>
Nostril to snouth distance	-	-	0.14-0.19 (0.16; 0.03) <sup>1</sup>	0.07-0.41 (0.19; 0.04) <sup>6</sup>
Mouth length o.s.	0.27	-	0.21-0.29 (0.25; 0.04)	0.24-0.50 (0.31; 0.03) <sup>6</sup>
Mouth length b.s.	0.23	-	0.21-0.28 (0.23; 0.03)	0.14-0.48 (0.26; 0.04) <sup>6</sup>
Ventral eye diameter	0.18	-	0.14-0.17 (0.15; 0.01)	0.13-0.40 (0.19; 0.03) <sup>6</sup>
Width of orbits	0.24	-	0.16-0.20 (0.18; 0.02)	0.18-0.38 (0.27; 0.05) <sup>6</sup>
Longest dorsal ray	-	-	0.71-0.87 (0.80; 0.07)	0.36-0.97 (0.74; 0.1) <sup>5</sup>
Longest anal ray	0.56	-	0.78-0.82 (0.79; 0.02)	0.37-1.03 (0.74; 0.1) <sup>5</sup>
IOD/V	0.24	-	0.08-0.12 (0.10; 0.02)	0.10-0.78 (0.33; 0.1) <sup>6</sup>
BPc/OPc	0.3	-	0.21-0.23 (0.22; 0.01) <sup>3</sup>	0.19-1.12 (0.40; 0.1) <sup>5</sup>
BPv/OPv	-	-	0.84-0.87 (0.85; 0.02) <sup>3</sup>	0.65-1.28 (0.95; 0.1) <sup>5</sup>

<sup>1</sup>: n=3; <sup>2</sup>: n=1; <sup>3</sup>: n=2; <sup>4</sup>: n=101; <sup>5</sup>: n=99; <sup>6</sup>: n=100; <sup>7</sup>: n=120.

**Geographic distribution:** *Z. zebra* has been reported from Indonesia, southeast Asia, and northward to Japan, including Java (Weber and Beaufort, 1929), the Gulf of Thailand (Shen, 1967), Sulawesi (Kottelat et al., 1993), Malaysia (Cantor, 1849), Taiwan (Jordan and Evermann, 1902; Chen and Weng, 1965; Shen, 1993), China (Gunther, 1862; Jordan and Snyder, 1901b; Wang et al., 2001; Cheng and Zhou, 1997), and Japan (Jordan and Snyder, 1901b; Ochiai, 1963). The species has also been reported from the Bay of Bengal (Cantor, 1849) and south Orissa, India (Mishra et al., 1999), but this is likely an error. Reported from depths of 20-57 m.

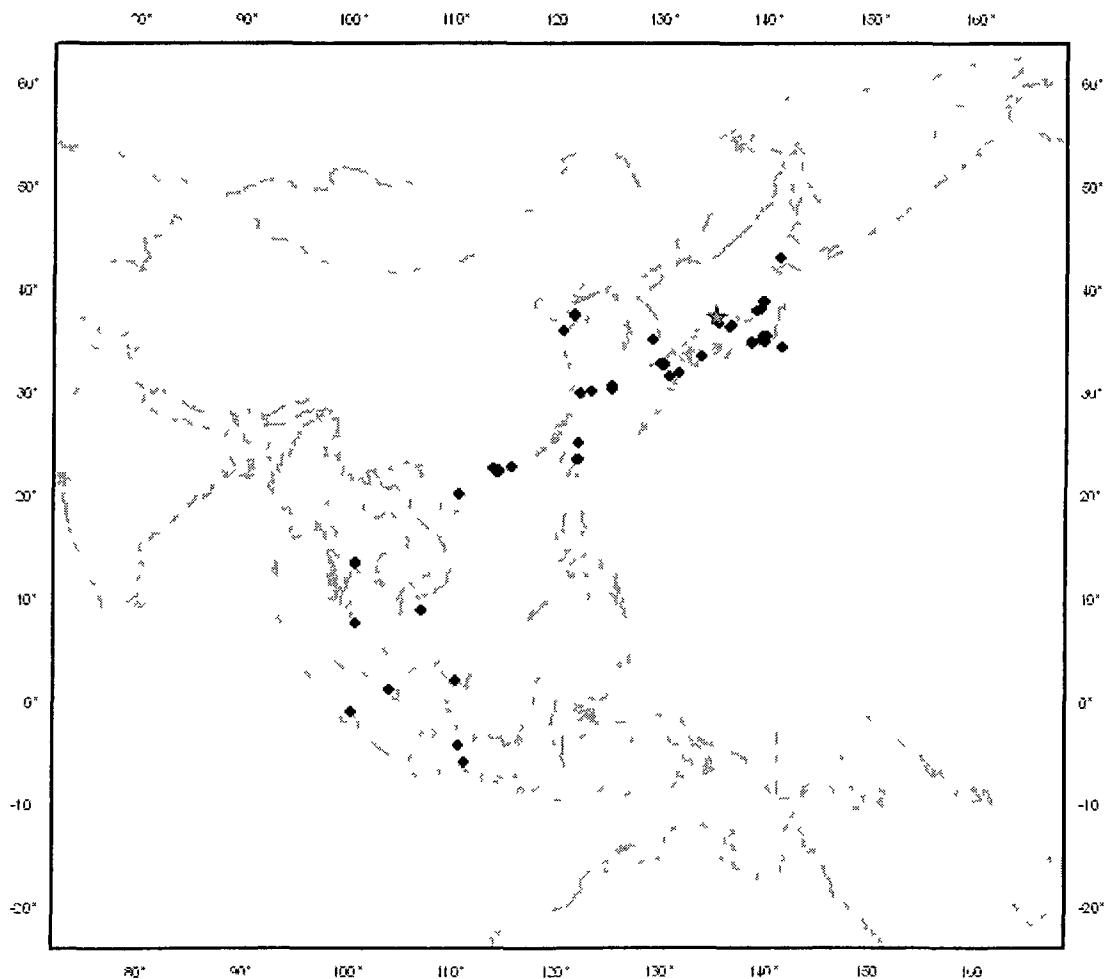


Figure 1.38. Geographic distribution of *Zebrias zebra*. Star denotes locality of type material.

The lectotype of *Pleuronectes zebra* is not represented as the locality, listed as “Indian Ocean”, was imprecise and possibly incorrect (see Remarks).

**Remarks:** As previously mentioned in the introduction, there has been a great deal of confusion surrounding the species complex comprised of *Zebrias zebra*, *Zebrias fasciatus* (Basilewsky, 1855), and *Zebrias zebrinus* (Temminck and Schlegel, 1847) and there does not appear to be a consensus about the validity of these species. When the genus *Zebrias* was first established, Jordan and Snyder (1900) designated *Z. zebrinus* as the type species. Soon after, the same authors synonymised *Z. zebrinus* with *Z. zebra*, stating that it was not evidently different from the Chinese form (Jordan and Snyder, 1901b). Jordan and Evermann (1902) identified a specimen of Bloch's *Z. zebra* from Taiwan; however, this specimen, corresponding to Gunther's (1862) description, was lost following an earthquake in 1923 (Oshima, 1927). Jordan and Starks (1906) later amended their initial identification of this specimen and stated that because it was found in Taiwanese waters, it could not correspond to Bloch's species. They identified the specimen as *Z. zebrinus*, in addition to Jordan and Snyder's *Z. zebra* from Yakohama, Japan (Jordan and Snyder, 1901b). Moreover, they proposed that the genus name, *Zebrias*, be replaced by *Aesopia*, as they were of the opinion that Bloch's *Pleuronectes zebra* was actually *Zebrias quagga* Kaup, 1858. Bloch's fish, having no ocular tentacles, separated eyes with a scaly interorbital space (*Z. quagga* has contiguous eyes each bearing an ocular tentacle), 49 vertebrae (38-44 for *Z. quagga*), 16 caudal fin rays (18 for *Z. quagga*), and 80 dorsal-fin rays (64-77 for *Z. quagga*) is not *Z. quagga*.

In their catalogue of fishes of Japan, Jordan, Tanaka and Snyder (1913) recognize only *Z. zebrinus*, whereas in Hubbs' "Flounders and Soles from Japan" (1915), both *Z. zebrinus* and *Z. zebra* are recognized; however, Hubbs describes *Z. zebra* as an East Indian species, closely allied to *Pseudaesopia japonica* (Bleeker, 1860) with a caudal fin that is not closely united to the dorsal and anal fins, and which has 18 caudal fin rays, both of which do not appear to correspond

to the lectotype of *Z. zebra*. Shen (1993) is of the opinion that the fish to which Hubbs refers actually corresponds to *Zebrias crossolepis* Zheng and Chang, 1965 (= *Pseudaesopia synapturoides* (Jenkins, 1910)).

Jordan and Hubbs (1925) recognize *Z. zebrinus* from Japan and synonymise *Z. fasciatus* with it. Weber and Beaufort (1929) recognize *Z. zebra* from the Indo-Australian Archipelago and synonymize Temminck and Schlegel's *Z. zebrinus* with it. Chabanaud (1930a) identifies *Solea zebrina* as a composite species, with five of the six types being synonymous with Bloch's *Zebrias zebra* and one being synonymous with *Pseudaesopia japonica* and in his revision of the genus *Zebrias*, Chabanaud (1934) only recognizes Bloch's fish. The present study found that two of the ethanol-preserved *Solea zebrina* paralectotypes actually correspond to *Pseudaesopia japonica* (RMNH3580). Boeseman (1947), who designated the lectotype for Temminck and Schlegel's species claimed the type material of *Solea zebrina* doubtless belongs to Bloch's "*Synaptura zebra*" and represents the type material of *Solea zebrina*. Matsubara (1955) and Ochiai (1963) consider *Zebrias zebrinus* to be a synonym of *Z. zebra* (Bloch), while Cheng and Weng (1965) recognize *Z. zebra* from the waters of Taiwan. Kottelat et al. (1993) and Cheng and Zhou (1997) also recognize Bloch's fish, *Zebrias zebra*, as valid, but make no synonymizations. Nakabo (2002) argues that *Z. zebrinus* differs from *Z. zebra* in body depth and body markings and should be regarded as a distinct species.

Compounding the confusion created by the conflicting opinions on the validity of these species in the literature is the nature of the original descriptions and type material itself. The type material for *Z. fasciatus* and *Solea ommatura* (Richardson, 1846) is missing. The type material for *Zebrias zebra* is in an extremely poor state, and that for *Z. zebrinus* is actually a combination of two species. The original description of *Z. zebra* is riddled with inaccuracies, as

described in the introduction, while the description for *Z. fasciatus* is entirely devoid of meristics and diagnostic characters. Bloch's description of *Z. zebra* is written in German, although Lacepède (1798) did provide a French translation of the key points from Bloch's paper.

The type material for Richardson's (1846) *Solea ommatura* was destroyed (Whitehead, 1970) but an illustration of the fish is provided by Gray (1851). Both the meristics reported in the original description and the illustration are consistent with *Zebrias zebra*. Thus, *Solea ommatura* is a synonym of *Zebrias zebra*.

An examination of the type material for both *Z. zebrinus* and *Z. zebra* reveals comparable meristics, as shown in Table 1.17. Temminck and Schlegel (1846) refer to a collection of banded soles from Java and distinguish them from Bloch's fish by their dorsal fin, said to commence in front of the eyes, and their greater body depth. As previously mentioned, Bloch's illustration is riddled with inaccuracies, including the insertion point of the dorsal fin. The body depth of his fish is narrower than any of the other specimens examined over the course of this study (Table 1.17), likely as a result of contraction due to preservation in alcohol. Temminck and Schlegel (1846) compare their collection from Java to their collection of soles from Japan, which they differentiate from the Java collection as having a larger body and longer pectoral fin. In the present study, specimens from Southeastern Asia (Thailand, Malaysia, Singapore, Indonesia) are compared to specimens from Eastern Asia (China, Taiwan, South Korea, North Korea, Japan) in Table 1.18. Meristics and morphometrics for both groups were found to be comparable, although the ranges of vertebral counts, dorsal-fin ray counts, ocular-side pectoral fin length and body depth among the fish from Eastern Asia do exceed those from Southeastern Asia. Given that the variation present in Southeast Asia is also found within Eastern Asia, the current data set does not support any distinction between these populations. It should be noted

that with only ten specimens from Southeastern Asia (x-ray data available for 22 specimens), the full range of meristics in this region may not be represented and thus an accurate comparison to the specimens from further north may not be possible. An examination of additional specimens from Southeastern Asia will provide a more comprehensive data set and accordingly, a more accurate interpretation of the data.

Jordan and Metz (1913), Oshima (1927), Matsubara (1955), Ochiai (1963), and Nakabo (2002) all recognize Basilewsky's (1855) species *Z. fasciatus* as valid. Jordan and Metz (1913) recognize this species from Korea and contend that it is indistinguishable from *Z. zebrinus*, the two being geminate species, the northern form being *Z. fasciatus* (from Korea), the southern form being *Z. zebrinus* (from Southern Japan and China). The authors state that *Z. fasciatus* has a higher number of fin rays, but do not provide a range for either *Z. fasciatus* or *Z. zebrinus*. The reported number of dorsal- and caudal-fin rays is comparable to that of the type material for *Z. zebra*. Oshima's description of *Z. fasciatus*, based on two specimens, agrees closely with *Z. zebra*. Both Matsubara and Ochiai record 107-123 lateral line scales and 51-52 vertebrae for *Z. fasciatus*, which is higher than the corresponding values observed for the type material of *Z. zebra* and *Z. zebrinus* in the present study, but falls within the range of the non-type specimens examined. Both Nakabo (2002) and Ochiai (1963) provide illustrations of *Z. fasciatus* and either *Z. zebra* or *Z. zebrinus*. In both cases, *Z. fasciatus* is depicted as having a shorter ocular-side pectoral fin, bands that appear to be splitting down their centers, and a caudal fin pattern that consists of a U shape at the base and spots at the distal end. In the present study, these splitting bands were observed in specimens having a large range of vertebral counts (41-52); in the majority of specimens having 51-53 vertebrae (16/18 specimens), broad, intact bands similar to those exhibited by the type material for *Z. zebrinus* were observed. The caudal fin pattern

depicted for *Z. fasciatus* in Nakabo's paper was observed in specimens having a vertebral count of 41-52. The pectoral fin length also varied among specimens of all vertebral counts.

Moreover, a clear bimodal distribution of vertebral counts, as reported by Ochiai (1963) and Nakabo (2002), was not observed (Table 1.2), making a clear separation difficult. A large, continuous range of values was also observed for ocular-side pectoral fin length (Figure 1.41), lateral-line scale counts (Table 1.6), and dorsal-fin ray counts (Table 1.5).

Several characters were found to be variable within this species, although no consistent combination of these characters was observed over the course of the present study. These characters include caudal fin pigmentation, the length of the ocular-side pectoral fin, band morphology, as well as a wide range of meristic values (vertebrae, vertical-fin rays, lateral-line scales). The large amount of variation present among the specimens observed suggests there might actually be more than one species present. In the absence of a consistent combination of these variable characters or a more evident division in the large range of meristics, any separation of this species would be arbitrary.

**Comparisons:** *Zebrias zebra* can be distinguished from all of its congeners by the barbels present on its chin and at the anterior end of the dorsal fin on the blind side. In addition, it can be easily differentiated from *Z. captivus* Randall, 1995 and *Z. quagga* (Kaup, 1858) by its separate eyes devoid of ocular tentacles and scaly interorbital space. *Z. scalaris* Gomon, 1987 and *Z. penescalaris* Gomon, 1987 differ from *Z. zebra* in having narrower, somewhat indistinct, singular bands, in addition to fewer lateral-line scales (67-93). *Z. cancellatus* (McCulloch, 1916) is easily distinguished from *Z. zebra* by its unique pigmentation consisting of dark parabolic shapes, contiguous eyes, singular bands, and rudimentary pectoral fins (10-19% HL). *Z.*

*annularis* (Fowler, 1934) and *Z. maculosus* (Oommen, 1977) are clearly distinct from *Z. zebra* in having irregular spots in place of bands. *Z. craticula* (McCulloch, 1916) is distinguished by its greyish pigmentation, singular bands that continue onto the caudal fin, contiguous eyes, and generally fewer scales along the lateral line (77-94). *Z. altipinnis* (Alcock, 1890) differs in having fewer, broad, singular bands (14-15), a generally higher number of pectoral-fin rays (9-12), none of which are elongate (average ocular-side pectoral fin length 18% HL), more pelvic-fin rays (5), and more caudal-fin rays (18).

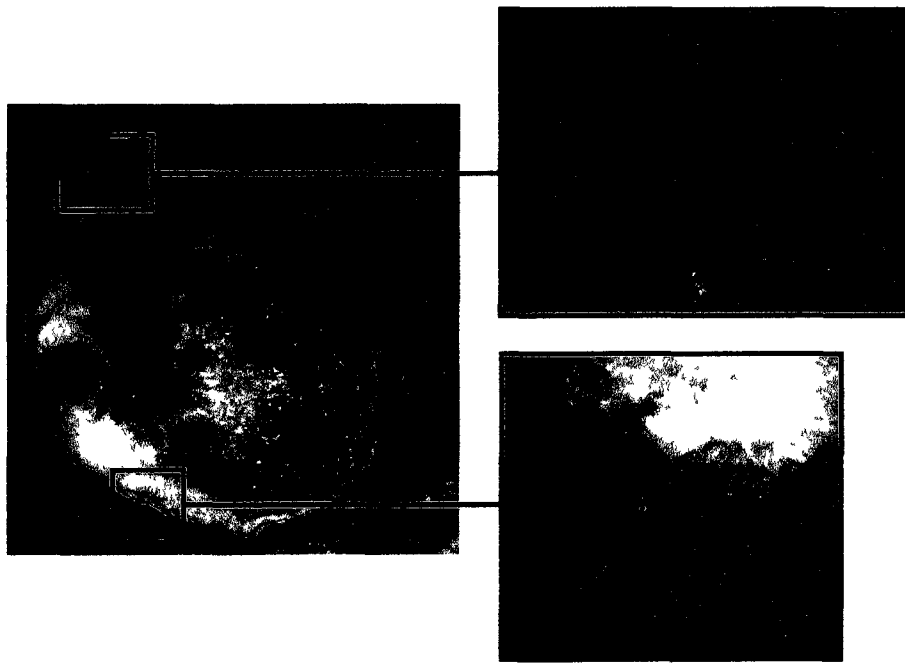


Figure 1.39. Photographs of *Zebrias zebra* showing the barbels around the anterior end of the dorsal fin and on the blind side of the chin, a character that is diagnostic of the species; CAS224633, 150 mm SL, Suruga Bay, Japan.

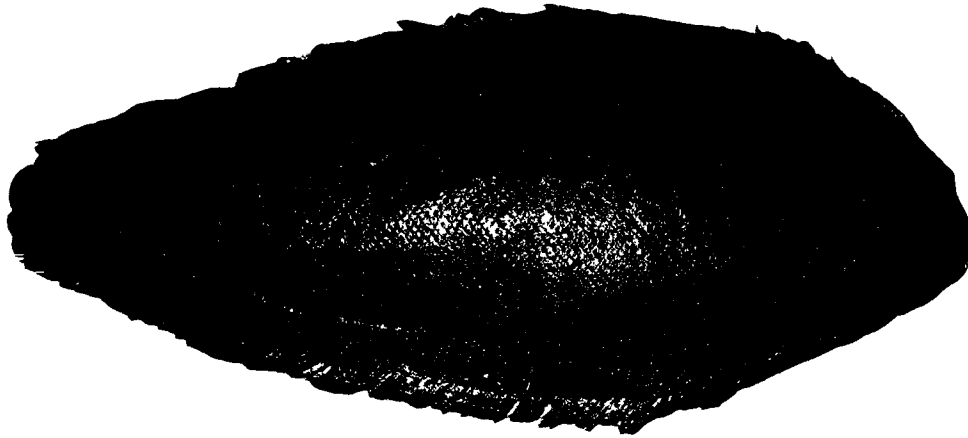


Figure 1.40. Photograph of *Solea zebrina*, lectotype, RMNH1308, 277 mm SL, Japan.

Table 1.18. Table comparing the meristics and morphometrics of *Zebrias zebra* (Bloch, 1787) specimens found in Southeastern Asia (Thailand, Malaysia, Singapore, Indonesia) to those from Eastern Asia (China, Taiwan, North Korea, South Korea, Japan). These values are also compared to the lectotype of *Z. zebra*. Note that the singular fish having 41 vertebrae has several vertebral abnormalities.

Meristics	Locality		<i>Z. zebra</i> lectotype (ZMB2423)
	Southeastern Asia n=22	Eastern Asia n=104	n=1
Dorsal-fin rays	70-81 (76; 2.8)	67-97 (82; 7.3)	80
Caudal-fin rays	15-16 (15.8; 0.4)	14-18 (16.0; 0.7) <sup>6</sup>	16
Vertebrae	41-47 (44.8; 1.3)	42-53 (49; 2.7) <sup>7</sup>	49
Lateral-line scales	96-120 (107.9; 6.9) <sup>1</sup>	90-133 (107.0; 9.7) <sup>4</sup>	108
Pectoral-fin rays o.s.	6-9 (7.5; 1.2) <sup>1</sup>	5-10 (8.3; 1.1) <sup>4</sup>	8
Pelvic-fin rays o.s.	4 (4; 0) <sup>1</sup>	3-5 (4; 0.2) <sup>5</sup>	damaged
Body depth (%SL)	0.30-0.38 (0.34; 0.03) <sup>2</sup>	0.29-0.43 (0.36; 0.03) <sup>5</sup>	0.26
Head length (%SL)	0.16-0.21 (0.18; 0.01) <sup>1</sup>	0.14-0.22 (0.17; 0.01) <sup>5</sup>	0.18
Pectoral fin length o.s. (%SL)	0.33-0.59 (0.44; 0.08) <sup>2</sup>	0.14-0.82 (0.54; 0.13) <sup>3</sup>	0.55

<sup>1</sup>: n=10; <sup>2</sup>: n=9; <sup>3</sup>: n=93; <sup>4</sup>: n=94; <sup>5</sup>: n=95; <sup>6</sup>: n=101; <sup>7</sup>: n=102.

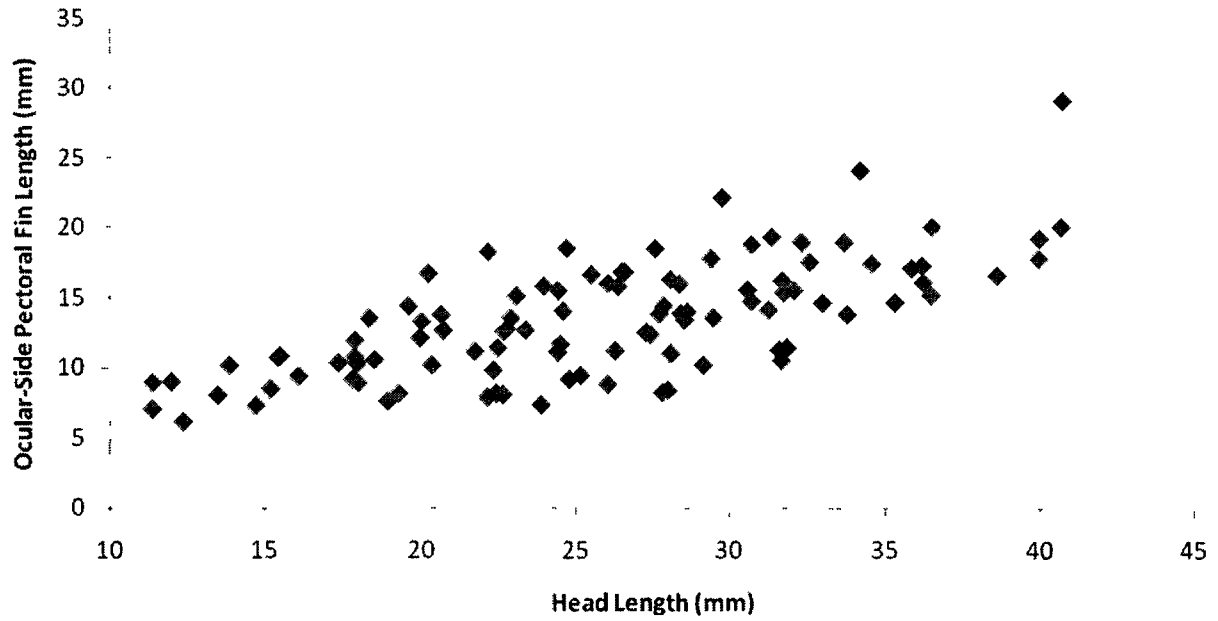


Figure 1.41. Graph depicting the relationship between the head length (mm) and ocular-side pectoral fin length (mm) among specimens of *Zebrias zebra* (Bloch, 1787). N=102.

## KEY TO SPECIES OF *ZEBRIAS*

- 1      Ocular side with large, irregular spots..... 2
- Ocular side with dark, transverse bands..... 3
- 2      71-74 dorsal-fin rays; 55-60 anal-fin rays; 93-100 lateral-line scales;  
head length 17-18% SL.....*Z. annularis* p. 59
- 58-66 dorsal-fin rays; 50-54 anal-fin rays; 120-135 lateral-line scales;  
head length 26-27% SL.....*Z. maculosus* p. 95
- 3      Eyes contiguous; interorbital scales absent..... 4
- Eyes separate; interorbital scales present..... 7
- 4      Ocular tentacle present on one or both eyes (Figure 1.21); ocular-side  
pectoral fin 27-37% HL (average); second ray from dorsal end of ocular-  
side pectoral fin the longest..... 5
- Ocular tentacles absent; ocular-side pectoral fin 15-24% HL (average);  
uppermost ray of ocular-side pectoral fin the longest..... 6
- 5      76-104 lateral-line scales; 12 bands that are singular, paired or a  
combination of the two; bands wider than inter-band spaces; 38-44  
vertebrae; 64-88 dorsal-fin rays; 52-64 anal-fin rays.....*Z. quagga* p. 110
- 74-75 lateral-line scales; 13 singular bands; bands of comparable width  
to adjacent inter-band spaces; 38-39 vertebrae; 63-66 dorsal-fin rays;  
51-54 anal-fin rays.....*Z. captivus* p. 77

- 6 17-24 dark grey, singular bands extending from snout to tip of caudal fin; lighter, indistinct bands present between darker bands; 41-43 vertebrae; 77-94 scales along the lateral line; ocular-side pectoral fin length 24% HL (average).....*Z. craticula* p. 85
- 11-20 singular bands extending from snout to base of caudal fin; dark blotches arranged along bands posterior to the operculum to form 2-3 parabolic shapes (Figure 1.16); 45-49 vertebrae; 105-129 scales along the lateral line; ocular-side pectoral fin length 15% HL (average); distal end of median fins thinly outlined with black and white.....*Z. cancellatus* p. 68
- 7 Bands narrow, indistinct; median fins uniformly dark; 67-93 scales along the lateral line; ocular-side pectoral fin length 7% HL (average); ocular-side anterior nasal tube reaches or surpasses anterior margin of ventral eye when flattened; genital papilla situated at base of posteriormost ocular-side pelvic-fin ray..... 8
- Bands broad, distinct; bands extend onto dorsal and anal fins where they become darker; 90-133 scales along the lateral line; ocular-side pectoral fin length 18-53% HL (average); ocular-side anterior nasal tube does not extend beyond posterior nasal tube when flattened; genital papilla situated submedian to anus on ocular side..... 9
- 8 76-93 scales along the lateral line; deep brown body.....*Z. scalaris* p. 122
- 67-77 scales along the lateral line; light brown body.....*Z. penescalaris* p. 100

- 9 Presence of 2-3 barbels on blind-side chin and around anterior end of dorsal fin (Figure 1.39); ocular-side pectoral fin length 52% (average); ocular-side mouth reaches midpoint of ventral eye, average length 31% HL; ocular-side anterior nasal tube reaches posterior nostril when flattened; 22-24 paired bands; 4 pelvic-fin rays; 5-10 ocular-side pectoral-fin rays; caudal fin dark with light spots, arranged more or less in a circle or randomly with a "U" shape at base; genital papilla attached to ocular-side pelvic fin; 16 caudal-fin rays; supracranial pattern 1-1-2-.....*Z. zebra* p. 131
- Absence of barbels (Figure 1.39); ocular-side pectoral fin length 18% HL (average); ocular-side mouth extends close to posterior margin of ventral eye, average length 37% HL; ocular-side anterior nasal tube does not reach posterior nostril when flattened; 14-15 singular bands; 5 pelvic-fin rays; 9-12 ocular-side pectoral-fin rays; caudal fin dark with two pale spots at its base; genital papilla free from ocular-side pelvic fin; 18 caudal-fin rays; supracranial pattern 1-1-4-.....*Z. altipinnis* p. 52

**Genus *Aesopia* Kaup, 1858**

Figures 1.42-1.45, Table 1.19

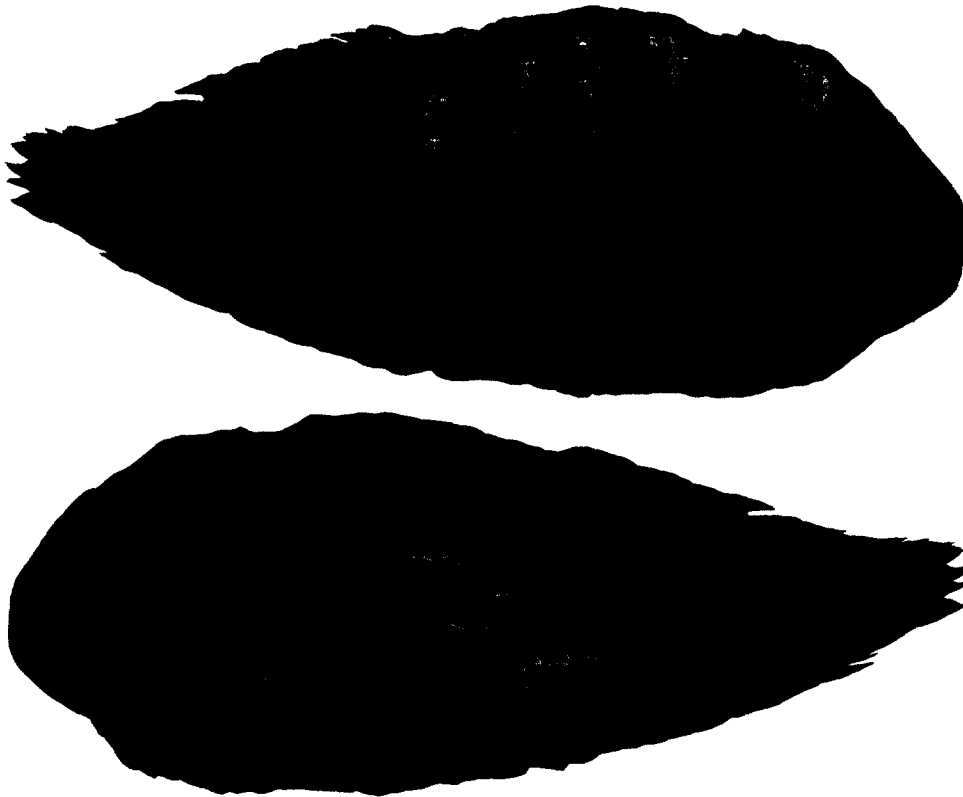


Figure 1.42. Photographs of *Aesopia cornuta*, WAM P.32293.001, 107 mm SL, Western Australia, Shark Bay, Point Quobba, 6.49 km WSW of 24°30.827'S, 113°21.721'E, depicting the ocular (above) and blind (below) sides.

**Material examined:** 31 specimens (64.69-239.45 mm TL)

**Non-type material:** AMS I.37574001, 1(x-ray only), SE Grafton, NSW; ASIZP0060304, 1(71.29 mm SL), Dahsi, Ylian, 24.94°N, 121.9°E; ASIZP0062198, 1(132.82 mm SL), open sea, Xingda Harbor, Kaohsiung, 22.88°N, 120.07°E; BPBM27561, 1(84.11 mm SL), India, Cochin; BPBM38586, 1(56.49 mm SL), Philippine, Luzon, Batangas; CAS46097, 1(x-ray only); Philippines, Manila Bay, Luzon Is.; CSIROCA2097, 1(x-ray only), WA, north of Joseph

Bonaparte Gulf, 13°16'S - 13°18'S, 128°21'E; CSIROH6511-01, 1(104.3 mm SL), Queensland, north of Townsville, 18°31'S, 147°20'E; CSIROH6512-01, 1(83.51 mm SL), Queensland, east of Gladstone, 23°37'S, 152°04'E; USNM Uncatalogued, 2(77.56 - 93.85 mm SL), India, Madras State, Porto Novo, 8 miles off mouth of Vellar Estuary (Bay of Bengal); NSMT-P54871, 1(126.67 mm SL), China, South Coast of Hainan Island, 100 km off Sanya; NSMT-P54963, 2(135.15-150.81 mm SL), East China Sea, 27°15'N, 121°45'E; NSMT-P6198, 1(209.93 mm SL), Japan, Sea of Japan, Nagasaki Pref., Tsushima Is., Tsutsu; QMI.36223, 1(102.42 mm SL), NE, Queensland, Australia, 18°38.1'S, 146°56.1'E; QMI.36596, 1(120.07 mm SL), NE, Queensland, Australia, 19°06.3'S, 148°36.9'E; QMI.40059, 1(112.21 mm SL), NE, Queensland, Australia, 23°47.7'S, 152°22.5'E; SAM24381, 1(77.57 mm SL), 29°23.0'S, 31°36.0'E; SAM28865, 1(116.74 mm SL), 3 miles off Tugela River, Sta No: K227, 29°14.0'S, 31°34.0'E; USNM106828, 1(x-ray only), Philippines; WAMP.32293.001, 1(107.13 mm SL), WA, Shark Bay, Point Quabba, 6.49 km WSW of Station: SB-11-031, 24°20.827'S to 24°31.431'S, 113°21.72'E to 113°21.723'E; WAMP.32420.001, 1(83.31 mm SL), WA, Shark Bay, Cape Ronsard, 21.58 km east of Cape, Station SB-13-174, 24°46.312'S to 24°46.857'S, 113°21.820'E to 113°21.840'E; WAMP11778.001, 1(x-ray only), WA, Shark Bay; WAMP11789.001, 1(x-ray only), WA, Shark Bay; AMSB.1682, 1(130.59 mm SL); CSIROCG034/673, 1(x-ray only); CSIRO S00580/69, 1(x-ray only); USNM Uncatalogued, 2(x-ray only), India; QMI23135, 1(x-ray only).

Table 1.19. Meristic and morphometric characteristics of type and non-type specimens of *Aesopia cornuta*. Means and standard deviations are shown in parentheses. Data for type material were obtained from the original species description (Kaup, 1858). Measurements and abbreviations are described in Appendix B.

	<i>Aesopia cornuta</i> syntypes (n=2)	<i>Aesopia cornuta</i> non-type specimens (n=31)
<b>Standard length (mm)</b>	-	56.49-209.93 (108.83; 34.4) <sup>1</sup>
<b>Total length (mm)</b>	-	64.69-239.45 (125.06; 38.9) <sup>1</sup>
<b>Counts</b>		
Dorsal-fin rays	72	67-79(74.4; 2.6) <sup>2</sup>
Anal-fin rays	62	58-66 (62.2; 2.2) <sup>2</sup>
Caudal-fin rays	17	12-17 (14.6; 1.2) <sup>2</sup>
Precaudal vertebrae	-	9-11 (9.8; 0.5)
Caudal vertebrae	-	34-38 (36.5; 1.0) <sup>2</sup>
Total vertebrae	-	44-48 (46.3; 1.0) <sup>2</sup>
Haemopophyses	-	5-7 (6.0; 0.4)
Pterygiophores	-	5-7 (6.0; 0.7) <sup>2</sup>
Pectoral-fin rays o.s.	10	12-19 (15.2; 1.8) <sup>1</sup>
Pectoral-fin rays b.s.	10	12-18 (14.9; 1.7) <sup>1</sup>
Pelvic-fin rays o.s.	3-4	4-5 (4.1; 0.3) <sup>1</sup>
Pelvic-fin rays b.s.	3-4	2-4 (3.9; 0.5) <sup>1</sup>
Lateral-line scales	-	80-108 (93.4; 7.4) <sup>1</sup>
Number of bands	12-13	13-27 (14.8; 4.3) <sup>3</sup>
<b>Measurements</b>		
<b>%SL</b>		
Head length	-	0.16-0.20 (0.18; 0.01) <sup>1</sup>
Head depth	-	0.17-0.22 (0.19; 0.01) <sup>1</sup>
Body depth	-	0.28-0.37 (0.33; 0.02) <sup>1</sup>
Caudal fin length	-	0.13-0.18 (0.15; 0.01) <sup>1</sup>
Width caudal peduncle	-	0.05-0.07 (0.06; 0.006) <sup>1</sup>
<b>%HL</b>		
Length of pectoral fin o.s.	-	0.07-0.22 (0.15; 0.04) <sup>1</sup>
Length of pectoral fin b.s.	-	0.13-0.24 (0.17; 0.03) <sup>1</sup>
Length of pelvic fin o.s.	-	0.18-0.35 (0.26; 0.04) <sup>1</sup>
Length of pelvic fin b.s.	-	0.17-0.32 (0.24; 0.04) <sup>4</sup>
Pre-orbital head length	-	0.16-0.28 (0.23; 0.03) <sup>1</sup>
Post-orbital head length	-	0.56-0.70 (0.62; 0.04) <sup>1</sup>
Snout length	-	0.22-0.33 (0.27; 0.03) <sup>1</sup>
Nostril to snouth distance	-	0.14-0.25 (0.19; 0.03) <sup>1</sup>
Mouth length o.s.	-	0.29-0.40 (0.33; 0.02) <sup>1</sup>
Mouth length b.s.	-	0.21-0.35 (0.28; 0.04) <sup>1</sup>
Ventral eye diameter	-	0.20-0.30 (0.25; 0.03) <sup>1</sup>
Width of orbits	-	0.27-0.40 (0.33; 0.04) <sup>1</sup>
Longest dorsal ray	-	0.51-0.82 (0.70; 0.09) <sup>1</sup>
Longest anal ray	-	0.51-0.86 (0.69; 0.1) <sup>1</sup>
IOD/V	-	0 <sup>1</sup>
BPc/OPc	-	0.73-2.17 (1.21; 0.4) <sup>1</sup>
BPv/OPv	-	0.67-1.13 (0.91; 0.1) <sup>4</sup>

<sup>1</sup>: n=20; <sup>2</sup>: n=27; <sup>3</sup>: n=18; <sup>4</sup>: n=19.

**Geographic distribution:** *Aesopia cornuta* has been reported from the coasts of India, the southern coast of Japan, southeast Asia and Australia, at depths of 19-85 m.

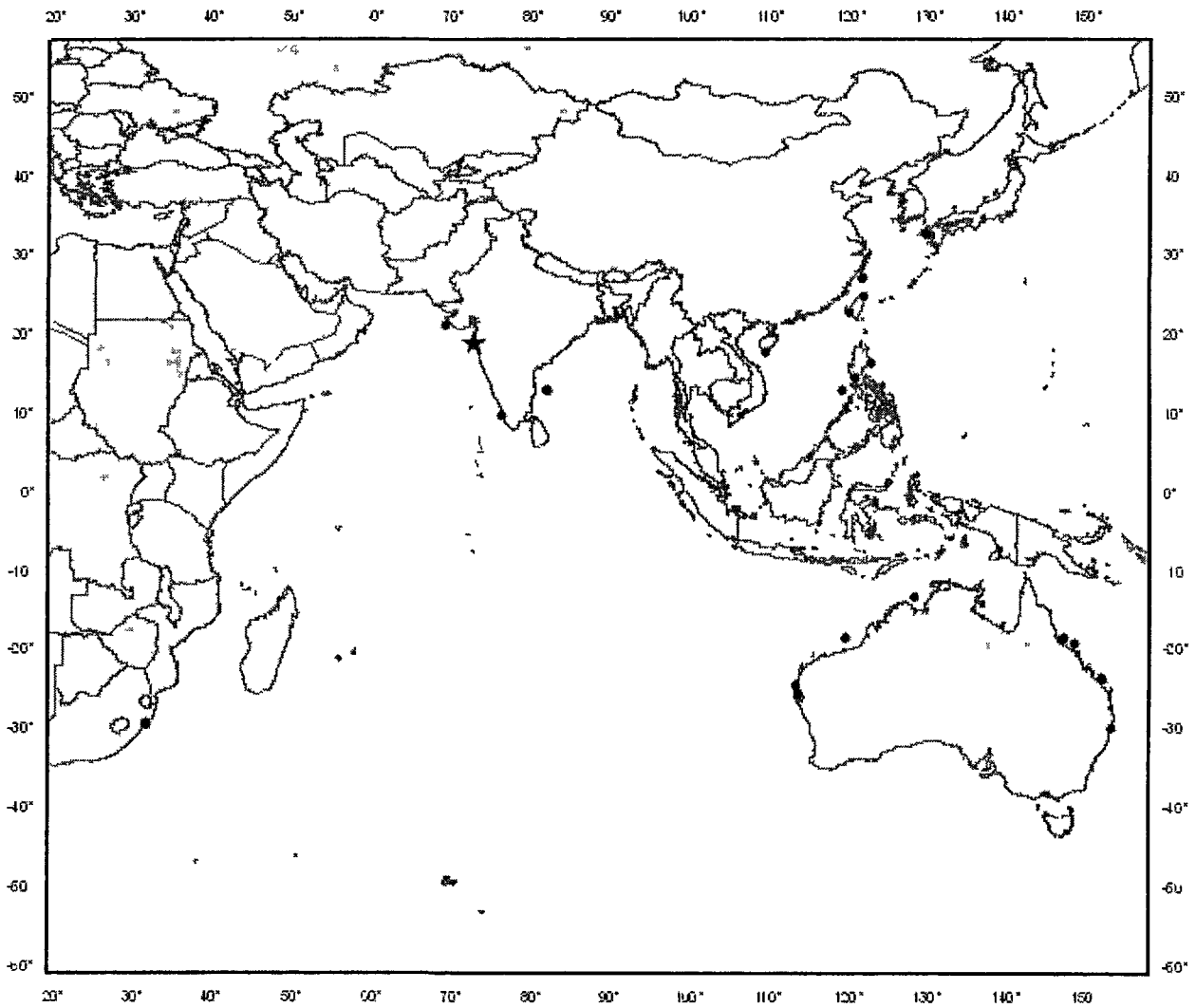


Figure 1.43. Geographic distribution of *Aesopia cornuta*. Star denotes locality of the syntype for *A. cornuta*, according to Kaup (1858).

**Remarks:** The genus *Aesopia* Kaup, 1858 bears a superficially striking resemblance to *Zebrias*, including the presence of completely confluent median fins and dark transverse bands. Due to its strong resemblance and the frequent misidentification of *Aesopia* species as *Zebrias* species, 31 representative specimens were examined in the present study to ascertain whether *A. cornuta* would be more appropriately placed in *Zebrias*. Kaup (1858) included six species in *Aesopia*: *A. zebra*, *A. cornuta*, *A. multifasciata*, *A. ommatura*, *A. quagga*, and *A. helotes*. Gunther (1862) restricted the genus to one species: *A. cornuta*. The other species were distributed among the genera *Soleichthys* and *Zebrias*. The current status of *Aesopia helotes*, however, is uncertain (Desoutter et al., 2001).

Chabanaud (1934) later reported a South African subspecies, *cornuta barnardi*, to which he assigned a new generic name: *Coryphaesopia*. The decision to create a new genus was based on the dissimilarity in appearance between *Aesopia cornuta* and the type species of the genus, *A. multifasciata* (this species has since been synonymised with the species *Soleichthys heterorhinos*). Günther (1862), however, proposed that the generic name *Aesopia* be retained for the single species, *A. cornuta*, rather than introduce a new generic name as dictated by the rules of nomenclature. The name *Coryphaesopia* has generally not been adopted by other taxonomists.

The monospecific genus, *Aesopia*, can be easily distinguished from *Zebrias* and *Pseudaesopia* by the presence of very weakly ctenoid scales (scale membrane completely conceals ctenii, giving the scales a cycloid appearance and texture), the presence of an enlarged and free first dorsal-fin ray, and an anterior blind-side nasal tube of comparable length to the posterior tube (in *Zebrias* and *Pseudaesopia*, the anterior blind nasal tube is nearly inconspicuous). Moreover, *A. cornuta* typically has 6 haemapophyses and 10 precaudal

vertebrae, whereas *Zebrias* and *Pseudaesopia* species typically have five and nine, respectively. In addition, *A. cornuta* typically has a higher number of pectoral-fin rays than both *Zebrias* and *Pseudaesopia* species (Table 1.4 and Table 2.3).

Chapleau (1989) noted different morphological types with respect to the supracranial complex of species in the family Soleidae. In this study, *Aesopia* was identified as having Type “A” morphology, characterized by an erisma of variable length, oriented parallel to the ocular orbit and rostrum. The anterior supracranial pterygiophore is attached directly to the erisma, while the posterior supracranial pterygiophore is attached directly to the cranium. The neural spine is straight and leans against the posterodorsal portion of the cranium, but barely surpasses it, if at all. *Zebrias* was found to have a markedly different supracranial complex and was identified as having Type “B” morphology, along with several other genera. The neural spine present among species of *Zebrias* was found to be relatively longer than species having morphological Type A. In this group, the first neural spine curves anteriorly to cover the posterior region of the cranium. It may also be relatively straight, with an enlarged distal extremity. In addition, the posterior supracranial pterygiophore is situated in the space between the first neural spine and the cranium, and is not directly anchored to either.

Schwarzans (1999) noted a difference in the otolith morphology of *Aesopia* in comparison to *Zebrias*, *Pseudaesopia*, *Soleichthys*, and *Typhlachirus*. According to his study, the otoliths of this genus are more elongate and, whereas the sulcus is rather short in the other genera and ends at a considerable distance from the posterior and anterior rims of the otolith, it extends close to the anterior tip of the otolith in *Aesopia*.

Although currently thought to be a monospecific genus, a cursory examination suggests that more than one species may, in fact, exist. Figure 1.42 and Figure 1.45 show markedly

dissimilar specimens, both exhibiting the diagnostic features of *Aesopia*. A revision of this genus is recommended.

There is no doubt that *Aesopia* is very closely related to both *Zebrias* and *Pseudaesopia*; however, at this point, it could be argued that the specimens examined differ sufficiently from the latter genera to warrant retaining them in their own, distinct genus until a proper phylogenetic study of the wider clade is done.

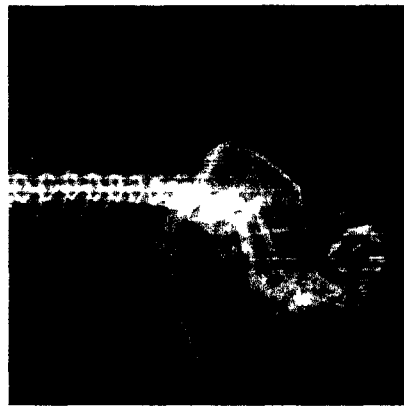


Figure 1.44. Radiograph showing the supracranial complex of *A. cornuta*, WAM P.32293.001, 107 mm SL, Western Australia, Shark Bay, Point Quobba, 6.49 km WSW of 24°30.827'S, 113°21.721'E to 24°31.431'S, 113°21.723'E.

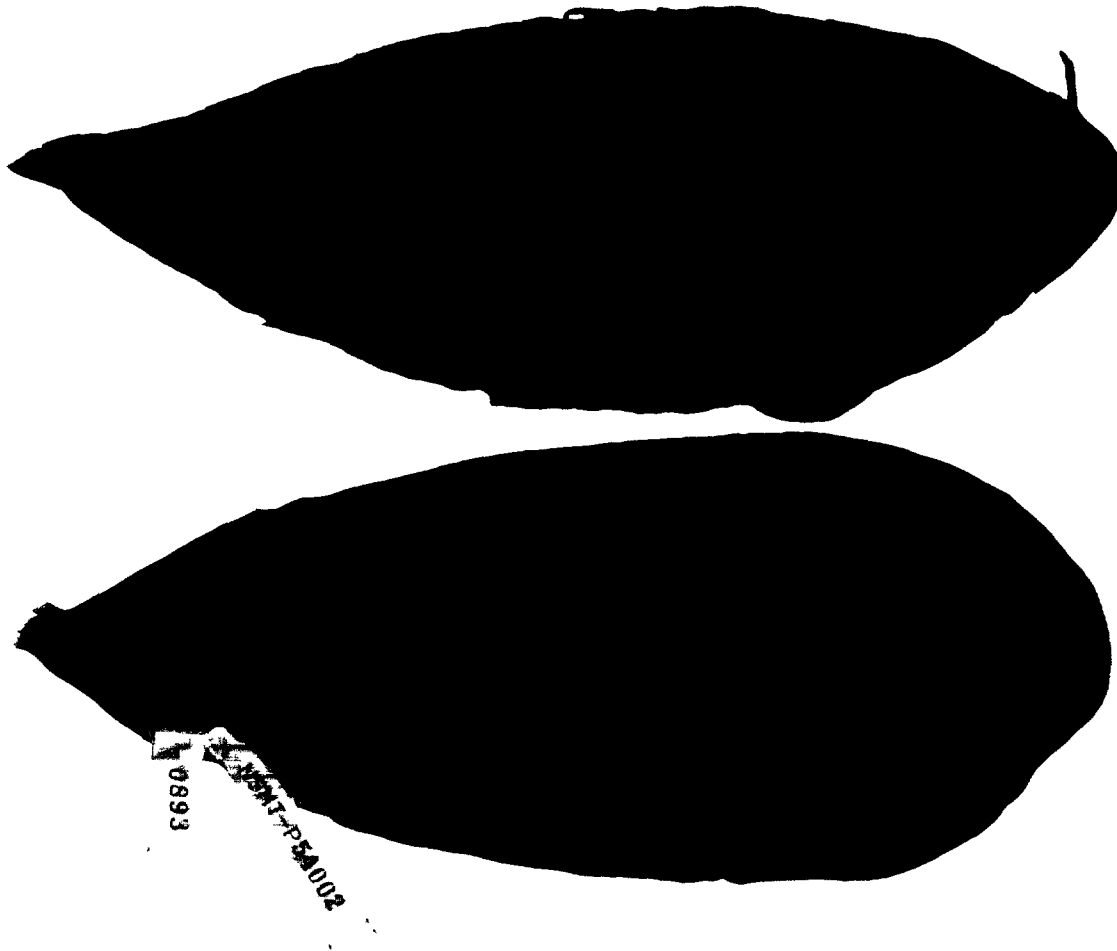


Figure 1.45. Photographs showing the striking similarity between *Aesopia cornuta* (Above: NSMT-P 6198, 210 mm SL, Sea of Japan, Nagasaki Pref., Tsushima Is., Tsutsu) and *Zebrias zebra* (Below: NSMT-P54002, 212 mm SL, Japan, Honshu, Chiba Pref., southern part of Boso Peninsula, Suno-saki Point).

## REFERENCES

Alcock, A. W. 1890. Natural history notes from H. M. Indian marine survey steamer 'Investigator,' Commander R. F. Hoskyn, R. N., commanding.--No. 20. On some undescribed shore-fishes from the Bay of Bengal. *Annals and Magazine of Natural History (Series 6)* v. 6 (no. 36): 425-443.

Amaoka, K. 1969. Studies on the sinistral flounders found in the waters around Japan -- taxonomy, anatomy and phylogeny. *Journal of the Shimonoseki University of Fisheries*. **18** (no.2): 65-340.

Amaoka, K., T. Kaga, and H. Misaki. 2008. A new sinistral flounder, *Engyprosopon kushimotoensis*, from Kushimoto, Kii Peninsula (Pleuronectiformes: Bothidae). *National Museums of Natural Sciences, Publications in Natural Sciences Suppl.* 2: 107-113.

Apte, D. and M. Rao. 1991. Food and feeding habits of *Zebrias quagga* (Kaup, 1858) with a note on abnormalities in the fish. *Environment & Ecology*. **9** (issue 3): 775 -777.

Apte, D. and M. Rao. 1992. Electrophoretic studies on eye lens and muscle proteins of some flat fishes off Bombay coast. *Fishery technology*. Society of Fisheries Technologists (India). **29** (no. 2): 147-150.

Australian Government. Department of Sustainability, Environment, Water, Population and Communities. A characterisation of the marine environment of the South-west Marine Region. A summary of an expert workshop convened in Perth, Western Australia, September 2006.

Department of the Environment and Water Resources, September 2007.

Azevedo, M. F. C., C. Oliveira, B.G. Pardo, P. Martínez and F. Foresti. 2008. Phylogenetic analysis of the order Pleuronectiformes (Teleostei) based on sequences of 12S and 16S mitochondrial genes. *Genetics and Molecular Biology*. **31 (1, suppl)**: 284-292.

Basilewsky, S. 1855. *Ichthyographia Chinae Borealis*. Nouveaux mémoires de la Société impériale des naturalistes de Moscou. **10**: 215-263, Pls. 1-9.

Berendzen, P. B. and W. W. Dimmick. 2002. Phylogenetic relationships of Pleuronectiformes based on molecular evidence. *Copeia* 2002, (no. 3): 642-652.

Berg, L.S. 1935. Sur les unités taxonomiques chez les poissons. *Bulletin du Muséum National d'Histoire Naturelle*, 2<sup>nd</sup> Série. **7 (1)**: 79-84.

Berg, L.S. 1940. Classification of fishes, both recent and fossil. *Trav. Inst. Zool. Acad. Sci. URSS*. **5**: 87-517, Figs. 1-190.

Bleeker, P. 1860. Zesde bijdrage tot de kennis der vischfauna van Japan. *Acta Societatis Regiae Scientiarum Indo-Neêrlandicae* v. **8**: 1-104.

Bleeker, P. 1870-75. Atlas ichthyologique des Indes Orientales Néerlandaises, publiés sous les auspices du Gouvernement colonial néerlandais. Tome VI. Pleuronectes, Scombrésoces, Clupées, Clupésoces, Chauliodontes, Saurides. Atlas ichthyologique des Indes Orientales Néerlandaises, publiés sous les auspices du Gouvernement colonial néerlandais. Tome VI.: 1-170, Pls. 232-278.

Bloch, M. E. 1787. Naturgeschichte der ausländischen Fische. Berlin. Naturgeschichte der Ausländischen Fische. **3**: i-xii + 1-146, Pls. 181-216.

Bloch, M. E. and J. G. Schneider. 1801. M. E. Blochii, Systema Ichthyologiae iconibus ex illustratum. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit Jo. Gottlob Schneider, Saxo. Berolini. Sumtibus Auctoris Impressum et Bibliopolio Sanderiano Commisum. M. E. Blochii, Systema Ichthyologiae.: i-lx + 1-584, Pls. 1-110.

Boeseman, M. 1947. Revision of the fishes collected by Burger and Von Siebold in Japan. Zoologische Mededelingen (Leiden). **28**: i-vii + 1-242, Pls. 1-5.

Bonaparte, C.L. 1846. Catalogo metodico dei pesci europei. Naples. Pp. 1-99.

Borsa, P. and J.-P. Quignard. 2001. Systematics of the Atlantic-Mediterranean soles *Pegusa impar*, *P. lascaris*, *Solea aegyptiaca*, *S. senegalensis*, and *S. solea* (Pleuronectiformes: Soleidae). Canadian Journal of Zoology. **79**: 2297-2302.

Burridge, C.P. 2000. Biogeographic history of geminate cirrhitoids (Perciformes: Cirrhitidae) with east-west allopatric distributions across southern Australia, based on molecular data. *Global Ecology & Biogeography*. **9**: 517-525.

Cantor, T. E. 1849. Catalogue of Malayan fishes. *Journal and Proceedings of the Asiatic Society of Bengal*. **18** (pt 2): i-xii + 983-1443, Pls. 1-14.

Chabanaud, P. 1928a. Remarques sur quelques genres de la famille des Soleidae. Extrait du *Bulletin de la Société zoologique de France*, Tom LIII: 272-279.

Chabanaud, P. 1928b. Revision des poissons Hétérosomes de la sous-famille des Achirinae, d'après les types de Kaup, de Günther et de Steindachner. *Bulletin de l'Institut Oceanographique (Monaco)* No. 523: 1-53.

Chabanaud, P. 1930a. Les genres de Poissons Hétérosomes [Pisces Heterosomata] appartenant à la sous-famille des Soleinae. *Bulletin de l'Institut Oceanographique (Monaco)* No. 555: 1-21.

Chabanaud, P. 1930b. Description d'un nouvel *Aseraggodes* [Pisces, Soleidae] du Queensland. *Annals and Magazine of Natural History (Series 10)*. **5** (no. 26): 241-243.

Chabanaud, P. 1931. Sur divers poissons soléiformes de la région Indo-Pacifique. *Bulletin de la Société Zoologique de France*. **56**: 291-305.

Chabanaud, P. 1934. Les soléidés du groupe *Zebrias*. Définition d'un sous-genre nouveau et description d'une sous-espèce nouvelle. Bulletin de la Société Zoologique de France **59**: 420-436.

Chabanaud, P. 1935. Les Soleidae de la sous-famille des Heteromycterinae. Bulletin de la Société Zoologique de France. **60**: 212-224.

Chabanaud, P. 1936. Sur divers soléidés apparentés au genre *Zebrias*. Bulletin de la Société Zoologique de France. **61**: 382-404, Pl. 6.

Chabanaud, P. 1937. Téléostéens dissymétriques du Mokkattam inférieur de Tourah. Mémoires de l'Institut d'Egypte. **32** : 1-121.

Chabanaud, P. 1940. Les espèces et les sous-espèces atlantiques du genre *Achirus* [Pisces Pleurinctoidea [sic] Achiridae]. Bulletin du Muséum National d'Histoire Naturelle (Série 2). **12** (no. 2): 86-90.

Chabanaud, P. 1943a. Notules ichthyologiques. (Sixième série). XX.--L'habitat du Soléidé *Pegusa lascaris* (Risso) ne serait-il pas circumafricain. XXI.--Le genre *Dexillus* Chabanaud. XXII.--Nouveaux genres de la famille des Soleidae. Bulletin du Muséum National d'Histoire Naturelle (Série 2). **15**(no. 5): 289-293.

Chabanaud, P. 1943b. Caractères ostéologiques et repartition géographique des Téléostéens vivants et fossiles appartenant à la famille des Soleidae. C R Séan Soc Biogeogr. 1943:39-42.

Chabanaud, P. 1947. Notules ichthyologiques (suite). XXXII.-- Description d'un nouveau *Cynoglossus* de la côte du Sénégal. Bulletin du Muséum National d'Histoire Naturelle (Série 2). **19** (no. 6): 441-443.

Chabanaud, P. 1948. Description de quatre espèces inédites du genre *Symphurus*. Bulletin du Muséum National d'Histoire Naturelle (Série 2). **20** (no. 6): 508-511.

Chabanaud, P. 1949. Révision des Cynoglossidae (s. str.) de l'Atlantique oriental. Bulletin du Muséum National d'Histoire Naturelle (Série 2). **21** (no. 1): 60-66.

Chabanaud, P. 1950. Description de nouveaux Soleidae, capturés au cours de l'Expédition océanographique belge dans les eaux africaines de l'Atlantique Sud (1948-1949). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. **26** (no. 55): 1-19.

Chabanaud, P. 1954. Revision des Soléidés du genre *Pegusa*. Description d'une espèce inédite. Bulletin de l'Institut Français d'Afrique Noire (Sér A) Sciences Naturelles. **16** (no. 1): 245-282.

Chanet, B. 1997. A cladistic reappraisal of the fossil falttfishes record consequences on the phylogeny of the Pleuornectiformes (Osteichthyes : Teleostei). Annales des Sciences naturelles, Zoologie et biologie animale. **18 (3)** : 105-117.

Chanet, B. and F. Chapleau. 2004. Darwin, Mivart et les poissons plats. Pour la science. Série : Les génies de la Science. Darwin, L'arbre de la vie: 76.

Chanet, B. and F. Chapleau. 2005. Darwin et l'origine des poissons plats. Bull. Soc. Sci. Nat. l'Ouest de la France, nouvelle série, tome 27. **3**: 101-108.

Chanet, B. and M. Desoutter-Meniger. 2008. French-English glossary of terms found in Chabanaud's published works on Pleuronectiformes. Cybium 2008, electronic publication no 1: 23p.

Chapleau, F. 1989. Étude de la portion supracrânienne de la nageoire dorsale chez les Soleidae (Téléostéens, Pleuronectiformes). Cybium. **13**(3): 271-279.

Chapleau, F. 1993. Pleuronectiform relationships: a cladistic reassessment. Bulletin of Marine Science. **52** (no. 1): 516-540.

Chapleau, F. and A. Keast. 1988. A phylogenetic reassessment of the monophyletic status of the family Soleidae, with comments on the suborder Soleoidei (Pisces: Pleuronectiformes). Canadian Journal of Zoology. **66**: 2797-2810.

Chen, W.-J., C. Bonillo and G. Lecointre. 2003. Repeatability of clades as a criterion of reliability: a case study for molecular phylogeny of Acanthomorpha (Teleostei) with larger number of taxa. Molecular Phylogenetics and Evolution. **26**: 262-288.

Chen, J.T.F., and H.T.C. Weng. 1965. Ichthyological series no. 5. A review of the flatfishes of Taiwan. *Biological Bulletin* 25 & 27. Department of Biology, College of Science, Tunghai University, Taichung, Taiwan, China. pp. 1-103.

Cheng, Q.-T. and C.-W. Zhou (Eds.). 1997. The fishes of Shandong Province. The fishes of Shandong Province. 1997: 1-549.

Cope, E.D. 1871. Contribution to the ichthyology of the Lesser Antilles. *Trans. Amer. Phil. Soc.* 14(2): 445-483.

Corrigan, S. and L.B. Beheregaray. 2009. A recent shark radiation: Molecular phylogeny, biogeography and speciation of wobbegong sharks (family: Orectolobidae). *Molecular Phylogenetics and Evolution.* 52: 205-216.

Cuvier, G. 1816. Poissons. *In: Le règne animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée.* 4, Paris, pp. 2: xviii – 532.

Darwin, C. 1872. *On the origin of species by means of natural selection* 6th Edition. Murray, London, 625 pp.

Dawson, M.N. 2005. Incipient speciation of *Catostylus mosaicus* (Scyphozoa, Rhizostomeae, Catostylidae), comparative phylogeography and biogeography in south-east Australia. *Journal of Biogeography*. **32**: 515-533.

Day, F. 1888. The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon. The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon. Suppl.: 779-816.

Desoutter, M. 1994. Révision des genres *Microchirus*, *Dicologlossa* et *Vanstraelenia* (Pleuronectiformes, Soleidae). *Cybium*. **18** (no. 3): 215-249.

Desoutter-Meniger M. 1997. Révision systématique des genres de la famille des Soleidae présents sur les côtes de l'Est-Atlantique et de la Méditerranée. PhD thesis, Muséum de National d'Histoire Naturelle, Paris, France.

Desoutter, M., F. Chapleau, T. A. Munroe, B. Chanet and M. Beaunier. 2001. Catalogue critique des types de poissons du Muséum national d'Histoire naturelle. Ordre des Pleuronectiformes. *Cybium* v. 25 (no.4 ): 299-368.

Dettai, A. and G. Lecointre. 2005. Further support for the clades obtained by multiple molecular phylogenies in the acanthomorph bush. *C.R. Biologies*. **328**: 674-689.

Dou, S. 1996. Life history cycles of flatfish species in the Bohai Sea, China. *Oceanographic Literature Review*. **43** (no. 8): 830.

Eschmeyer, W. 2010. *Catalog of Fishes*. Online update on October 25, 2010. California Academy of Sciences, San Francisco. 2905 pages. [www.calacademy.org](http://www.calacademy.org).

Environmental Systems Research Institute (ESRI). 2006. Arc/INFO. Version 9.2. ESRI Limited, Redlands, California, USA.

Evseenko, S.A. 2000. Family Achiropsettidae and its position in the taxonomic and ecological classification of Pleuronectiformes. *Journal of Ichthyology*. **40** (suppl. 1): 110-138.

FAO Fisheries and Aquaculture Information and Statistics Service. 2009. *FAO yearbook*.

*Fishery and Aquaculture Statistics*. 2007. Rome, FAO. 72p.

Fowler, H. W. 1934. Descriptions of new fishes obtained 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *Proceedings of the Academy of Natural Sciences of Philadelphia* v. 85 (for 1933): 233-367.

Fowler, H. W. 1956. *Fishes of the Red Sea and southern Arabia*. I. Branchiostomida to Polynemida. Weizmann Sci. Press, Jerusalem. *Fishes of the Red Sea and southern Arabia*.: 1-240.

Fraser, C.I., H.G. Spencer, and J.M. Waters. Glacial oceanographic contrasts explain phylogeography of Australian bull kelp. *Molecular Ecology*. **18**: 2287-2296.

Friedman, M. 2008. The evolutionary origin of flatfish asymmetry. *Nature*. **454**: 209-212.

Gibson, R.N. (Ed.). 2005. Flatfishes. Biology and Exploitation. Blackwell Publishing, Oxford. pp. 1-391.

Gomon, M. F. 1987. New Australian fishes. Part 6. New species of *Lepidotrigla* (Triglidae), *Choerodon* (Labridae) and *Zebrias* (Soleidae). *Memoirs of the Museum of Victoria* v. 48 (no. 1): 17-23.

Gonzales, Benjamin J., Okamura, Osamu, Nakamura, Katsuhiko, and Miyahara, Hajime. 1994. New record of the annular sole, *Synaptura annularis* (Soleidae, Pleuronectiformes) from Japan. *Japan J. Ichthyol.* 40(4): 491-494.

Gray, J. E. 1851. List of the specimens of fish in the collection of the British Museum. Part I.-- Chondropterygii. London.: i-x + 1-160, Pls. 1-2.

Gronow, L. T. 1854. *In*: Gray, J. E. 1854. Catalogue of fish collected and described by Laurence Theodore Gronow, now in the British Museum. London.: i-vii + 1-196.

Günther, A. 1862. Catalogue of the fishes in the British Museum. Catalogue of the Acanthopterygii, Pharyngognathi and Anacanthini in the collection of the British Museum. Catalogue of the fishes in the British Museum. 4: i-xxi + 1-534.

Heemstra, P. C. and O. Gon. 1986. Family No. 262: Soleidae (pp. 868-874). *In*:

Smith, M. M. and P. C. Heemstra (eds.). 1986. Smiths' Sea Fishes. Macmillan South Africa, Johannesburg. i-xx + 1-1047, Pls. 1-144.

Hoese, D. F. and D. J. Bray. 2006. Families and subfamilies: p. 88, 113-115, 116-117, 188-189, 675-685, 1000-1001, 1029-1030, 1031-1033, 1047, 1073-1077, 1176-1182, 1212-1217, 1264-1274, 1280, 1317-1327, 1350-1352, 1363-1365, 1476-1478, 1495-1496, 1497-1499, 1500-1504, 1505-1506, 1507-1508, 1540-1566, 1568-1576, 1578-1592, 1711-1712, 1729, 1787-1792, 1793-1797, 1800-1801, 1804-1805, 1807-1809, 1810-1823, 1824-1825, 1826-1830, 1831-1837, 1838-1840, 1841-1852, 1853-1858. *In*: Zoological Catalogue of Australia. Volume 35. Fishes.

Hubbs, C. L. 1915. Flounders and soles from Japan collected by the United States Bureau of Fisheries steamer "Albatross" in 1906. Proceedings of the United States National Museum. 48 (no. 2082): 449-496, Pls. 25-27.

Hubbs, C.L. 1945. Phylogenetic position of the Citharidae, a family of flatfishes. Miscellaneous publications Museum of Zoology, University of Michigan, No. 63: 1-38.

Hubbs, C.L. and K.F. Lagler. 1958. Fishes of the Great Lakes region. Bulletin-Cranbrook Institution of Science. **26**: 1-213.

Hutchins, J. B. 2001. Checklist of the fishes of Western Australia. Records of the Western Australian Museum Supplement No. 63: 9-50.

Jenkins, J. T. 1910. Report on the fishes taken by the Bengal Fisheries Steamer "Golden Crown" Part IV. Pleuronectidae. Memoirs of the Indian Museum. **3**(no. 1): 23-31.

Joglekar, A. 1976. On a new species of the genus *Zebrias* Jordan and Snyder, 1900 (Pisces: Soleidae) from Kerala coast (India). Zoologischer Anzeiger v. 197 (no. 1-2): 67-70.

Jordan, D. S. and B. W. Evermann. 1898. The fishes of North and Middle America III. Bull. U.S. Nat. Mus. **47**(3): 2602-2712.

Jordan, D. S. and B. W. Evermann. 1902. Notes on a collection of fishes from the island of Formosa. Proceedings of the United States National Museum. **25** (no. 1289): 315-368.

Jordan, D. S. and C. L. Hubbs. 1925. Record of fishes obtained by David Starr Jordan in Japan, 1922. Memoirs of the Carnegie Museum. **10**(no. 2): 93-346, Pls. 5-12.

Jordan, D. S. and C. W. Metz. 1913. A catalog of the fishes known from the waters of Korea. Memoirs of the Carnegie Museum. **6** (no. 1): 1-65, Pls. 1-10.

Jordan, D. S. and J. O. Snyder. 1900. A list of fishes collected in Japan by Keinosuke Otaki, and by the United States steamer Albatross, with descriptions of fourteen new species. Proceedings of the United States National Museum. **23**(no. 1213): 335-380, Pls. 9-20.

Jordan, D. S. and J. O. Snyder. 1901a. A preliminary check list of the fishes of Japan. *Annotationes Zoologicae Japonenses*. **3** (pts 2 & 3): 31-159.

Jordan, D.S. and J.O. Snyder. 1901b. List of fishes collected in 1883 and 1885 by Pierre Louis Jouy and preserved in the United States National Museum, with descriptions of six new species. Proceedings of the United States National Museum. **23**(no. 1235): 739-769, Pls. 31-38.

Jordan, D. S., S. Tanaka, and J. O. Snyder. 1913. A catalogue of the fishes of Japan. Journal of the College of Science. Imperial University, Tokyo. **33** (art. 1): 1-497.

Jordan, D. S. and E. C. Starks. 1906. A review of the flounders and soles of Japan. Proceedings of the United States National Museum. **31** (no. 1484): 161-246.

Kaup, J. 1858. Uebersicht der Soleinae, der vierten Subfamilie der Pleuronectidae. *Archiv für Naturgeschichte*. **24** (no. 1): 94-104.

Kawai, T., K. Amaoka, and B. Séret. 2008. *Samariscus multiradiatus*, a new dextral flounder (Pleuronectiformes: Samaridae) from New Caledonia. *Ichthyological Research*. **55**: 17-21.

Kawai, T., K. Amaoka, and B. Séret. 2010. A new righteye flounder, *Poesilopsetta multiradiata* (Teleostei: Pleuronectiformes: Poecilopsettidae), from New Zealand and New Caledonia (South-West Pacific). *Ichthyological Research*. **57**: 193-198.

Kottelat, M., A. J. Whitten, S. N. Kartikasari and S. Wirjoatmodjo. 1993. Freshwater fishes of Western Indonesia and Sulawesi. Periplus Editions, Hong Kong. i-xxxviii + 1-259, Pls. 1-84.

Krishnan, S. and S. S. Mishra. 1993. On a collection of fish from Kakinada--Gopalpur sector of the east coast of India. *Records of the Zoological Survey of India*. **93** (nos. 1-2): 201-240, 1 pl.

Krishnan, S. and S. S. Mishra. 1994. On a collection of fish from middle and south Andaman Group of islands. *Records of the Zoological Survey of India*. **94** (nos. 2-4): 265-306.

Lacepède, B. G. E. 1798. *Histoire naturelle des poissons*. *Histoire naturelle des poissons*. v. 1: 1-8 + i-cxlvii + 1-532, Pls. 1-25, 1 table.

Lee, M.-Y., H.-M. Chen, and K.-T. Shao. 2009a. A new species of deep-water tonguefish genus *Symphurus* (Pleuronectiformes: Cynoglossidae) from Taiwan. *Copeia* 2009 (no. 2): 342-347.

Lee, M.-Y., T. A. Munroe, and H.-M. Chen. 2009b. A new species of tonguefish (Pleuronectiformes: Cynoglossidae) from Taiwanese waters. *Zootaxa* No. 2203: 49-58.

Leviton, A. E., R. H., Jr. Gibbs, E. Heal and C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985 (no. 3): 802-832.

Li, S.-Z. and H.-M. Wang. 1995. *Fauna Sinica. Osteichthyes. Pleuronectiformes*. Science Press. Beijing. 1-433.

Lindberg, G. U. and V. V. Fedorov. 1993. Fishes of the Sea of Japan and the adjacent parts of the Sea of Okhotsk and the Yellow Sea. Part 6. Teleostomi. Osteichthyes. Actinopterygii. XXI. Pleuronectiformes (Fam. CXC.V. Psettodidae -- Fam. CCI. Cynoglossidae). Handbook on the Identification of Animals, Zoological Institute of the Russian Academy No. 166: 1-271.

Linnaeus, C. 1758. *Systema Naturae*, 10<sup>th</sup> Edn, Vol. 1, Laurentii Slviii Holmiae, Stockholm.

Love, M.S. and J. Vucci. 1973. Partial ambicoloration in three California flat fishes. *Cali. Fish. Game*. 4: 59.

Macleay, W. 1882. Notes on the Pleuronectidae of Port Jackson, with descriptions of two hitherto unobserved species. *Proceedings of the Linnean Society of New South Wales*. 7 (pt 1): 11-15.

Malm, A.W. 1868. Bidrag till kannedom af Pleuronektoidermas utveckling och byggnad, *Kongliga Svenska Vetenskaps – Akademiens Handlinger*. 7(4): 1-28.

Matsubara, K. 1955. Fish morphology and hierarchy. Parts I-III. Ishizaki-shoten, Tokyo, xii+790pp., vi+791-1605pp., xiv+135pls.

McCulloch, A. R. 1916. Ichthyological items. Memoirs of the Queensland Museum v. 5: 58-69, Pls. 7-9.

McCulloch, A. R. 1929. A check-list of the fishes recorded from Australia. Part I. Memoirs of the Australian Museum, Sydney Memoir 5: 1-144.

Mishra, S., R. Gouda, L. Nayak and R. C. Panigrahy. 1999. A check list of the marine and estuarine fishes of south Orissa, east coast of India. Records of the Zoological Survey of India. **93** (no. 3): 81-90.

Mishra, S. S. and S. Krishnan. 2003. Marine fishes of Pondichery and Karaikal. Records of the Zoological Survey of India. Miscellaneous Publication, Occasional Paper No. 216: 1-53.

Mivart, St.G.J. 1871. On the Genesis of Species. Mac Millan (ed.), London.

Mohsin, A. K. M. and M. A. Ambak. 1996. Marine fishes and fisheries of Malaysia and neighbouring countries. Marine fishes and fisheries of Malaysia and neighbouring countries. 1996: iv - xxxvi; 1 - 744.

Muchhala, N. and T. A. Munroe. 2004. A new species of *Soleichthys* (Soleidae: Pleuronectiformes) from tropical seas off northern Australia. *Ichthyological Research*. **51**(no. 1): 57-62.

Munroe, T. A. 2001. Families Soleidae, Cynoglossidae. *In*: Carpenter, K.E. and V.H. Niem. 2001. Species identification guide for fishery purposes. The living marine resources of the western central Pacific. Bony fishes part 4 (Labridae to Latimeriidae), estuarine crocodiles, sea turtles, sea snakes and marine mammals. FAO, Rome. Species identification guide for fishery purposes. Bony fishes part 4. **6**: 3878-3901.

Munroe, T. A. 2005. Systematic diversity of the Pleuronectiformes. *In*: Gibson, R.N. (Ed.), *Flatfishes Biology and Exploitation*. Blackwell Publishing, Iowa, pp. 10-41.

Nair, R. J. 2006. First record of the annular sole, *Synaptura annularis* (Fowler, 1933) (Pleuronectiformes: Soleidae) from India. *Journal of the Marine Biological Association of India*. **48** (no. 1): 118-120.

Nakabo, T. (Ed.). 2002. *Fishes of Japan with pictorial keys to the species*, English edition. Tokai University Press. *Fishes of Japan with pictorial keys to the species*. Second edition. **2**: i-vii + 867-1749.

Nelson, J. S. 1994. *Fishes of the World*. 3rd edition. John Wiley & Sons. *Fishes of the World*. 3rd edition.: i-xvii + 1-600.

Norman, J. R. 1928. The flatfishes (Heterosomata) of India, with a list of the specimens in the Indian Museum. Part II. Records of the Indian Museum (Calcutta). **30** (pt 2): 173-215, Pls. 4-7.

Nixon, K.C. and Q.D. Wheeler. 1990. An amplification of the phylogenetic species concept. *Cladistics*. **6**: 211-223.

Norman, J. R. 1934. A systematic monograph of the flatfishes (Heterosomata). Vol. I. Psettodidae, Bothidae, Pleuronectidae. British Museum (Natural History). A systematic monograph of the flatfishes (Heterosomata): i-viii + 1-459.

Ochiai, A. 1963. Fauna Japonica. Soleina (Pisces). Biogeographical Society of Japan (Tokyo) 1963: i-vi + 1-114, Pls. 1-24.

Oommen, V. P. 1977. New records of bathypelagic fishes from the Arabian Sea with description of a new species. *Journal of the Bombay Natural History Society* v. 74 (pt 2): 282-287.

Oshima, M. 1927. List of flounders and soles found in the waters of Formosa, with descriptions of hitherto unrecorded species. *Japanese Journal of Zoology*. **1** (no. 5): 177-204.

Paepke, H.-J. 1999. Bloch's fish collection in the Museum für Naturkunde der Humboldt Universität zu Berlin: an illustrated catalog and historical account. *Theses Zoologicae*. **32**: 1-216, Pls. 1-32 (unpaginated).

Pardo, B.G., A. Machordom, F. Foresti, F. Porto-Foresti, M.F.C. Azevedo, R. Bañón, L. Sánchez and P. Martínez. 2005. Phylogenetic analysis of flatfish (Order Pleuronectiformes) based on mitochondrial 16s rDNA sequences. *Scientia Marina*. **69(4)**: 531-543.

Policansky, D. 1982. The asymmetry of flounders. *Scientific American*. **246**: 116-122.

Pradhan, R.M. and M.J. Pradhan. 1962. An instance of partial ambicoloration in oriental sole *Brachirus orientalis*. *J. Bom. Nat. Hist. Soc.* **59**: 967-968.

Rama-Rao, K.V. 1967. A new sole *Zebrias cochinchensis* from India. *Journal of the Zoological Society of India*. **19**(nos. 1-2): 99-100.

Ramos, R. T. C., T. P. A. Ramos, and P. R. D. Lopes. 2009. New species of *Achirus* (Pleuronectiformes: Achiridae) from northeastern Brazil. *Zootaxa* No. 2113: 55-62.

Randall, J. E. 1995. *Zebrias captivus*, a new species of sole (Pleuronectiformes: Soleidae) from the Persian Gulf. *Journal of South Asian Natural History* v. 2 (no. 2): 241-246.

Randall, J. E. and M. Desoutter-Meniger. 2007. Review of the soles of the genus *Aseraggodes* (Pleuronectiformes: Soleidae) from the Indo-Malayan region, with description of nine [actually ten] new species. *Cybium*. **31** (no. 3): 301-331.

Randall, J. E. and T. A. Munroe. 2008. *Soleichthys dori*, a new sole (Pleuronectiformes: Soleidae) from the Red Sea. *Electronic Journal of Ichthyology, Bulletin of the European Ichthyology Society*. **2**: 76-84.

Regan, C.T. 1903. Notes on the genus *Synaptura* Cantor, with descriptions of two new species. *Annals and Magazine of Natural History (Series 7)*. 11(61): 56-58, Pl. 6.

Regan, C. T. 1910. The origin and evolution of the teleostean fishes of the order Heterosomata. *Annals and Magazine of Natural History (Series 8)*. **6** (no. 35): 484-496.

Richardson, J. 1846. Report on the ichthyology of the seas of China and Japan. Report of the British Association for the Advancement of Science 15th meeting [1845]: 187-320.

Sainsbury, K.J., P.J. Kailola, G.G. Leyland, and CSIRO. 1985. Continental shelf fishes of Northern and North-Western Australia: an illustrated guide. Clouston & Hall and Peter Pownall Fisheries Information Service, Canberra, Australia. viii, 375p.

Schwarzhan, W. 1999. *Piscium Catalogus: Part Otolithi piscium*, Vol. 2, A comparative morphological treatise of recent and fossil otoliths of the order Pleuronectiformes. Verlag Dr Friedrich Pfeil, München.

Seigel, Jeffrey A. and Adamson, Thomas A. 1985. First record of the genus *Zebrias* (Pisces: Pleuronectiformes: Soleidae) from the Philippine Islands, with the description of a new species. Proc. Biol. Soc. Wash. 98(1): 13-16.

Sharina, S.N. and Yu.P. Kartavtsev. 2010. Phylogenetic and taxonomic analysis of flatfish species (Teleostei, Pleuronectiformes) inferred from the primary nucleotide sequence of cytochrome oxidase 1 gene (Co-1). Russian Journal of Genetics. **46(3)**: 356-361.

Shen, S.-C. 1967. Studies on the flatfishes (Pleuronectiformes or Heterosomata) in the adjacent waters of Hong Kong. Quarterly Journal of the Taiwan Museum (Taipei). **20** (nos. 1-2): 149-281.

Shen, Shih-Chieh, and Lee, Chian-Hsing. 1981. Study on sole fishes (family Soleidae) from Taiwan. Bull. Inst. Zool., Academia Sinica. **20(2)**: 29-39.

Shen, S.-C. (Chief editor). 1993. Fishes of Taiwan. Fishes of Taiwan. 1993: 1-956, Pls. 1-208, 4 unnumbered. Published by the National Taiwan University, Taipei, Taiwan.

Sivaprakasam, T.E. 1965. Ambicoloration in two species of flat fishes from Madras. J. Bom. Nat. Hist. Soc. **63**: 758-759.

Suzuki, S., T. Kawashima, and T. Nakabo. 2009. Taxonomic review of East Asian *Pleuronichthys* (Pleuronectiformes: Pleuronectidae), with description of a new species. Ichthyological Research. **56**: 276-291.

Swainson, W. 1838. The natural history and classification of fishes, amphibians, & reptiles, or monocardian animals. A. Spottiswoode, London. The natural history and classification of fishes, amphibians, & reptiles, or monocardian animals. v. 1: i-vi + 1-368.

Taki, I. 1938. On the abnormal arrangement of scales and colour bands in a sole (*Zebrias*), with special reference to its adverse scales. Journal of Science of the Hiroshima University. Series B, Div. 1, Vol. 6, Art. 3. pp.1-14, Pls. I-II.

Talwar, P. K. and S. Chakrapany. 1967. A new flatfish of the genus *Zebrias* Jordan and Snyder [Soleidae] from the Orissa coast, India. Proceedings of the Zoological Society of Calcutta. v. 20 (no. 2): 119-121.

Temminck, C. J. and H. Schlegel. 1846. Fauna Japonica, sive descriptio animalium quae in itinere per Japoniam suscepto annis 1823-30 collegit, notis observationibus et adumbrationibus illustravit P. F. de Siebold. Parts 10-14: 173-269.

The International Commission on Zoological Nomenclature. 1999. International code of zoological nomenclature, fourth edition. The International Trust for Zoological Nomenclature 1999. <http://www.nhm.ac.uk/hosted-sites/iczn/code/>

Vachon, J., Chapleau, F., and M. Desoutter-Meniger. 2008. Révision taxinomique du genre *Solea* et réhabilitation du genre *Barnardichthys* (Soleidae; Pleuronectiformes). Cybium. 32 (no. 1): 9-26.

Venkataramanujam, K., Ramanathan, N., and V.K. Venkataramani. 1988. On the egg and larval stages of the zebra sole, *Zebrias quagga* (Kaup) (Pisces: Soleidae) reared in the laboratory. *Matsya*. No. 14: 41-46.

Voronina, E. P. 2009. New species of righteye flounder *Samariscus leopardus* sp. nov. (Samaridae, Pleuronectiformes) from the Saya de Malha Bank (Indian Ocean). *Journal of Ichthyology*. **49** (no. 8): 575-584.

Wang, S.-A., Wang, Z.-M., Li, G.-L., Cao, Y.-P., et al. 2001. The fauna of Hebei, China. Pisces. Hebei Science and Technology Publishing House. The fauna of Hebei, China. Pisces. 2001: 1-366.

Waters, J.M., T.M. King, P.M. O'Loughlin, and H.G. Spencer. 2005. Phylogeographical disjunction in abundant high-dispersal littoral gastropods. *Molecular Ecology*. **14**: 2789-2802.

Waters, J.M., P.M. O'Loughlin, and M.S. Roy. 2004. Cladogenesis in a starfish species complex from southern Australia: evidence for vicariant speciation? *Molecular Phylogenetics and Evolution*. **32**: 236-245.

Waters, J.M and M.S. Roy. 2003. Marine biogeography of southern Australia: phylogeographical structure in a temperate sea-star. *Journal of Biogeography*. **30**: 1787-1796.

Weber, M. and L. F. de Beaufort. 1929. The fishes of the Indo-Australian Archipelago. V. Anacanthini, Allotriognathi, Heterostomata, Berycomorphi, Percomorphi: families Kuhliidae, Apogonidae, Plesiopidae, Pseudoplesiopidae, Priacanthidae, Centropomidae. E. J. Brill Ltd., Leiden. The Fishes of the Indo-Australian Archipelago. v. 5: i-xiv + 1-458.

Whitehead, P. J. P. 1970. The Reeves Collection of Chinese fish drawings. Bulletin of the British Museum (Natural History) Zoology. **3** (no. 7): 191-233, Pls. 1-29.

Whitley, G. P. 1966. Notes on some Queensland fishes. Australian Zoologist. **13**(pt 3): 235-243, Pls. 13-14.

Wilson, B.R. and G.R. Allen (Eds.). 1987. Major components and distribution of marine fauna. Australian Government Publishing Service, Canberra.

Wu, H.-W. 1932. Contribution à l'étude morphologique, biologique et systématique des poissons hétérosomes (Pisces Heterosomata) de la Chine. [Thèses présentées à la faculté des Sciences de l'Université de Paris.]. Contribution à l'étude morphologique, biologique et systématique des poissons hétérosomes (Pisces Heterosomata) de la Chine: 1-178.

Yazdani, G. M. 1976. The specific identity of the sole, *Zebrias zebra* (Bloch) in Indian waters. Journal of the Bombay Natural History Society. **73**(pt 2): 408.

Yokogawa, K., H. Endo, and H. Sakaji. 2008. *Cynoglossus ochiaii*, a new tongue sole from Japan (Pleuronectiformes: Cynoglossidae). Bulletin of the National Museum of Nature and Science (Ser. A) Suppl. 2: 115-127.

York, K.L., M.J. Blackett, and B.R. Appleton. The Bassian Isthmus and the major ocean currents of southeast Australia influence the phylogeography and population structure of a southern Australian intertidal barnacle *Catomerus polymerus* (Darwin). Molecular Ecology. **17**: 1948-1961.

Zheng, P.-S. and Y.-W. Chang. 1965. Studies on the Chinese soleoid fishes of the genus *Zebrias*, with description of a new species from the South China Sea. Acta Zoologica Sinica. **2**(no. 4): 267-278.

## **CHAPTER 2**

**A taxonomic revision of the flatfish genus**

***Pseudaesopia* Chabanaud, 1934 (Pleuronectiformes:**

**Soleidae)**

## ABSTRACT

The flatfish genus *Pseudaesopia* Chabanaud, 1934 (Pleuronectiformes: Soleidae) is re-described and the taxonomic status of its nominal species is revised based on a morphological study of 101 specimens. Previous authors have treated *Pseudaesopia* as a distinct genus or subgenus of an expanded *Zebrias*. Evidence is presented to demonstrate the monophyly of *Pseudaesopia*, distinct from *Zebrias*. The genus is diagnosed by the combination of the attachment of the posteriormost dorsal- and anal-fin rays along their entire lengths to the basal halves of the distal caudal-fin rays; a rounded caudal fin distinct from the dorsal and anal fins; supracranial morphology with 1-2 pterygiophores attached to the erisma, 1-2 pterygiophores present between the erisma and the first neural spine (not directly anchored to the cranium), and 1-4 pterygiophores attached to the first neural spine (= neural spine of the second precaudal vertebra); presence of transverse bands on the ocular side; and the attachment of the pectoral fins to the branchiostegal membrane. Prior to this study, only a single species (*Pseudaesopia japonica* (Bleeker, 1860)) was recognized in the genus *Pseudaesopia*. In the present study, ten nominal species are placed in this genus. Of these ten nominal species, six were recognized as valid and are re-described. These species, along with their synonyms in parentheses, are as follows: *P. callizona* Regan, 1903, *P. cochinchensis* Rama-Rao, 1967 (*Zebrias keralensis* Joglekar, 1976), *P. japonica* Bleeker, 1860 (*Zebrias annandalei* Talwar and Chakrapany, 1967, *Synaptura smithii* Regan, 1903), *P. lucapensis* Seigel and Adamson, 1985, *P. regani* Gilchrist, 1906, and *P. synapturoides* Jenkins, 1910 (*Zebrias crossolepis* Zheng and Chang, 1965). An identification key to the species of *Pseudaesopia* is provided.

## RÉSUMÉ

Le genre de poisson plat *Pseudaesopia* Chabanaud, 1934 (Pleuronectiformes: Soleidae) est re-décrit et le statut taxinomique de ses espèces nominales est examiné suite à une étude morphologique de 101 spécimens. Précédemment, *Pseudaesopia* a été traité en tant que genre distinct ou en tant que sous-genre de *Zebrias*. Dans cette étude, le statut monophylétique de *Pseudaesopia* est confirmé. Ce genre est distinct de *Zebrias*. Les caractères diagnostiques du genre incluent l'ensemble des caractères suivants : une nageoire caudale avec le dernier rayon des nageoires anale et dorsale attachés sur toute leur longueur à la moitié proximale des rayons de la nageoire caudale; une nageoire caudale ronde distincte des nageoires anale et dorsale; 1-2 ptérygiophores attachés à l'érisme, 1-2 ptérygiophores entre l'érisme et la première épine neurale (non ancrée sur le crâne) 1-4 ptérygiophores attachés directement à la première épine neurale (= épine neurale de la seconde vertèbre précaudale); la présence de bandes transversales sur la face oculée; et l'attachement des nageoires pectorales à la membrane branchiostège. Avant notre étude, une seule espèce (*Pseudaesopia japonica* (Bleeker, 1860)) étant reconnue dans ce genre. Maintenant, le genre *Pseudaesopia* contient 10 espèces nominales. De ces dix espèces, six espèces sont valides et sont re-décrites. Les espèces valides et leurs synonymes (indiqués entre parenthèses) sont: *P. callizona* Regan, 1903, *P. cochinensis* Rama-Rao, 1967 (*Zebrias keralensis* Joglekar, 1976), *P. japonica* Bleeker, 1860 (*Zebrias annandalei* Talwar and Chakrapany, 1967, *Synaptura smithii* Regan, 1903), *P. lucapensis* Seigel and Adamson, 1985, *P. regani* Gilchrist, 1906, and *P. synapturoides* Jenkins, 1910 (*Zebrias crossolepis* Zheng and Chang, 1965). Une nouvelle clé d'identification des espèces de *Pseudaesopia* est offerte.

## INTRODUCTION

Evident from the historical literature dealing with the nominal genera *Zebrias* Jordan and Snyder 1900 and *Pseudaesopia* Chabanaud, 1934 is that considerable confusion persists regarding whether to recognize *Pseudaesopia* as distinct from *Zebrias*, and if recognized, what species should be assigned to this genus. *Pseudaesopia* was initially established as a subgenus of *Zebrias* Jordan and Snyder 1900 by Chabanaud (1934), who designated *Synaptura regani* Gilchrist, 1906 as the type species for this subgenus. The subgenus was poorly defined with the only distinctive character noted by Chabanaud (1934) being the deeply indented membrane connecting the posteriormost dorsal- and anal-fin rays to the adjacent caudal-fin rays. Chabanaud described the membrane, which extends from the distal ends of the posteriormost dorsal- and anal-fin rays and adjacent caudal-fin rays, as having a deep indentation reaching only to the proximal quarter of the posteriormost dorsal- and anal-fin rays. He used the indentation in the fin membrane as the main character distinguishing this subgenus from the subgenus *Zebrias*, which has fully confluent dorsal, anal and caudal fins without any indentation in the membranous connection between these fins.

In a later study, Chabanaud (1936), after re-examining a syntype of *Synaptura regani* (which he referred to as the paratype; currently BMNH 1903.12.31.12), realized that the deeply indented membrane he observed connecting the posteriormost dorsal- and anal-fin rays to the adjacent caudal-fin rays actually was only a tear in the membrane. As a result, he proposed that the subgenus *Pseudaesopia* Chabanaud, 1934 be eliminated from nomenclature, and also that *Synaptura regani* remain associated with *Zebrias*.

Despite Chabanaud's recommendation to disregard his subgenus *Pseudaesopia*, subsequent authors continued to recognize *Pseudaesopia* as a valid genus distinct from *Zebrias* (Ochiai, 1963; Kamohara, 1964; Lindberg and Federov, 1993; Sakamoto, 1997; Schwarzhans, 1999; Munroe in Randall and Lim, 2000; Shinohara et al., 2001; Nakabo, 2002; Hoese and Bray, 2006; Eschmeyer, 2010). Six of these publications recognizing *Pseudaesopia* are checklists and catalogues, none of which include critical assessment of the validity of this genus.

Ochiai's study (1963) was the first to treat *Pseudaesopia* as a distinct genus, rather than including it as a subgenus of *Zebrias*. Ochiai apparently did not examine the syntype or any other specimens of *Synaptura regani*, but instead recognized *Pseudaesopia* Chabanaud based on his study of *Aesopia japonica* Bleeker, 1860. Of interest is that although *Synaptura regani* is the type species of the genus *Pseudaesopia*, the generic name *Pseudaesopia* is currently most often associated with the species *P. japonica*, following the study of Ochiai.

Ochiai (1963), expanding on Chabanaud's original description of *Pseudaesopia*, provided the first comprehensive description of the genus based on numerous external and internal morphological features. Some of the distinguishing characteristics of the genus according to Ochiai (1963) are the distinct caudal fin that is only partially confluent with the dorsal and anal fins, contiguous eyes, the higher number of pectoral-fin rays, the short, asymmetrical pectoral fins, a comparatively long ocular-side anterior nasal tube reaching to the anterior rim of the ventral eye, and the number of caudal-fin rays (18).

Ochiai distinguished *Pseudaesopia* from *Zebrias* on the basis of several characters including the moderately long ocular-side anterior nasal tube that reaches the anterior margin of the ventral eye when flattened, the well-elevated interorbital space, a caudal fin scarcely or nearly confluent with the vertical fins, a greater number of pelvic- and caudal-fin rays, and well-diverged hypurals. It should be noted that Ochiai's diagnoses of these two genera were restricted only to those species of these genera occurring in Japanese waters. He did not report on the presence of diagnostic characters in other species of *Zebrias* occurring beyond this region.

In his remarks on the genus *Pseudaesopia*, Ochiai noted that some features of this genus were intermediate between those occurring in *Soleichthys* Bleeker 1860 and *Zebrias*. These included a partially distinct caudal fin, somewhat wavy or irregular bands (seen only in *P. japonica*), and the frequently longer ocular-side anterior nasal tube. Both *Zebrias* and *Soleichthys* were noted as sharing several of the characters that Ochiai identified as defining *Pseudaesopia*. Ochiai contended that despite these similarities, the characters distinguishing *Zebrias* from *Pseudaesopia* warranted separating them as distinct genera.

Few other studies have commented on the status of *Pseudaesopia*. As mentioned above, most studies citing this genus are regional checklists or catalogues with no taxonomic comments provided. For example, Lindberg and Federov (1993) who examined two specimens of *P. japonica* (Bleeker, 1860), provided a detailed account of the genus *Pseudaesopia* and *P. japonica*, however, much of their chapter on this species and the genus *Pseudaesopia* was information cited directly from Ochiai (1963).

Schwarzahns (1999) examined otoliths of a diverse number of flatfish species, including otoliths from *Pseudaesopia japonica* and a variety of species in related genera. He observed that otoliths of *Pseudaesopia* closely resemble those of *Zebrias* and *Soleichthys*. In fact, due to the particularly strong similarity in otolith morphology (nearly rectangular otoliths) between *Pseudaesopia* and *Zebrias*, he commented that *Pseudaesopia* could be retained as a subgenus within *Zebrias* rather than recognizing this as a separate genus. Despite this statement, Schwarzahns (1999) nevertheless recognized the genus *Pseudaesopia* and included three species in this genus: *P. regani*, *P. crossolepis* Zheng and Chang, 1965, and *P. japonica*. He also proposed, again based primarily on similarities in their otolith morphology to other species assigned to *Pseudaesopia*, that three additional nominal species, *Zebrias altipinnis* (Alcock, 1890), *Pseudaesopia synapturoides* (Jenkins, 1910) and *Zebrias cancellatus* (McCulloch, 1916), could also be placed in *Pseudaesopia*.

In the most recent edition of the *Catalogue of Fishes*, Eschmeyer (2010) considers *Pseudaesopia* Chabanaud, 1934 as a subgenus of *Zebrias* Jordan and Snyder 1900. He does not indicate subgeneric assignment of species within the concept of *Zebrias*.

Throughout the history of *Pseudaesopia*, from creation of the subgenus by Chabanaud (1934), through the treatments of Ochiai (1963) and Schwarzahns (1999), to the most current listing of genera and species (Eschmeyer, 2010), no consistent application of nomenclature has been available for this nominal taxon (subgenus or genus). Even when recognized as a distinct taxon, there also has been no agreement as to how many species should be assigned to it. The primary goal of this chapter is to evaluate the status of *Pseudaesopia* Chabanaud relative to *Zebrias* and other related

nominal genera through detailed morphological examination of the type and other species of each of the nominal genera. The second objective of the chapter, once the status of this taxon is established, is to evaluate all of the nominal species currently associated with *Zebrias* and *Pseudaesopia* and to determine their appropriate taxonomic assignment.

#### **Recognition of *Pseudaesopia* Chabanaud, 1934**

Chabanaud's (1934) erection of the subgenus *Pseudaesopia* was based on *Synaptura regani*. His primary character for recognizing this as a distinct subgenus was the purported presence of a deep indentation in the membranous connection between the dorsal and anal fins and the caudal fin. In a later study, Chabanaud (1936) realized that the deep indentation was not a reliable diagnostic character for recognition of a distinct subgenus, but rather the indentation resulted merely from a tear in the fin membrane. Consequently, he recommended that *Pseudaesopia* not be recognized. Although Chabanaud (1936) discounted this feature as an important diagnostic character to distinguish *Pseudaesopia*, re-examination of the syntypes of *Synaptura regani* reveal that the degree of attachment of the posteriormost dorsal- and anal-fin rays with the adjacent caudal-fin rays is distinct from that observed in other species of *Zebrias*, including the type species *Z. zebra* (Bloch, 1787). Other distinguishing characters of *Synaptura regani* include contiguous eyes and a high pectoral-fin ray count (9-11 rays each fin).

Ochiai (1963) resurrected the genus *Pseudaesopia* Chabanaud based on his study of *Aesopia japonica* and *Zebrias zebra* from Japanese waters. Because he examined only *P. japonica* and *Zebrias zebra*, observed differences between these nominal genera are largely limited to differences between these species. Although he did not directly

compare *Aesopia japonica* with the type species of *Pseudaesopia*, *Synaptura regani*, the two species share many similarities. Like *S. regani*, *Aesopia japonica* is characterized by having: a distinct caudal fin only partially confluent with the dorsal and anal fins; contiguous eyes; comparable numbers of pectoral-fin rays; short pectoral fins; a comparatively long ocular-side anterior nasal tube reaching the anterior rim of the ventral eye; and these species also have the same number of caudal-fin rays (18). Some of the characters Ochiai thought to be diagnostic for *Pseudaesopia* are not found in the type species. For example, Ochiai commented that the genus is further defined as having five pelvic-fin rays; however, this count is not diagnostic of the genus because it differs from the fin-ray count in the type species, *Synaptura regani*, which only has four rays in each pelvic fin. Furthermore, Ochiai stated that the position of the genital papilla of *Aesopia japonica*, which is connected to the ocular-side pelvic fin by a membrane, is diagnostic for the genus *Pseudaesopia*. Again, this is not a diagnostic feature of the genus because the genital papilla is free from the pelvic fin in *Synaptura regani*.

Ochiai (1963) recognized an overall similarity among several nominal genera in his study including *Pseudaesopia*, *Zebrias* and *Soleichthys*. Some features of *Pseudaesopia* were found to be intermediate between those of *Zebrias* and *Soleichthys*, including the partially distinct caudal fin, somewhat wavy or irregular bands (seen only in *Pseudaesopia japonica*), and frequently longer ocular-side anterior nasal tube. Ochiai contended that although there were overlaps in these characters, there were sufficient differences to warrant recognizing *Pseudaesopia* from *Zebrias* as distinct genera.

Retention of the genus *Pseudaesopia* Chabanaud is proposed for the following reasons: 1- the nominal species of *Pseudaesopia* differ from species of *Zebrias*, *Aesopia*

and *Soleichthys* in the degree of attachment of the posteriormost dorsal- and anal-fin rays with the adjacent caudal-fin rays and this character is unique to this genus; 2- preliminary evidence based on otolith morphology (Schwarzhan, 1999) suggests that two different taxa (either genera or subgenera) are represented among species currently assigned to either *Zebrias* or *Pseudaesopia*.

Several nominal species currently assigned to *Zebrias* share characters exhibited by *Synaptura regani*, including a distinct caudal fin with the posteriormost dorsal- and anal-fin rays attached only to the basal half of the adjacent caudal-fin rays; contiguous eyes; and a high pectoral-fin ray count. The following nominal species fit the current definition of *Pseudaesopia*: *Zebrias annandalei* Talwar and Chakrapany, 1967; *Synaptura callizona* Regan, 1903; *Zebrias cochinchensis* Rama-Rao, 1967; *Zebrias crossolepis* Zheng and Chang, 1965; *Aesopia japonica* Bleeker, 1860; *Zebrias (Nematozebias) keralensis* Joglekar, 1976; *Zebrias lucapensis* Seigel and Adamson, 1985; *Synaptura regani* Gilchrist, 1906; *Synaptura smithii* Regan, 1903; and *Solea synapturoides* Jenkins, 1910. These differentiations are thought to be sufficient to warrant removing these species from their current generic assignments and placing them in *Pseudaesopia*.

### **Biological Studies**

As with *Zebrias*, few studies other than taxonomic revisions, species descriptions, and catalogues of species inhabiting particular regions have been published on the subject of *Pseudaesopia* species. A study by Taki (1938) on the arrangement of scales and transverse bands present in the species *Pseudaesopia japonica* (Bleeker, 1860) is one of

the few examples of biological studies dealing with this genus. Consequently, little is known of their behaviour and ecology.

### **Genus *Pseudaesopia* Chabanaud, 1934**

*Pseudaesopia*: Chabanaud, 1934: 424 (original description based on *Synaptura regani* Gilchrist, 1906; Natal, South Africa); Ochiai, 1963: 49 (expanded concept of genus *Pseudaesopia* based on *Aesopia japonica* Bleeker, 1860)

*Zebrias* (*Pseudaesopia*) – Eschmeyer, 2010 (*Pseudaesopia* considered subgenus of *Zebrias*)

**Type species:** *Synaptura regani* Gilchrist, 1906: 160 (original designation; type locality Natal, South Africa).

**Diagnosis:** Caudal fin only partially confluent with vertical (= dorsal and anal) fins, posteriormost vertical-fin rays extending only as far as basal half of caudal fin; posteriormost vertical-fin rays attached by thin membrane along their entire lengths to adjacent caudal-fin rays; eyes contiguous; pectoral-fin ray count usually 9-14 (one species with 6-10); transverse bands on ocular side from base of caudal fin to snout; branchiostegal membrane connected to upper pectoral-fin rays; supracranial morphology with 1-2 pterygiophores attached directly to erisma, 1-2 pterygiophores in space between cranium and first neural spine (not directly anchored to either) and 1-4 pterygiophores attached to first neural spine (= neural spine of the second precaudal vertebra); 18 caudal-fin rays.

**Description:** Epicranial morphology with 3-6 ( $\bar{x}$  = 4.3, SD = 0.7) supracranial pterygiophores (Table 2.2): 1-2 pterygiophores attached directly to erisma, 1-2

pterygiophores between erisma and first neural spine (not directly anchored to either), and 1-4 pterygiophores attached to first neural spine. Commonly observed pattern is 1-1-2. Erisma in close proximity to first neural spine without being in contact. First neural spine either curving anteriorly over posterior portion of cranium or straight with enlarged distal end. Precaudal vertebrae have a neural spine, except for the anteriormost, which is just a centrum. Precaudal vertebrae typically 9, infrequently 8 or 10 (Table 1.1). Vertebrae 40 to 45 (Table 2.1). Haemapophyses observed on last 4-6 precaudal vertebrae; usually 5 (Table 2.1). Lateral-line scales from opercular margin to caudal peduncle 58-103 (Table 2.5). Dorsal-fin rays 67-83 (Table 2.4); anal-fin rays 53-71 (Table 2.4); caudal-fin rays typically 18 (Table 2.4). Ocular-side pectoral-fin rays 6-14 (5/6 species with 9-14 ocular-side pectoral-fin rays; see Table 2.3); blind-side pectoral-fin rays 6-13. Pelvic-fin rays 4-5 (Table 2.3).

Small-sized group of soles, attaining total lengths to about 19 cm. Body oblong with greatest depth and thickness just posterior to opercular margin; body tapering at posterior end. Head shape somewhat wider than long.

Eyes contiguous; slightly subequal. Ventral eye situated in posterior groove of upper lip. Dorsal eye aligned with ventral eye or situated slightly anterior to it. Ocular tentacles absent.

Ocular-side anterior nostril a posteriorly oriented, elongate tube. When flattened posteriorly, tube minimally reaching posterior nasal tube and usually extending as far as anterior margin of ventral eye. Base of anterior nasal tube wider than aperture. Ocular-side posterior nostril a short, ventrally oriented, circular tube, situated directly adjacent to ventral eye; its length typically two to three times shorter than anterior tube. Blind-side

anterior nostril a short, uneven tube, higher end covering nasal aperture in preserved specimens; anterior tube often inconspicuous, hidden amidst dense patch of cirri.

Anterior nasal tube situated slightly dorso-anteriorly to dorsalmost point of mouth.

Blind-side posterior nasal tube situated dorso-posteriorly relative to anterior nasal tube, at vertical through posterior edge of mouth and at posterior margin of dense patch of cirri on anterior region of head. Blind-side posterior nasal tube slightly larger than ocular-side counterpart, tapering toward its distal end; oriented posteriorly.

Mouth longer and less strongly curved on ocular side, posterior margin of jaws extending no farther posteriorly than vertical through midpoint of ventral eye. Ocular-side lips smooth. Blind-side lower lip plicate. Teeth minute, villiform, restricted to blind-side jaws; often restricted to posterior end of jaws.

Anterior margin of blind-side head with nearly continuous patch of conspicuous cirri, originating near anterior end of dorsal fin and curving ventrally around posterior margin of mouth, cirri also covering chin and opercular margin. Cirri sometimes associated with blind-side lateral line. Mid-head region on blind side occasionally with sparsely distributed cirri between scales posterior to dense patch on anterior end of head. Cirri often present along a small portion of lateral line in region posterior to opercular margin. When present, ocular-side cirri restricted to opercular margin.

Branchiostegal membrane attaching to upper rays of pectoral fin on both sides.

Lateral line well developed on both sides. On ocular side, mediolateral line extending along middle of body from point slightly anterior to opercular margin to caudal peduncle. On head, supraorbital line curving around dorsal eye before straightening

towards snout. Blind-side mediolateral line extending horizontally from opercular margin to caudal peduncle; absent or inconspicuous on head.

Scales moderately to strongly ctenoid on both sides; lateral-line scales cycloid. Scales present or absent in interorbital space; interorbital scales smaller than body scales. Body scales of comparable size on ocular and blind sides.

Anterior end of dorsal fin at, or slightly anterior to, vertical at anterior margin of dorsal eye. First anal-fin ray just posterior to anus, near distal ends of pelvic fins. Vertical-fin rays increasing in length posteriorly in fins; longest rays situated in vicinity of caudal fin, but not those directly adjacent to it. Caudal fin rounded and distinct from dorsal and anal fins. Posteriormost anal-fin ray length 30% to 62% relative to caudal fin length (Figure 1.10). Thin membrane attaching posteriormost vertical-fin rays along their entire lengths to basal halves of adjacent caudal-fin rays. Scales smaller than those on body extending onto dorsal, anal and caudal fins on both ocular and blind sides of these fins.

Scales present on base of ocular-side pectoral fin; scales absent on blind-side fin. Pectoral fins rudimentary, fin rays decreasing in length toward ventral end. Pectoral fins typically asymmetrical, ocular-side fin somewhat longer than blind-side counterpart. Pectoral-fin rays simple, arranged in parallel.

Pelvic fins inserted just anterior to anus, often partially or completely covering it. Pelvic fins not attached to anal fin; generally asymmetrical, ocular-side fin slightly longer.

Anus on midline of body or slightly submedian on blind side. Genital papilla submedian on ocular side. Some species with genital papilla attached to posteriormost ocular-side pelvic-fin ray by thin membrane.

**Pigmentation of preserved specimens:** Ocular side with series of transverse bands from base of caudal fin to snout. Bands may be arranged in pairs, as singular bands, or a combination of these two. Band morphology and arrangement varies interspecifically and, to a lesser degree, intraspecifically. Bands typically relatively uniform in width across body, those on head becoming narrower. Ocular-side pigmentation ranging from light to dark- grey or brown. Blind side typically pale, whitish, with no conspicuous pigmentation. Minute, almost inconspicuous dark spots often present on blind side along posterior median-fin margins; may be found in higher concentration and extend onto head, creating a dusky appearance. Ocular-side anterior nasal tube pigmented; posterior tube typically whitish with few, minute, dark spots. Blind-side nasal tubes whitish. Interior of mouth typically pale with minute, dark spots or uniformly charcoal. Bands extending onto dorsal and anal fins, becoming darker and bending posteriorly to follow direction of vertical-fin rays. Ocular-side caudal fin pigmentation varying interspecifically with subtle intraspecific variations. Ocular-side pectoral fin darkly pigmented; blind-side fin transparent or mostly transparent with minute, dark spots. Pelvic fins whitish.

**Geographic distribution:** *Pseudaesopia* is an Indo-Pacific genus, ranging from eastern South Africa, and extending to the Persian Gulf, India, Indonesia, Australia, China, and Japan.

**Comparisons:** *Pseudaesopia* is most closely related to *Zebrias* Jordan and Snyder, 1900, with which it shares similar meristic values. The genera are distinguished by the attachment of the caudal fin. The caudal fin among species of *Pseudaesopia* is quite rounded and distinct, whereas the caudal fin is completely or nearly confluent with the dorsal and anal fins among species of *Zebrias* (Figure 1.10; Chapter 1). Within *Pseudaesopia*, the posteriormost anal-fin ray extends 30% to 62% of the caudal-fin length; within *Zebrias*, the posteriormost anal-fin ray length is 59% to 95% relative to the caudal-fin length; within The longest vertical-fin ray of *Pseudaesopia* species is 54% HL on average (standard deviation = 0.06); the corresponding value for *Zebrias* species is 67% HL (standard deviation = 0.09).

*Pseudaesopia* can be easily distinguished from *Aesopia* Kaup, 1858 by the presence of moderately to strongly ctenoid scales (those of *Aesopia* are very weakly ctenoid and have the appearance and texture of being cycloid), the absence of an enlarged first dorsal-fin ray, and an inconspicuous blind-side anterior nasal tube (that of *Aesopia* is of comparable length to the posterior tube on the same side). Moreover, *Pseudaesopia* species typically have five haemapophyses and nine precaudal vertebrae, whereas *Aesopia* typically has six and ten, respectively (Table 2.1 and Table 1.1). In addition, *Aesopia* typically has a higher number of pectoral-fin rays (Table 1.4 and Table 2.3).

*Pseudaesopia* differs from *Phyllichthys* McCulloch, 1916 in having the anal fin free from the ocular-side pelvic fin (in *Phyllichthys*, they are attached) and regular, transverse bands (absent in *Phyllichthys*, apart from *P. munroi* which has highly irregular, wavy bands; Figure 1.5).

*Soleichthys* Bleeker, 1860 bears a strong resemblance to *Pseudaesopia*. Both genera are characterized by having a distinct caudal fin; however, in *Soleichthys*, the caudal fin is attached to the adjacent vertical fins by a thin membrane at its base. *Soleichthys* is also readily distinguished by its longer ocular-side anterior nasal tube, which minimally reaches the middle of the ventral eye when flattened posteriorly.

Table 2.1. Frequency distribution of vertebral counts and haemapophyses on the abdominal vertebrae among recognized species of *Pseudaesopia*. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material.

Species	Vertebrae						n	Mean	SD
	40	41	42	43	44	45			
<i>P. callizona</i>					4	1*	5	44.2	0.4
<i>P. japonica</i>	2	6	27*	5	4		44	42.1	0.9
<i>P. cochinensis</i>		1	1	6			8	42.6	0.7
<i>P. lucapensis</i>		2*	2*				4	41.5	0.6
<i>P. regani</i>			1	6*		1	8	43.1	0.8
<i>P. synapturoides</i>			7	16*	1		24	42.8	0.5

Species	Haemapophyses			n	Mean	SD
	4	5	6			
<i>P. callizona</i>	1	2*	2	5	5.2	0.8
<i>P. japonica</i>		35*	11	46	5.2	0.4
<i>P. cochinensis</i>		7	1	8	5.1	0.4
<i>P. lucapensis</i>		4*		4	5	0
<i>P. regani</i>		6*	2	8	5.3	0.5
<i>P. synapturoides</i>		23*	1	24	5.0	0.2

Table 2.2. Frequency distribution of supracranial complex patterns of the dorsal fin and the number of supracranial pterygiophores of the dorsal fin on and anterior to the first neural spine among recognized species of *Pseudaesopia*. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material. See Materials and Methods for definition of supracranial complex.

Species	Supracranial Pattern											n		
	0-2-2-	1-0-2-	1-1-1-	1-1-2-	1-1-3-	1-1-4-	1-2-1-	1-2-2-	1-2-3-	2-1-1-	2-1-2-			
<i>P. lucapensis</i>				1*	3*							4		
<i>P. synapturoides</i>			1	8	12*	2			1			24		
<i>P. japonica</i>			6	20*	2	1	3	3		2	8	45		
<i>P. regani</i>	1		1*	6*								8		
<i>P. callizona</i>		1	1*	3								5		
<i>P. cochinchensis</i>				7				1				8		
	Number Supracranial Pterygiophores											n	Mean	SD
	3	4	5	6										
<i>P. callizona</i>	2*	3										5	3.6	0.5
<i>P. japonica</i>	6	25*	13	1								45	4.2	0.7
<i>P. regani</i>	1*	7*										8	3.9	0.4
<i>P. cochinchensis</i>		7	1									8	4.1	0.4
<i>P. lucapensis</i>		1*	3*									4	4.8	0.5
<i>P. synapturoides</i>	1	8	12*	3								24	4.7	0.8

Table 2.3. Frequency distribution of ocular-side pectoral- and pelvic-fin rays among recognized species of *Pseudaesopia*. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote the value for type material.

<b>Ocular-Side Pectoral-Fin Rays</b>												
Species	6	7	8	9	10	11	12	13	14	n	Mean	SD
<i>P. japonica</i>	3	12	14*	12	5			1		47	8.2	1.3
<i>P. cochinchensis</i>						1	1	4	1	7	12.7	1.0
<i>P. lucapensis</i>					3*	1*				4	10.3	0.5
<i>P. regani</i>				2	4*	2				8	10.0	0.8
<i>P. synapturoides</i>				3	6*	7	8			24	10.8	1.0
<i>P. callizona</i>			1	4*						5	8.8	0.4
<b>Ocular-Side Pelvic-Fin Rays</b>												
	3	4	5	6								
<i>P. japonica</i>		8	40*									
<i>P. cochinchensis</i>	1	7										
<i>P. lucapensis</i>			3*	1								
<i>P. regani</i>		7*	1									
<i>P. synapturoides</i>		5	19*									
<i>P. callizona</i>			5*									

Table 2.4. Frequency distribution of dorsal-, anal-, and caudal-fin rays among recognized species of *Pseudaesopia*. The sample size (n), mean, and standard deviation (SD) are presented. Asterisks denote value for type material.

Species	Dorsal-Fin Rays															n	Mean	SD			
	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81				82	83	85
<i>P. callizona</i>											1	2		1			1*	5	79.2	2.4	
<i>P. japonica</i>				3		2	2*	5	3	8*	7	3	5	1	2	2			43	76.2	3.0
<i>P. cochinensis</i>	1		1	1		2	1	1		1								8	71.6	2.9	
<i>P. lucapensis</i>				1	1	1*	1*											4	70.5	1.3	
<i>P. regani</i>	1	2*	2	1*	1	1												8	69.3	1.7	
<i>P. synapturoides</i>			2			2	3	3	9	2	1	1	1*					24	74.3	2.3	

Species	Anal-Fin Rays															n	Mean	SD		
	53	55	56	57	58	59	60	61	62	63	64	65	66	67	68				70	71
<i>P. callizona</i>									1		1	2				1*		5	65.2	2.9
<i>P. japonica</i>					1	2	5	6	5*	6*	7	5	2	1	3		1	44	63.1	2.8
<i>P. cochinensis</i>	1			3	1	2	1											8	57.5	2.1
<i>P. lucapensis</i>	1	1*		1*	1													4	55.8	2.2
<i>P. regani</i>		1		2*	1	1*	2	1										8	58.4	2.0
<i>P. synapturoides</i>			2	1	2	3	8	2	4	1*	1							24	60.0	2.0

Species	Caudal-Fin Rays				n	Mean	SD
	16	17	18	19			
<i>P. callizona</i>			4*		4	18.0	0
<i>P. japonica</i>		5	39*	2	46	17.9	0.4
<i>P. cochinensis</i>			8		8	18.0	0
<i>P. lucapensis</i>			4*		4	18.0	0
<i>P. regani</i>			8*		8	18.0	0
<i>P. synapturoides</i>	1	22*			23	18.0	0.2



*Pseudaesopia callizona* (Regan, 1903)

Figures 2.1-2.2, Table 2.6



Figure 2.1. Photographs of *Pseudaesopia callizona*, QM I. 28002, 84 mm SL, Gulf of Carpentaria, depicting the ocular (above) and blind (below) sides.

**Synonym(s):** *Synaptura callizona* Regan 1903.

**Common name(s):** None known.

**Material Examined:** 5 specimens (69.05-128.8 mm TL)

**Type material:** BMNH1879.514.68, Holotype, 1(113.2 mm SL), Arafura Sea

**Non-type material:** LACM Uncategorized, 1(89 mm SL), Alpha Helix Station, Southeast Asia; NTMS.14280-003, 1(61.6 mm SL), NW of Weipa, Gulf of Carpentaria, Queensland, Gulf20; QMI.28002, 1(83.63 mm SL), Gulf of Carpentaria; CSIROH4193-01, 1(58.91 mm SL), NT, Arafura Sea, north of Wessel Islands.

**Diagnosis:** A species of *Pseudaesopia* with the following combination of characters: 14-17 thinly-demarcated, singular bands; 77-83 dorsal-fin rays; 62-70 anal-fin rays; 44-45 vertebrae; 90-100 lateral-line scales; ocular-side pectoral-fin length 61-82% HL with upper two rays elongate; genital papilla attached to ocular-side pelvic fin; caudal fin with solid black distal end, or whitish with 4-5 oblong black spots at its distal end; blind side with minute dark spots around head and median-fin margins.

**Description:** Meristic and morphometric characters are indicated in Table 2.6. Small sole, attaining a total length of 13 cm. Supracranial pterygiophores 3-4; formula: 1-1-(1-2). Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes contiguous without ocular tentacles. Dorsal eye slightly in advance of ventral eye with posterior margin of dorsal eye situated approximately at vertical through midpoint of ventral eye. Interorbital scales present. Ocular-side anterior nasal tube surpassing anterior margin of ventral eye when flattened; aperture of tube narrower than base, oriented posteriorly. Ocular-side posterior nasal tube approximately 1/3 the length of anterior; located directly adjacent to ventral eye,

oriented ventrally. Blind-side anterior nostril inconspicuous; nostril a short, uneven tube, bordered by cirri. Anterior nostril slightly dorso-anterior to dorsalmost point of mouth. Posterior nasal tube dorso-posterior to anterior nasal tube, at a vertical through posterior edge of mouth. Posterior tube whitish with dark pigment spots, aperture narrower than base. Posterior margin of ocular-side jaws just surpassing anterior margin of ventral eye. Ocular-side lips smooth. Blind-side lower-lip plicate. Teeth minute, restricted to blind-side jaws. Ocular-side cirri restricted to short fringe along opercular margin. Cirri densely distributed at anterior end of blind-side head, extending along snout, chin and opercular margin. More sparsely-distributed cirri often found on mid-head region between scales posterior to dense patch of cirri on anterior region, cirri not extending posterior to opercular margin. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line well developed on both sides. Supraorbital line present on ocular-side head. Blind-side lateral line not extending anterior to opercular margin. Lateral-line scales cycloid. Scales on body moderately ctenoid, rectangular, with 10-18 ctenii on ocular-side scales and 12-14 ctenii on blind-side scales. Anterior end of dorsal fin at vertical through midpoint of dorsal eye or slightly anterior to vertical through anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Caudal fin rounded and distinct. Scales extending onto median fins. Ocular-side pectoral fin relatively long (61-82% HL); upper two rays elongate and of comparable length. Third dorsalmost ray roughly one third to one half length of upper rays; more ventral rays decreasing gradually in length. Blind-side pectoral fin short (14-24% HL); dorsalmost ray longest with more ventral rays decreasing gradually in length. Ocular-side and blind-side pelvic fins of comparable length. Anus slightly submedian on blind side in holotype;

in other specimens, anus more or less centralized along ventral midline. Genital papilla submedian on ocular side, adjacent to anus; attached to ocular-side pelvic fin by thin membrane.

**Pigmentation of preserved specimens:** Ocular side greyish with series of 14-17 singular, darkly-bordered brown bands: 3-5 on head, 10-12 on body. Bands relatively uniform in width across body, those on head becoming narrower. Blind side whitish with minute black spots, primarily concentrated on head and along median-fin margins. Interior of mouth charcoal or whitish with minute, black spots. Bands extending onto vertical fins, becoming black at their distal ends. Inter-band spaces on dorsal and anal fins whitish-grey. Blind sides of median fins uniformly dark. Proximal half of ocular-side caudal fin dark brown, distal end white with 4-5 elongate, black, oval blotches. Alternatively, proximal end brown, middle white or grey, distal end solid black. Upper two rays of ocular-side pectoral fin darkly pigmented. Blind-side pectoral fin of most specimens mostly transparent with minute black spots; others with transparent fins. Pelvic fins whitish.

Table 2.6. Meristic and morphometric characteristics of type and non-type specimens of *Pseudaesopia callizona*. Means and standard deviations are shown in parentheses. Measurements and abbreviations are described in Appendix B.

	<i>Synaptura callizona</i> holotype	<i>Pseudaesopia callizona</i> non-type specimens (n=4)
<b>Standard length (mm)</b>	113.2	58.91-89.00 (73.29; 15.2)
<b>Total length (mm)</b>	128.8	69.05-102.36 (84.23; 17.0)
<b>Counts</b>		
Dorsal-fin rays	83	77-83 (79; 2.7)
Anal-fin rays	70	62-70 (65.5; 3.3)
Caudal-fin rays	18	18 (18; 0) <sup>1</sup>
Precaudal vertebrae	9	8-9 (8.8; 0.5)
Caudal vertebrae	36	35-36 (35.5; 0.6)
Total vertebrae	45	44 (44; 0)
Haemopophyses	5	4-6 (5; 0.8)
Pterygiophores	7	6-7 (6.7; 0.6)
Pectoral-fin rays o.s.	9	8-9 (8.8; 0.5)
Pectoral-fin rays b.s.	6	6-9 (8; 1.4)
Pelvic-fin rays o.s.	5	5 (5; 0)
Pelvic-fin rays b.s.	5	4-5 (4.8; 0.5)
Lateral-line scales	100	90-100 (94.8; 4.6)
Number of bands	15	14-15 (14.3; 0.5)
<b>Measurements</b>		
<b>%SL</b>		
Head length	0.18	0.17 (0.17; 0.004)
Head depth	0.19	0.18-0.20 (0.19; 0.009)
Body depth	0.37	0.31-0.36 (0.35; 0.02)
Caudal fin length	0.14	0.14-0.17 (0.15; 0.02)
Width caudal peduncle	0.06	0.06-0.07 (0.07; 0.009)
<b>%HL</b>		
Length of pectoral fin o.s.	0.66	0.61-0.82 (0.71; 0.09)
Length of pectoral fin b.s.	0.24	0.14-0.22 (0.18; 0.04)
Length of pelvic fin o.s.	0.36	0.30-0.47 (0.40; 0.08)
Length of pelvic fin b.s.	0.35	0.31-0.47 (0.39; 0.07)
Pre-orbital head length	0.21	0.17-0.20 (0.18; 0.01)
Post-orbital head length	0.57	0.56-0.68 (0.64; 0.05)
Snout length	0.22	0.23-0.26 (0.25; 0.01)
Nostril to snouth distance	0.08	0.14-0.19 (0.17; 0.03)
Mouth length o.s.	0.24	0.27-0.46 (0.35; 0.08)
Mouth length b.s.	0.20	0.24-0.29 (0.26; 0.02)
Ventral eye diameter	0.21	0.28-0.31 (0.29; 0.01)
Width of orbits	0.26	0.35-0.43 (0.39; 0.04)
Longest dorsal ray	0.62	0.63-0.85 (0.69; 0.1)
Longest anal ray	0.72	0.61-0.71 (0.65; 0.04)
IOD/V	0	0
BPc/OPc	0.36	0.23-0.32 (0.25; 0.05)
BPv/OPv	0.99	0.92-1.05 (0.99; 0.07)

<sup>1</sup>: n=3.

**Geographic distribution:** Species has been reported from the Arafura Sea and the Gulf of Carpentaria at depths of 15-55 m.

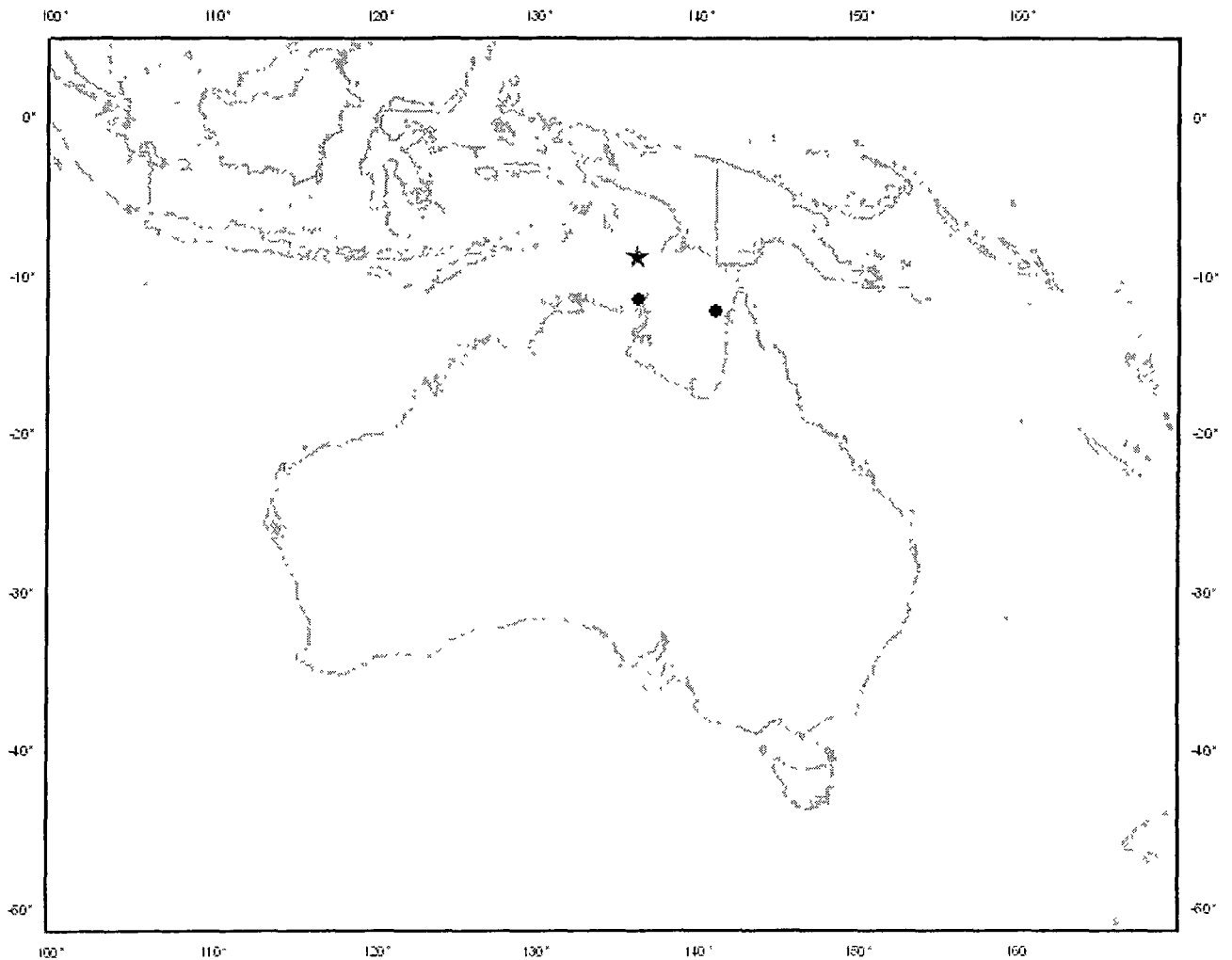


Figure 2.2. Geographic distribution of *Pseudaesopia callizona*. Star denotes locality of type material.

**Remarks:** The original description states that the anterior seven bands in this species bifurcate at the dorsal or ventral end, whereas the posterior seven bands do not. Based on specimens examined in the present study, the bifurcation of bands appears to be random. As previously discussed, banding pattern variations and band abnormalities are relatively common within this genus. Banding irregularities are particularly common among specimens of *Pseudaesopia japonica* (Bleeker, 1860), the most closely allied species to *P. callizona*. A discrepancy was noted in the median-fin ray counts reported in the original description; Regan (1903) reported 15 caudal-, 82 dorsal-, and 68 anal-fin rays for the holotype, whereas the present authors recorded 18, 83, and 70 rays, respectively.

**Comparisons:** With the exception of its most closely allied species, *P. japonica*, *P. callizona* can be easily distinguished from all of its congeners by its caudal fin pigmentation (other species with light spots), pectoral-fin morphology and length (other species without upper two rays elongate; mean length 14-39% HL), higher number of scales along the lateral line (other species with 58-85), and the attachment of the genital papilla to the ocular-side pelvic fin (detached in other species). *P. japonica* differs from *P. callizona* by its blind-side pigmentation (pale, conspicuous pigmentation absent), irregular band morphology and arrangement (somewhat wavy, thickly-demarcated bands in pairs, singular, or a combination of the two), and generally fewer vertebrae (40-44).

*Pseudaesopia cochinensis* (Rama-Rao, 1967)

Figures 2.3-2.5, Table 2.7

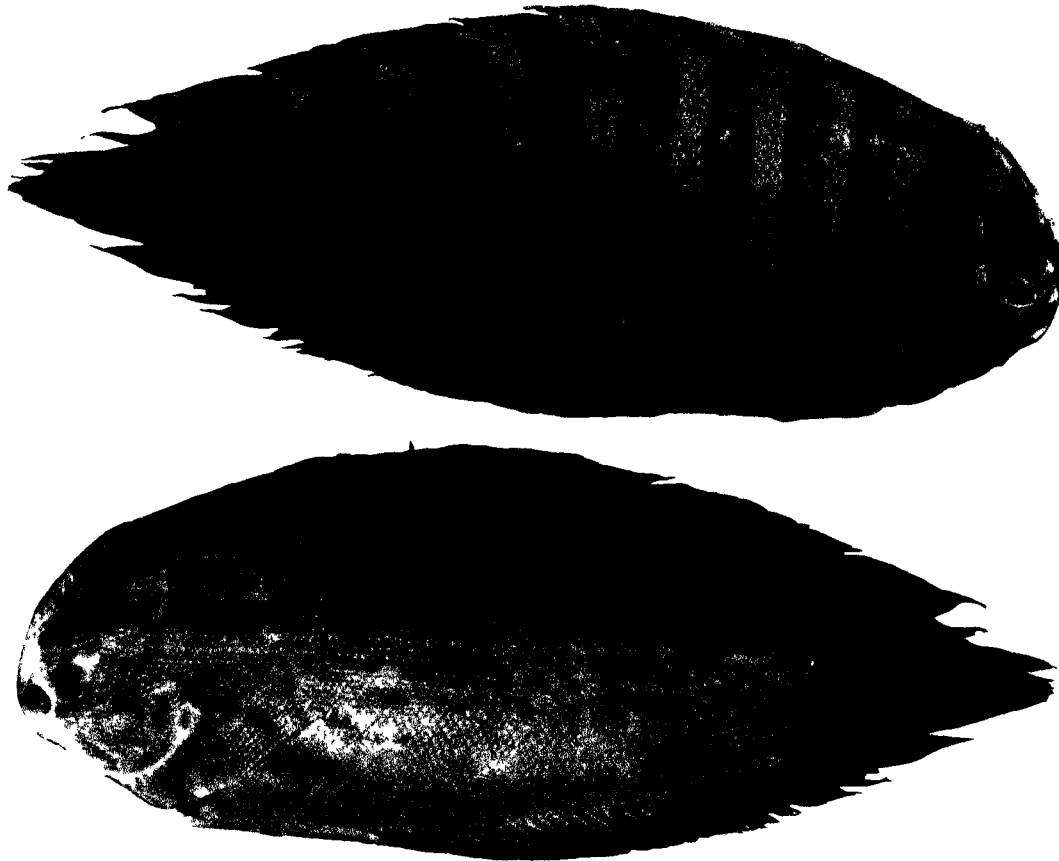


Figure 2.3. Photographs of *Pseudaesopia cochinensis*, USNM uncatalogued, 138 mm SL, India, depicting the ocular side (above) and the blind side (below).

**Synonym(s):** *Zebrias cochinensis* Rama-Rao, 1967; *Zebrias (Nematozebrias) keralensis* Joglekar, 1976.

**Common name(s):** None known.

**Material examined:** 8 specimens (78.54 to 158.68 mm TL)

**Type material (not examined):** ZSI F.6822/2, Holotype 1(122 mm SL), Aleppy Kerala coast; ZSI F.6823/2, Paratypes, 3(82-114 mm SL), Aleppy Kerala coast.

**Non –type material:** LACM38128-10, 1(91.25 mm SL), Pakistan, Sind, Hawkes Bay, just west of Karachi; USFWS-1965-1966 Acc. 261501, 2(115.42-134.47 mm SL), Vizhinjam, India; BPBM uncatalogued, 3(68.30-127.46 mm SL), India, Cochin; USNM uncatalogued, 1(137.89 mm SL), India; MNHN 1981-1169, 1(134.36 mm SL), Cochin, Kerala State, South India, Sector 5124, 9°933'N, 76°083'E, fish harbour.

**Diagnosis:** A species of *Pseudaesopia* with the following combination of characters: thirteen singular, darkly demarcated bands on body; 11-14 pectoral-fin rays on ocular side (11-13 on blind side); 4 pelvic-fin rays; ocular-side pectoral-fin length 28-48% HL (average 39% HL) with upper 4-5 rays of comparable length, more ventral rays decreasing gradually in length; 75-85 lateral-line scales; interorbital scales present; ocular-side anterior nasal tube just reaching posterior nasal tube when flattened; average 4 supracranial pterygiophores anterior to the first neural spine.

**Description:** Meristic and morphometric characters are indicated in Table 2.7. Small sole, attaining a total length of 16 cm. Supracranial pterygiophores 4-5 ( $\bar{x} = 4$ ); formula: 1-1-2, rarely 1-2-2. Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes contiguous or nearly so, usually with a few interorbital scales. Ocular tentacles absent. Ocular-side anterior nasal tube reaching posterior nasal tube when flattened, but not reaching anterior margin

of ventral eye. Posterior nasal tube nearly half the length of anterior tube. Blind-side anterior nostril a short, uneven tube located slightly dorso-anteriorly to dorsalmost point of mouth. Posterior nostril a longer tube located dorso-posteriorly from anterior tube at vertical through posterior edge of mouth and at posterior margin of dense patch of cirri on anterior region of head. Posterior margin of ocular-side jaws reaching as far as vertical through midpoint of ventral eye. Ocular-side lips smooth. Blind-side lower lip plicate. Teeth minute, restricted to blind-side jaws. Ocular-side cirri restricted to opercular margin. Cirri densely distributed at anterior end of blind-side head, extending along snout, chin and opercular margin. Infrequently, cirri sparsely distributed between scales on mid-head region posterior to dense patch of cirri on anterior region, cirri not extending posterior to opercular margin. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line well developed on both sides of body; supraorbital line present on ocular-side head. Lateral-line scales cycloid. Scales on body moderately ctenoid with 8-13 ctenii. Anterior end of dorsal fin at, or slightly anterior to, vertical at anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Longest dorsal- and anal-fin rays located at posterior end of body, not directly adjacent caudal fin. Caudal fin distinct, somewhat rectangular. Scales extending onto median fins. Pectoral fins asymmetrical, ocular-side fin nearly twice as long as blind-side fin (ocular-side fin 28-48% HL). Ocular-side pectoral fin broad with 11-14 rays; upper 4-5 rays of comparable length, more ventral rays decreasing gradually in length. Dorsalmost ray of blind-side pectoral fin longest; more ventral rays decreasing gradually in length. Pelvic fins of comparable length, the ocular-side fin sometimes slightly longer. Anus

slightly submedian on blind side. Genital papilla submedian on ocular side; free from ocular-side pelvic fin.

**Pigmentation of preserved specimens:** Ocular side greyish-brown with series of 13 singular, darkly demarcated, deep brown bands: ten bands on body, with one situated at base of caudal fin, and three bands on head. Bands flanking operculum are usually joined at their dorsal ends. Bands becoming narrower toward anterior end. Blind side generally pale, whitish; infrequently, minute, dark spots present along posterior median-fin margins. Interior of mouth pale. Tongue may be light grey or brown, or speckled with dark spots. Bands extending onto ocular-side dorsal and anal fins, becoming darker. Ocular-side caudal fin dark brown with light spots and a thin, cream-colored strip at its distal end. Distal end of ocular-side pectoral fin dark brown or black. Blind-side pectoral fin of most specimens mostly transparent with minute black spots; others with transparent fins. Pelvic fins whitish.

Table 2.7. Meristic and morphometric characteristics of type and non-type specimens of *Pseudaesopia cochinensis*. Means and standard deviations are shown in parentheses. Data for type material were obtained from the original species descriptions (Rama-Rao, 1967; Joglekar, 1976). Measurements and abbreviations are described in Appendix B.

	<i>Zebrias keralensis</i> holotype	<i>Zebrias keralensis</i> paratypes (n=3)	<i>P. cochinensis</i> holotype	<i>P. cochinensis</i> non-type specimens (n=8)
<b>Standard length (mm)</b>	122	82-114	-	68.3-137.89 (104.8; 32.4)
<b>Total length (mm)</b>	-	-	150	78.54-162.77 (121.69; 37.9)
<b>Counts</b>				
Dorsal-fin rays	72	65-73 (70)	69	67-76 (71.6; 2.9)
Anal-fin rays	63	56-62 (60)	56	53-60 (57.5; 2.1)
Caudal-fin rays	17	17-18 (17.2)	14	18 (18; 0)
Precaudal vertebrae	-	8 <sup>1</sup>	-	9 (9; 0)
Caudal vertebrae	-	35 <sup>1</sup>	-	32-34 (33.6; 0.7)
Vertebrae	-	43 <sup>1</sup>	-	41-43 (42.6; 0.7)
Haemopophyses	-	-	-	5-6 (5.1; 0.4)
Pterygiophores	-	-	-	5-6 (5.9; 0.4)
Pectoral-fin rays o.s.	11	10-13 (11.2)	14	11-14 (12.7; 1.0) <sup>2</sup>
Pectoral-fin rays b.s.	11	10-11 (10.5)	14	11-13 (12.3; 0.9)
Pelvic-fin rays o.s.	4	4	5	3-4 (3.9; 0.4)
Pelvic-fin rays b.s.	4	4	5	4 (4; 0)
Lateral-line scales	74	75-78 (75.7)	90	75-85 (80.5; 3.5)
Number of bands	13	13	13	13 (13; 0)
<b>Measurements</b>				
<b>%SL</b>				
Head length	0.204	0.196-0.219 (0.204)	-	0.19-0.21 (0.20; 0.006)
Head depth	-	-	-	0.21-0.24 (0.22; 0.01)
Body depth	0.409	0.348-0.421 (0.392)	-	0.34-0.39 (0.37; 0.01)
Caudal fin length	-	-	-	0.15-0.18 (0.16; 0.01)
Width caudal peduncle	-	-	-	0.07-0.09 (0.08; 0.008)
<b>%HL</b>				
Length of pectoral fin o.s.	0.42	0.333-0.440 (0.399)	-	0.28-0.48 (0.39; 0.07) <sup>2</sup>
Length of pectoral fin b.s.	0.20	0.166-0.240 (0.199)	-	0.19-0.25 (0.22; 0.02)
Length of pelvic fin o.s.	-	-	-	0.27-0.32 (0.29; 0.02) <sup>2</sup>
Length of pelvic fin b.s.	-	-	-	0.24-0.32 (0.28; 0.03)
Pre-orbital head length	-	-	-	0.14-0.23 (0.18; 0.04)
Post-orbital head length	0.60	0.601-0.640 (0.613)	-	0.63-0.75 (0.68; 0.05)
Snout length	0.24	0.208-0.320 (0.254)	-	0.18-0.28 (0.24; 0.04)
Nostril to snouth distance	-	-	-	0.14-0.28 (0.19; 0.04)
Mouth length o.s.	0.34	0.320-0.342 (0.333)	-	0.26-0.34 (0.31; 0.02)
Mouth length b.s.	-	-	-	0.20-0.26 (0.24; 0.02)
Ventral eye diameter	0.20	0.200-0.208 (0.202)	-	0.18-0.24 (0.21; 0.02)
Width of orbits	-	-	-	0.27-0.37 (0.32; 0.03)
Longest dorsal ray	-	-	-	0.45-0.62 (0.54; 0.06)
Longest anal ray	-	-	-	0.45-0.66 (0.55; 0.06)
IOD/V	-	-	-	0-0.15 (0.03; 0.06)
BPc/OPc	-	-	-	0.52-0.68 (0.58; 0.06) <sup>2</sup>
BPv/OPv	-	-	-	0.84-1.06 (0.98; 0.07) <sup>2</sup>

<sup>1</sup>: n=1.

<sup>2</sup>: n=7.

**Geographic Distribution:** *Pseudaesopia cochinensis* has been reported from the northwestern Indian Ocean, Arabian Sea, and along the western coast of India and Pakistan (Manilo and Bogorodsky, 2003). The type material is described from the Kerala Coast, India. Specimens examined in the current study were reported at depths of 19-34m. Reported from depths of 19-34 m.

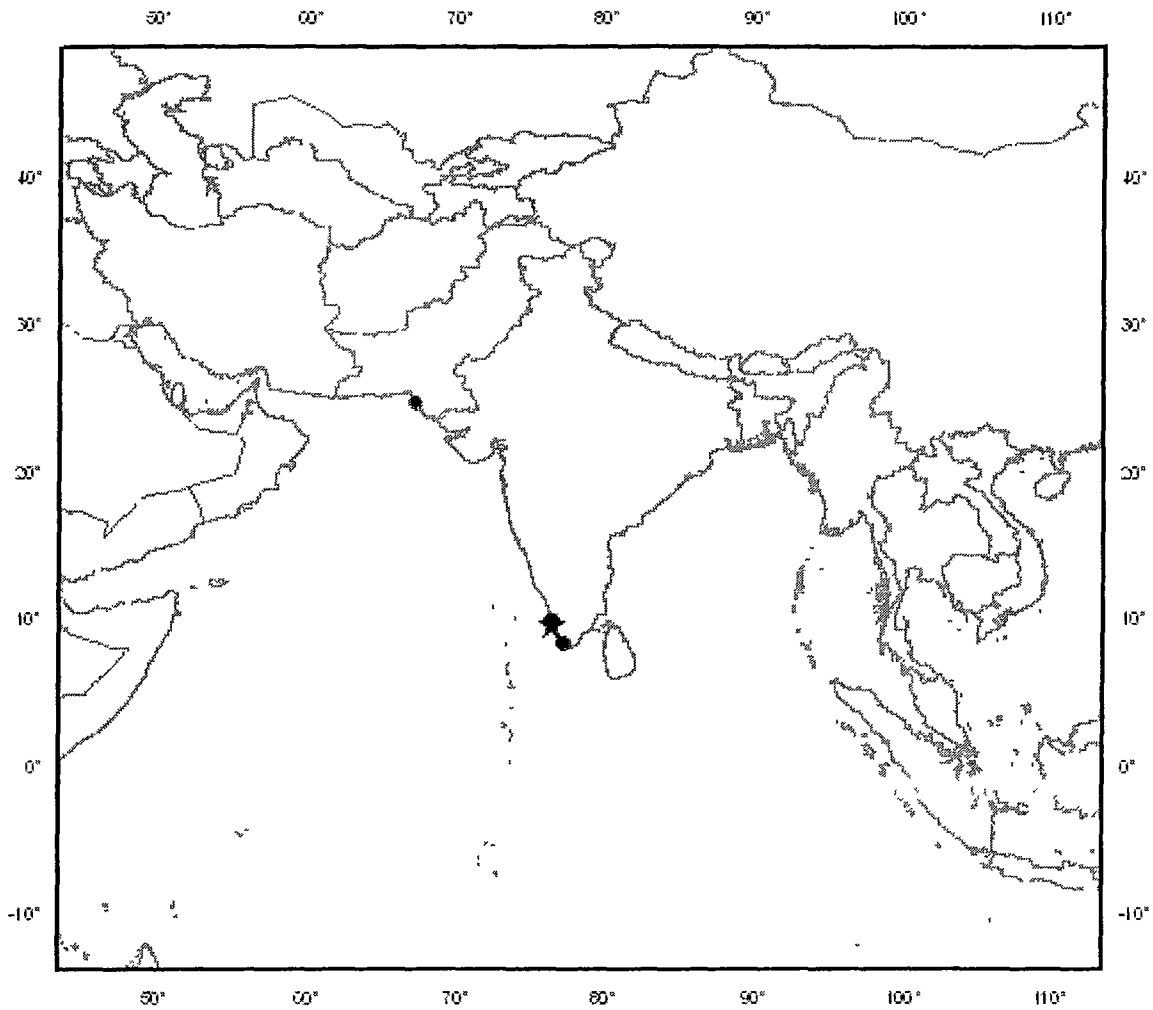


Figure 2.4. Geographic distribution of *Pseudaesopia cochinensis*. Star denotes locality of type material according to Rama-Rao (1967).

**Remarks:** *Zebrias cochinensis* was originally distinguished from all other species of *Zebrias* by its unique banding pattern. As previously discussed in the introduction, banding irregularities are not uncommon within the genera *Pseudaesopia* and *Zebrias*. The location of the holotype is currently unknown and there does not appear to be any non-type material present in museum collections. This apparent absence of both type and non-type material suggest that the holotype of *Z. cochinensis* may have simply exhibited an abnormal banding pattern. Talwar and Kacker (1984) synonymised *Z. cochinensis* with *P. synapturoides*; however, the attributes of *Zebrias keralensis* (Joglekar, 1976), described from the Kerala Coast, much more closely resemble those reported for *P. cochinensis*. In addition to their comparable meristics (Table 2.7), both species are depicted as having a similar ocular-side pectoral fin length and morphology (Figure 2.5), comparable pigmentation (apart from banding abnormality), and more or less contiguous eyes. The ocular-side pectoral fin morphology is unique within the genus. Moreover, both species are reported as having moderately ctenoid scales with 10-12 ctenii and a short ocular-side anterior nasal tube. *Pseudaesopia synapturoides*, having symmetrical, rudimentary pectoral fins, fewer pectoral-fin rays (9-12), strongly ctenoid scales, a longer ocular-side anterior nasal tube (frequently reaching or surpassing anterior margin of ventral eye when flattened), and a different band arrangement and morphology (12-24 bands in pairs, singular, or a combination of the two) is clearly closely-related, but not synonymous with *P. cochinensis*. The count of 14 caudal-fin rays reported for *P. cochinensis* is likely an error or an abnormality of the fish, as no *Pseudaesopia* species has fewer than 16 caudal-fin rays (Table 2.4).

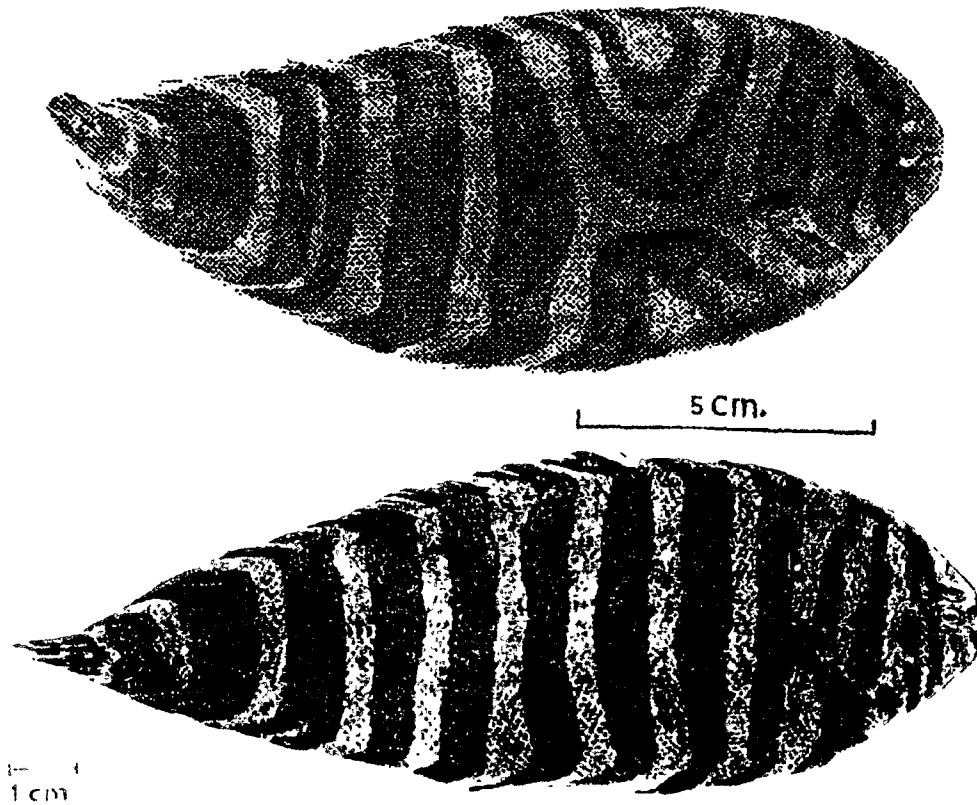


Figure 2.5. Scans of photographs depicting holotypes of *Zebrias cochinensis* Rama-Rao, 1967 (above) and *Zebrias keralensis* Joglekar, 1976 (below), as presented in their original descriptions.

**Comparisons:** *Pseudaesopia regani* (Gilchrist, 1906), which most closely resembles *P. cochinensis*, differs by the absence of interorbital scales, the shorter ocular-side pectoral fin (19-30% HL), and the smaller number of ocular-side pectoral-fin rays (9-11).

*Pseudaesopia japonica* (Bleeker, 1860) and *P. callizona* (Regan, 1903) differ from *P. cochinensis* in having fewer pectoral-fin rays (6-10), the upper two ocular-side pectoral-fin rays elongate, five pelvic-fin rays, a caudal fin with a solid distal black end or 4-5 oblong black spots, more scales along the lateral line (85-103), the genital papilla

attached to the ocular-side pelvic fin, and longer ocular-side anterior nasal tubes, which reach or surpass the anterior margin of the ventral eye when flattened. *Pseudaesopia lucapensis* (Seigel and Adamson, 1985) is easily distinguished by its more numerous bands (24-27), five pelvic-fin rays, fewer lateral-line scales (58-66), longer ocular-side anterior nasal tube (reaches or surpasses anterior margin of ventral eye), and shorter ocular-side pectoral fin (13-15% HL). *P. synapturoides* (Jenkins, 1910) differs in having five pelvic-fin rays, a shorter ocular-side pectoral fin (18-31% HL), and thickly-demarcated or paired bands.

*Pseudaesopia japonica* (Bleeker, 1860)

Figures 2.6-2.10, Table 2.8

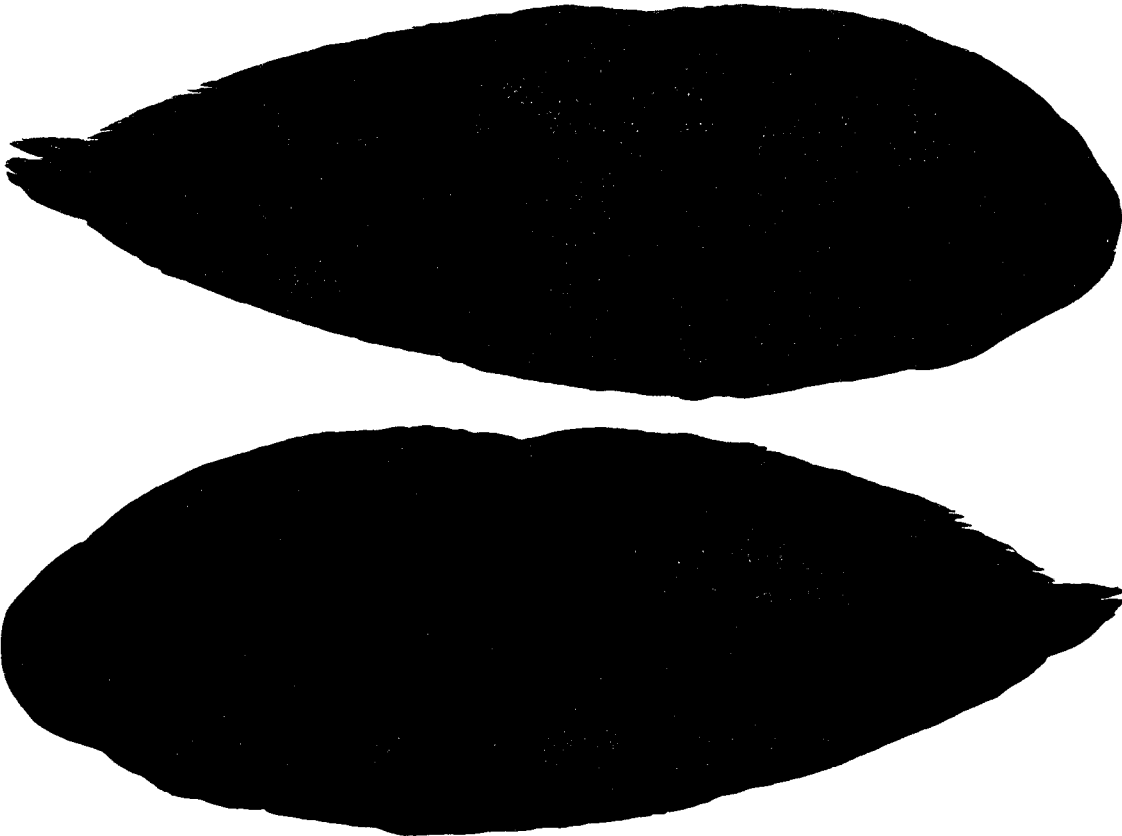


Figure 2.6. Photographs of *Pseudaesopia japonica*, UMMZ159582, 126 mm SL, Sea of Japan, NE of Oki-No-Jima (off Miyazu), Kyoto-Fu (Miyazu Market), Japan, 40-70 fathoms, depicting ocular side (above) and blind side (below).

**Synonym(s):** *Aesopia japonica* Bleeker, 1860; *Synaptura smithii* Regan, 1903; *Zebrias annandalei* Talwar and Chakrapany, 1967; *Solea zebrina* Temminck and Schlegel, 1846 [note: only two of the three paralectotypes preserved in ethanol represent specimens of *P. japonica*: RMNH3580]

**Common name(s):** Seto-ushinoshita (= Channel-sole); Japanese sole

**Material examined:** 50 specimens (81.44 to 185.32 mm TL)

**Type material:** *Pseudaesopia japonica*: holotype lost; *Synaptura smithii*:

BMNH1902.10.31.152, holotype, 1(112.7 mm SL), inland sea, Japan; *Zebrias zebrinus*: RMNH3580, paralectotypes, 2(74.8-105 mm SL), Japan; *Zebrias annandalei*: ZSI F5011/2 (holotype) and ZSI F5012/2 (paratype), unavailable for examination.

**Non-type material:** ASIZP0061416, 1(111.95 mm SL), open sea, Jinshan, Taipei; ASIZP0061543, 1(112.71 mm SL), open sea, Jinshan, Taipei; BPBM23162, 2(116.17-127.74 mm SL), Taiwan, N shore; Keelung market; CAS109970, 3(103.09-139.42 mm SL), NW and Central Pacific, Japan, Tokyo, Honshu Is., Tokyo Wan (Tokyo Bay); CAS214464, 2(108.55-116.72 mm SL), Indo-West Pacific, Taiwan, Suao Fish Market; CSIRO H6295-10, 1(121.17 mm SL), Taiwan, Tashi Fish market, near I-Lan (NE); FMNH57276, 1(107.88 mm SL), Asia, Pacific Ocean, Japan; FMNH5763, 1(99.4 mm SL), Japan, Inland Sea of Japan; FMNH58820, 1(85.5 mm SL), Asia, Japan, Misaki; FMNH89177, 3(122.51-136.68 mm SL), Asia, Japan, Yokohama Market; FMNH89242, 1(148.45 mm SL), Asia, Yokohama Market, Japan; FMNH89875, 1(111.39 mm SL), Nagasaki, Japan; USNM Uncatalogued, 1(x-ray only), India; MNHN1976-389, 1(138.2 mm SL), Aburatsu, Japan, Sector 6131, 31°583'N, 131°383'E; NSMT-P19754, 1(159.88 mm SL), Japan, Honshu, Chiba Pref., off Choshi, southern Japan; SIO 64-259-64A, 1(131 mm SL), Japan, Sea of Amakusa-Nada; SMF15477, 2(98.8-109.94 mm SL), Japan, Kochi-Ken, Tosa-Bucht, Mimase, M. Turkay; UMMZ159579, 2(127.11-162.9 mm SL), Asia, Korea, near Fusan, at Fusan market (no fishes shipped in from far away);

UMMZ159582, 5(125.82-141.99 mm SL), Asia, Japan, Sea of Japan, NE of Oki-No-Jima (off Miyazu), Kyoto-Fu (Miyazu Market), some probably from east of Oki-No-Jima, 40-70 fathoms; UMMZ159587, 6(78.17-111.34 mm SL), Asia, Japan, Toyama Bay near Namerikawa (Namerikawa Market), all fisheries very close; UMMZ159704, 2(110.95-127.65 mm SL), Asia, Japan, Toba Market; Uncatalogued label 37591-2, tag: M-549, 2(89.79-123.81 mm SL); USNM059761, 1(96.48 mm SL), Pacific Japan, Kagoshima, Japan; USNM071956, 2(107.91-111.96 mm SL), Pacific Japan, Hakodate, Japan; USNM072081, 2(104.77-147.31 mm SL), Pacific Japan, Hakodate (Market), Japan; USNM151712, 1(122.77 mm SL), Pacific Japan, Fukui-Ken, Japan.

**Diagnosis:** A species of *Pseudaesopia* with the following combination of characters: somewhat irregular, thickly-demarcated, often wavy bands that are randomly arranged as pairs or singular; distal end of caudal fin solid black or dark brown, spots absent; ocular-side pectoral-fin length 49% HL (average) with upper two rays elongate; 40-44 vertebrae; 85-103 lateral-line scales; genital papilla attached to ocular-side pelvic fin; blind side pale, devoid of conspicuous pigmentation.

**Description:** Meristic and morphometric characters are indicated in Table 2.8. Small sole, attaining a total length of 19 cm. Supracranial pterygiophores 3-5; formula: (1-2)-(1-2)-(1-4). Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes contiguous or nearly so; dorsal eye slightly in advance of ventral eye. Ocular tentacles absent. Scales present in interorbital space. Ocular-side anterior nasal tube long, reaching or more frequently

surpassing anterior margin of ventral eye when flattened. Aperture of anterior nasal tube considerably narrower than its base. Ocular-side posterior nasal tube one quarter to one half length of anterior tube. Blind-side anterior nostril an uneven tube with longer side folding over to conceal nasal aperture. Anterior nasal tube dorso-anterior to dorsalmost point of mouth. Blind-side posterior nasal tube slightly larger than ocular-side counterpart, its aperture narrower than its base. Blind-side posterior nasal tube dorso-posterior to anterior nasal tube at vertical through posterior edge of mouth and at posterior margin of dense patch of cirri on anterior region of head. Posterior margin of ocular-side jaws typically extending to a vertical just posterior to anterior margin of ventral eye, infrequently reaching vertical through midpoint of ventral eye. Ocular-side lips smooth. Blind-side lower lip plicate. Teeth restricted to blind-side jaws. Ocular-side cirri restricted to short fringe along opercular margin. Cirri densely distributed at anterior end of blind-side head, extending along snout, chin and opercular margin. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line well developed on both sides. Supraorbital line present on ocular-side head. Lateral-line scales cycloid. Blind-side lateral line associated with patches of cirri. Scales on body strongly ctenoid on both sides with 10-18 ctenii. Anterior end of dorsal fin at, or slightly anterior to, vertical at anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Longest dorsal- and anal-fin rays located close to caudal fin, but not directly adjacent to it. Caudal fin rounded and distinct; posteriormost vertical-fin ray length 34-58% relative to length of caudal fin. Basal third to half of median fins covered in scales on both sides. Ocular-side pectoral fin of moderate length ( $\bar{r} = 49\%$  HL), upper two rays elongate; more ventral rays decreasing gradually in length. Blind-side pectoral

fin short; dorsalmost ray longest with more ventral rays decreasing gradually in length. Pelvic fins of comparable length; ocular-side pelvic fin often a bit longer. Anus slightly submedian on blind side. Genital papilla submedian on ocular side. Genital papilla attached to ocular-side pelvic fin by thin membrane.

**Pigmentation of preserved specimens:** Ocular side light brown or grey-brown with series of 10-26 thickly and darkly bordered brown or grey bands. Banding pattern somewhat irregular, bands often wavy and randomly arranged in pairs or as singular bands. Band abnormalities, such as bifurcating or incomplete bands, frequently observed. Bands on head becoming narrower. Blind side typically pale, devoid of conspicuous pigmentation; infrequently, minute, dark spots present along posterior median-fin margins (3/50 specimens). Interior of mouth charcoal or black. Bands extending onto dorsal and anal fins, becoming darker. Dark brown or black blotches at distal ends of interband spaces on dorsal and anal fins. Ocular-side caudal fin greyish with solid dark brown or black distal end. Ocular-side pectoral fin grey, dark brown or black. Blind-side pectoral fin transparent or mostly transparent with minute, black spots; black spots may be present on skin beneath fin. Pelvic fins whitish.

Table 2.8. Meristic and morphometric characteristics of type and non-type specimens of *Pseudaesopia japonica*. Means and standard deviations are shown in parentheses.

	<i>Synaptura smithii</i> holotype	<i>Solea zebrina</i> <sup>1</sup> paralectotypes (n=2)	<i>Pseudaesopia japonica</i> non- type specimens (n=45)
<b>Standard length (mm)</b>	112.7	74.8-105	78.17-162.90 (117.96; 19.2)
<b>Total length (mm)</b>	123.7	88-119.1	87.61-185.32 (134.44; 21.7)
<b>Counts</b>			
Dorsal-fin rays	73	76	70-82 (76.3; 3.0) <sup>5</sup>
Anal-fin rays	62	63	58-71 (63.1; 2.8) <sup>4</sup>
Caudal-fin rays	18	18	17-19 (17.9; 0.4) <sup>3</sup>
Precaudal vertebrae	9	8-9	8-10 (8.9; 0.4) <sup>3</sup>
Caudal vertebrae	33	-	31-35 (33.2; 0.8) <sup>3</sup>
Total vertebrae	42	-	40-44 (42.1; 0.9) <sup>5</sup>
Haemopophyses	5	5	5-6 (5.3; 0.4) <sup>3</sup>
Pterygiophores	7	4	5-8 (6.6; 0.7) <sup>3</sup>
Pectoral-fin rays o.s.	8	8	6-10 (8.2; 1.3)
Pectoral-fin rays b.s.	9	6-7	6-10 (7.5; 0.9)
Pelvic-fin rays o.s.	5	4-5	4-5 (4.8; 0.4)
Pelvic-fin rays b.s.	5	5	4-5 (4.8; 0.4)
Lateral-line scales	90	91-92	85-103 (92.5; 4.2) <sup>2</sup>
Number of bands	18	21-24	10-26 (17.7; 5.4) <sup>5</sup>
<b>Measurements</b>			
<b>% SL</b>			
Head length	0.18	0.16-0.20	0.15-0.20 (0.18; 0.01)
Head depth	0.18	0.18	0.16-0.22 (0.19; 0.01)
Body depth	0.35	0.36-0.40	0.29-0.40 (0.35; 0.02)
Caudal fin length	0.10	0.13-0.18	0.11-0.17 (0.14; 0.01)
Width caudal peduncle	0.08	0.06-0.08	0.06-0.09 (0.07; 0.007)
<b>% HL</b>			
Length of pectoral fin o.s.	0.50	0.66-0.67	0.25-0.74 (0.49; 0.1)
Length of pectoral fin b.s.	0.19	0.19-0.29	0.12-0.27 (0.19; 0.03)
Length of pelvic fin o.s.	0.41	0.28	0.26-0.45 (0.37; 0.05)
Length of pelvic fin b.s.	0.38	0.27	0.21-0.41 (0.33; 0.04)
Pre-orbital head length	0.23	0.12-0.31	0.15-0.28 (0.22; 0.04)
Post-orbital head length	0.59	0.59-0.72	0.51-0.69 (0.59; 0.04)
Snout length	0.23	0.21-0.22	0.20-0.35 (0.26; 0.03)
Nostril to snouth distance	0.10	0.12-0.13	0.14-0.25 (0.19; 0.03)
Mouth length o.s.	0.17	0.25-0.31	0.25-0.37 (0.31; 0.02)
Mouth length b.s.	0.19	0.25	0.23-0.32 (0.28; 0.02)
Ventral eye diameter	0.21	0.24-0.27	0.18-0.31 (0.25; 0.03)
Width of orbits	0.24	0.28-0.30	0.21-0.41 (0.33; 0.04)
Longest dorsal ray	0.50	0.49	0.44-0.62 (0.53; 0.05)
Longest anal ray	0.52	0.49	0.40-0.62 (0.52; 0.04)
IOD/V	0	0.08-0.09	0-0.52 (0.15; 0.1)
BPc/OPc	0.37	0.29-0.43	0.21-0.82 (0.41; 0.1)
BPv/OPv	0.94	0.98	0.66-1.10 (0.91; 0.1)

<sup>1</sup>: 2/3 of the alcohol-preserved paralectotypes represent *P. japonica*, while the third specimen represents *Z. zebra* (Bloch, 1787); <sup>2</sup>: n=44; <sup>3</sup>: n=43; <sup>4</sup>: n=42; <sup>5</sup>: n=41.

**Geographic Distribution:** *Pseudaesopia japonica* has been reported from Japan, Korea, Taiwan, the Gulf of Carpentaria, New Caledonia, Taipei (off-China), and the Bay of Bengal (India) at depths of 15-127 m.

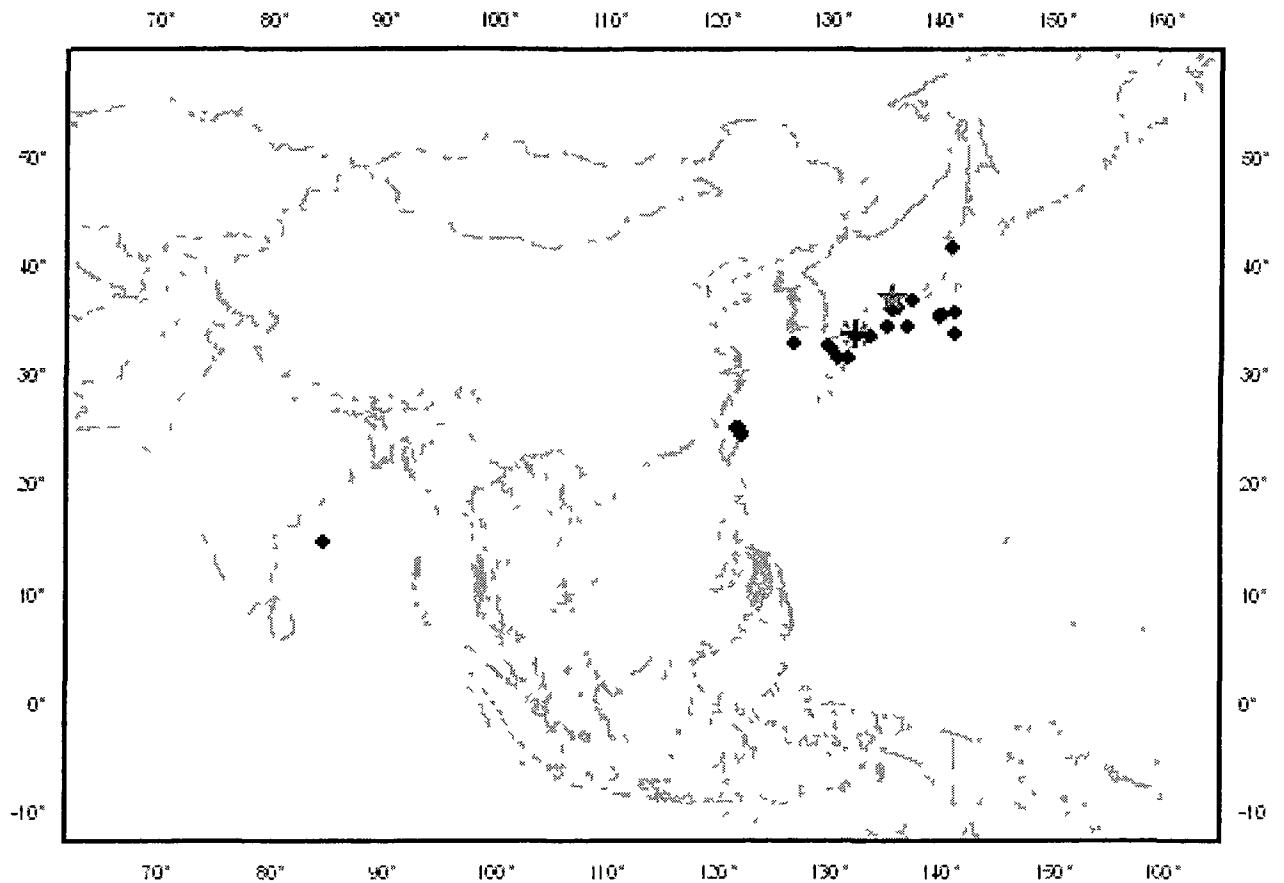


Figure 2.7. Geographic distribution of *Pseudaesopia japonica*. The locality of the holotype of *P. japonica* is unknown. Stars denote locality of the holotype of *Synaptura smithi* (= *P. japonica*) and the two paralectotypes of *Solea zebrina* (Temminck and Schlegel, 1846) that actually represent *P. japonica* specimens.

**Remarks:** An examination of the holotype of *Synaptura smithii* Regan, 1903 leaves no doubt that this specimen is synonymous with *P. japonica*, as evidenced by its caudal fin pigmentation, pectoral fin morphology, number of lateral line scales, and the presence of thickly-demarcated, wavy bands (Figure 2.8). Temminck and Schlegel's (1846) *Solea zebrina* was determined to be a composite species with four of the six type specimens being synonymous with Bloch's (1787) *Zebrias zebra*, and two being synonymous with *Pseudaesopia japonica* (Figure 2.9).

The type material for *Zebrias annandalei* Talwar and Chakrapany, 1967 could not be obtained for examination and therefore, it was necessary to rely on the original description to make an assessment of the species' validity. *Z. annandalei* was described from Indian waters at a time when *Pseudaesopia japonica* was known only to exist in the waters surrounding Japan. Since then, *P. japonica* has been reported from the Bay of Bengal, off Visakhapatnam, India (Rao and Murty, 1981); in addition, a representative specimen from India was examined in the present study, which confirms its presence in these waters. The illustration provided by Talwar and Chakrapany (Figure 2.10) depicts a species bearing a strong resemblance to *P. japonica*; however, the banding pattern is shown to consist of 22-24 narrow, singular bands across the body and head, which is unlike the slightly irregular, thickly-demarcated bands of *P. japonica*. It is possible that the depicted banding pattern is inaccurate, or that some of the bands may actually represent thick demarcations as observed in *P. japonica*. Talwar and Chakrapany (1967) distinguish *Zebrias annandalei* from *Pseudaesopia japonica* by its higher number of caudal-fin rays (18), smaller body-depth (3.3 times in TL), smaller head (6.1-6.8 times in TL), and larger eyes (3.4-3.7 times in HL). As shown in Table 2.8, *P. japonica* typically

has 18 caudal-fin rays. Moreover, the body depth, head length, and eye diameter of this species was found to coincide with the ranges provided by Talwar and Chakrapany: body depth 2.9-3.9 times in the TL ( $\bar{x}$  = 3.3, SD = 0.2); head length 5.8-7.7 times in TL ( $\bar{x}$  = 6.5, SD = 0.4); eye diameter 3.3-5.5 times in HL ( $\bar{x}$  = 4.1, SD = 0.5). *Zebrias annandalei* is also purported to differ from *Pseudaesopia japonica* in having a higher number of scales in the lateral series and a lower number of scales in the transverse series. The method of counting scales was not indicated and therefore, it is difficult to make a comparison with *P. japonica*. The lateral line scale count recorded for *Zebrias annandalei* appears to be at the higher end of the range of values recorded for *Pseudaesopia japonica* in the present study. All other meristics are consistent with *P. japonica*. Accordingly, *Zebrias annandalei* has been synonymised with *Pseudaesopia japonica*. An examination of the type material for *Zebrias annandalei* is required to better assess the validity of this nominal species.

**Comparisons:** With the exception of its most closely allied congener, *Pseudaesopia callizona* (Regan, 1903), *P. japonica* can be distinguished from all of its congeners by its irregular band morphology and arrangement, caudal fin pigmentation (solid black distal end; spots absent), ocular-side pectoral fin morphology (upper two rays elongate, mean length 49% HL), the attachment of the genital papilla to the ocular-side pelvic fin, and its high lateral-line scale count (85-103). *P. callizona* differs from *P. japonica* in its band morphology and arrangement (14-17 thinly-demarcated, singular bands), greater number of vertebrae (44-45), the presence of minute, black spots on the blind-side along the

median-fin margins and head, and the generally longer ocular-side pectoral fin ( $\bar{x} = 71\%$  HL).



Figure 2.8. Photograph depicting the holotype of *Synaptura smithii* (= *Pseudaesopia japonica*), BMNH1902.10.31.152, 113 mm SL, inland sea, Japan.

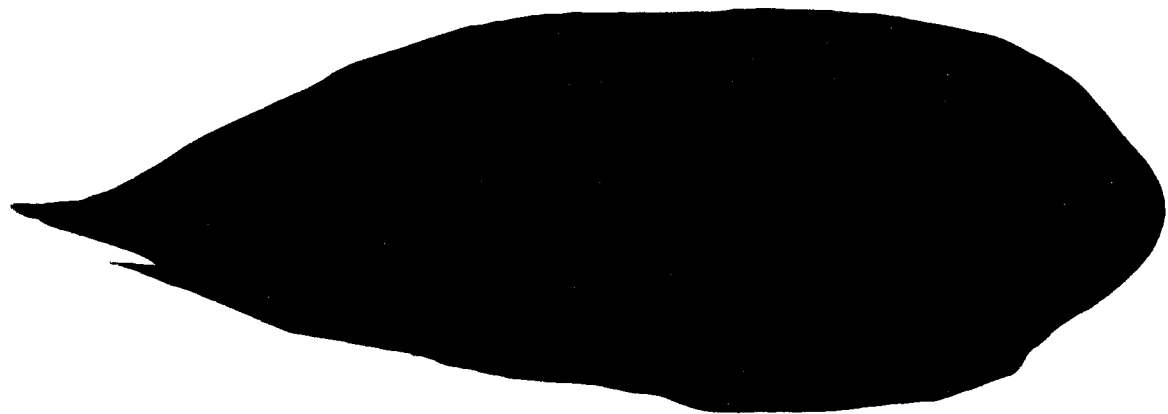


Figure 2.9. Photograph depicting one of the three ethanol-preserved paralectotypes of *Solea zebrina* (= *Pseudaesopia japonica*), RMNH3580, 75 mm SL, Japan.

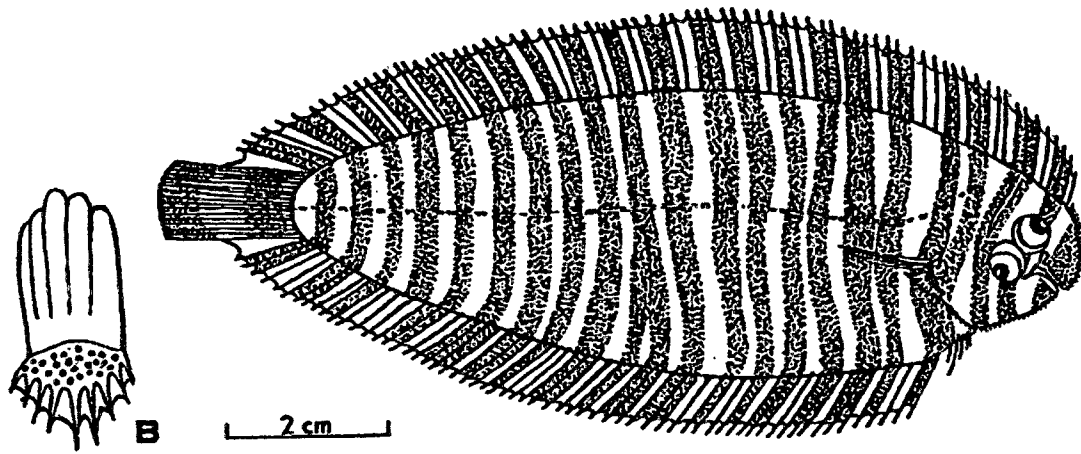


Figure 2.10. An illustration of *Zebrias annandalei*, as depicted in the original type description (Talwar and Chakrapany, 1967), 97 mm SL, Puri Beach, Orissa, India.

*Pseudaesopia lucapensis* (Seigel and Adamson, 1985)

Figures 2.11-2.12, Table 2.9

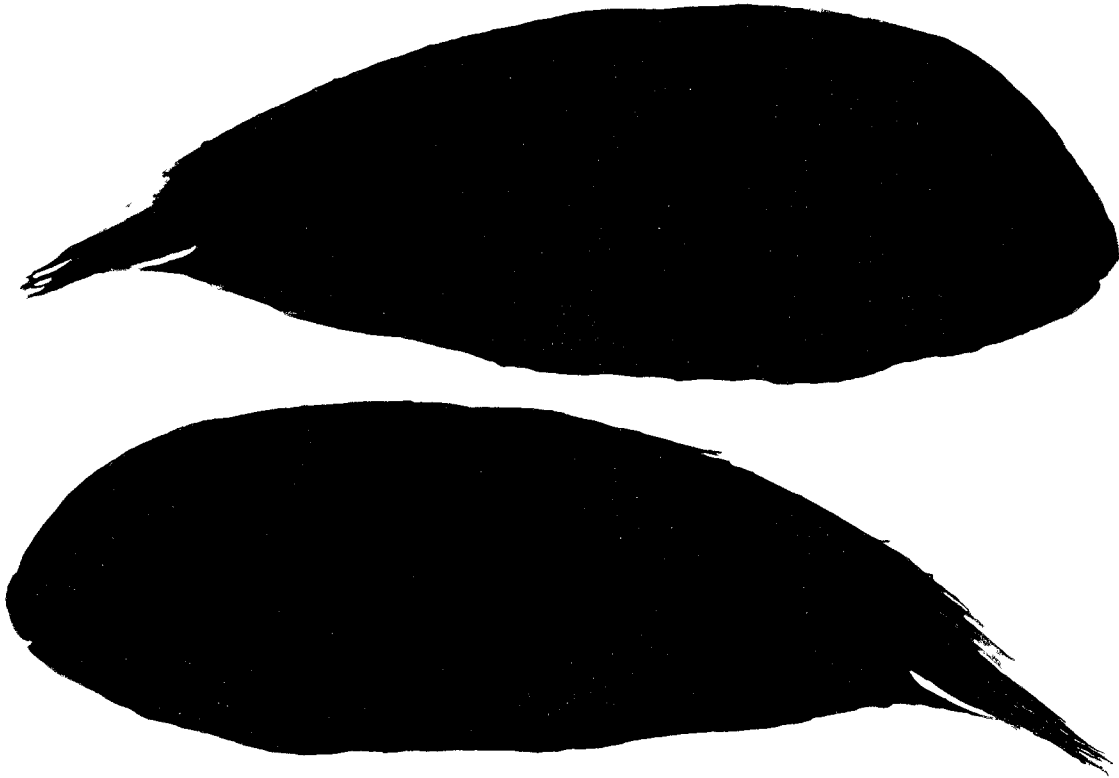


Figure 2.11. Photographs of *Pseudaesopia lucapensis*, LACM37436-6, holotype, 81 mm SL, Philippines, Lingayen Gulf, Pangasinan, Lucap Bay, depicting the ocular (above) and blind (below) sides.

**Synonym(s):** *Zebrias lucapensis* Seigel and Adamson, 1985.

**Common name(s):** None known.

**Material examined:** 4 specimens (73.89-102.21 mm TL)

**Type material:** LACM37436-6, Holotype, 81.26 mm SL, Philippines: Lingayen Gulf; Pangasinan, Lucap Bay; LACM37436-8, Paratype, 79.61 mm SL, Philippines: Lingayen Gulf; Pangasinan, Lucap Bay.

**Non-type material:** NMVA11516, 2(58.57- 80.06 mm SL), Philippines, Camotes Sea, west of Leyte Is., 10°57.5'S - 10°52.0'S, 124°36.5'E - 124°35.1'E.

**Diagnosis:** A species of *Pseudaesopia* with the following combination of characters: Ocular side with 24-27 narrow, singular bands; 58-66 lateral-line scales; scales very strongly ctenoid; blind side dusky.

**Description:** Meristic and morphometric characters are indicated in Table 2.10. Small sole, attaining a total length of 10 cm. Supracranial pterygiophores 4-5; formula: 1-1-(2-3). Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes contiguous, dorsal eye slightly in advance of ventral eye. Scales absent in interorbital space. Ocular tentacles absent. Ocular-side anterior nasal tube narrow, reaching or just surpassing anterior margin of ventral eye when flattened. Ocular-side posterior nasal tube approximately one fifth to one quarter the length of anterior tube, located directly adjacent to ventral eye. Blind-side anterior nostril slightly anterior to dorsalmost point of mouth; anterior nostril a short, uneven tube with higher end covering nasal aperture in preserved specimens. Blind-side posterior nasal tube small, postero-dorsal to anterior tube at vertical through posterior edge of mouth. Both tubes inconspicuous. Posterior margin of ocular-side jaws nearly

reaching vertical through midpoint of ventral eye. Ocular-side lips smooth. Blind-side lower lip plicate. Teeth minute, restricted to blind-side jaws. Cirri absent on ocular side. Cirri densely distributed at anterior end of blind-side head, extending along snout, chin and opercular margin. Smaller patches of cirri may be associated with lateral line on blind-side head. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line well developed on both sides of body; mediolateral line extending horizontally from caudal peduncle to opercular margin. Supraorbital line present on ocular-side head. Blind-side lateral line inconspicuous on head. Lateral-line scales cycloid. Scales on body strongly ctenoid, long, narrow with 8-12 ctenii on ocular-side scales and 12-13 ctenii on blind-side scales. Anterior end of dorsal fin at, or slightly anterior to, vertical at anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Dorsal- and anal-fin rays bifurcating at their distal ends. Caudal fin rounded, distinct. Scales extending onto bases of median fins. Pectoral fins rudimentary (11-15% HL on ocular side), more or less symmetrical and broad-based; rays gradually decreasing in length toward ventral end. Ocular-side pectoral fin covered by thick layer of skin. Ocular-side pelvic fin slightly longer than blind-side fin. Anus submedian on blind side, anterior to first anal-fin ray and posterior to junction of pelvic fins. Genital papilla submedian on ocular side, adjacent to anus. Genital papilla free from ocular-side pelvic fin.

**Pigmentation of preserved specimens:** Body greyish-beige with series of 24-27 narrow, darkly-demarcated, brown bands (8-9 on head; 16-18 on body). Bands on head becoming narrower. Inter-band width comparable to width of bands. Blind side white with minute,

charcoal grey spots primarily concentrated at anterior end of body and along median fin margins. Bands extending onto dorsal and anal fins, becoming darker. Blind-side median fins uniformly dark brown. Ocular-side caudal fin dark grey in middle with solid black distal end. Light spots faintly visible at distal end of ocular-side caudal fin in paratype. Base of caudal fin same colour as body. Pectoral fins charcoal grey. Pelvic fins whitish.

Table 2.9. Meristic and morphometric characteristics of type and non-type specimens of *Pseudaesopia lucapensis*. Means and standard deviations are shown in parentheses. Measurements and abbreviations are described in Appendix B.

	<i>Zebrias lucapensis</i> holotype	<i>Zebrias lucapensis</i> paratype (n=1)	<i>Pseudaesopia lucapensis</i> non-type specimens (n=2)
<b>Standard length (mm)</b>	81.26	79.61	58.57-80.06
<b>Total length (mm)</b>	98.48	98.39	73.89-102.21
<b>Counts</b>			
Dorsal-fin rays	72	71	69-70
Anal-fin rays	57	55	53-58
Caudal-fin rays	18	18	18
Precaudal vertebrae	9	8	9
Caudal vertebrae	33	33	32-33
Total vertebrae	42	41	41-42
Haemopophyses	5	5	5
Pterygiophores	6	6	6-7
Pectoral-fin rays o.s.	10	11	10
Pectoral-fin rays b.s.	10	11	9-10
Pelvic-fin rays o.s.	5	5	5-6
Pelvic-fin rays b.s.	4	5	5
Lateral-line scales	58 <sup>1</sup>	66	60-66
Number of bands	24	27	24
<b>Measurements</b>			
<b>%SL</b>			
Head length	0.20	0.21	0.22
Head depth	0.22	0.23	0.21-0.24
Body depth	0.33	0.35	0.31-0.36
Caudal fin length	0.21	0.24	0.26-0.28
Width caudal peduncle	0.08	0.08	0.07-0.09
<b>%HL</b>			
Length of pectoral fin o.s.	0.15	0.13	0.11-0.13
Length of pectoral fin b.s.	0.18	0.17	0.10-0.17
Length of pelvic fin o.s.	0.30	0.30	0.28-0.36
Length of pelvic fin b.s.	0.27	0.27	0.25-0.30
Pre-orbital head length	0.17	0.21	0.20-0.27
Post-orbital head length	0.57	0.55	0.54-0.55
Snout length	0.32	0.31	0.28-0.30
Nostril to snouth distance	0.19	0.21	0.21-0.25
Mouth length o.s.	0.44	0.37	0.38-0.39
Mouth length b.s.	0.33	0.32	0.31-0.35
Ventral eye diameter	0.26	0.26	0.24-0.28
Width of orbits	0.27	0.25	0.39-0.42
Longest dorsal ray	0.65	0.58	0.61-0.69
Longest anal ray	0.65	0.57	0.59-0.73
IOD/V	0	0	0
BPc/OPc	1.25	1.30	0.93-1.27
BPv/OPv	0.89	0.91	0.84-0.89

<sup>1</sup>: approximation, a few scales missing.

**Geographic Distribution:** *Pseudaesopia lucapensis* has been reported from the Western Pacific, off the Philippine Islands at depths up to 80.5m.

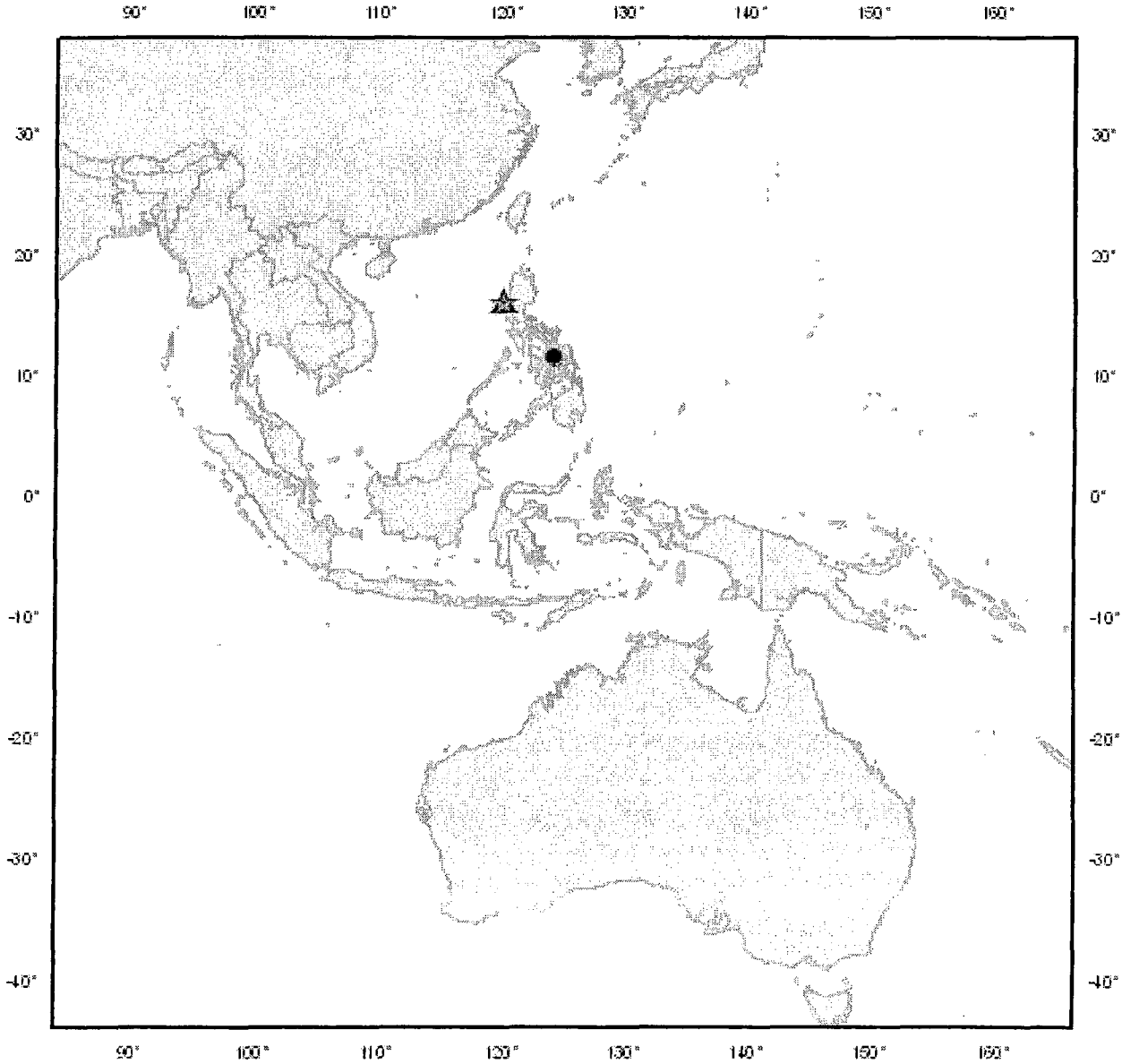


Figure 2.12. Geographic distribution of *Pseudaesopia lucapensis*. Stars denote locality of type material.

**Remarks:** None.

**Comparisons:** *Pseudaesopia lucapensis* can be distinguished from all of its congeners by its numerous, narrow, singular bands (24-27), and low lateral-line scale count (58-66).

With the exception of *Pseudaesopia callizona* (Regan, 1903), it can also be distinguished by its dusky blind side. Among its congeners, *P. lucapensis* appears to be most closely allied to *Pseudaesopia synapturoides* (Jenkins, 1910), with which it shares many characters. *P. synapturoides* is easily distinguished by its thickly-demarcated or paired bands, higher number of vertebrae (42-44), generally higher number of scales along the lateral line (62-82), and generally higher number of anal-fin rays (56-64). *Pseudaesopia regani* (Gilchrist, 1906) differs from *P. lucapensis* in having more scales along the lateral line (76-84), fewer pelvic-fin rays (4), and generally more vertebrae (42-45).

*Pseudaesopia cochinensis* (Rama-Rao, 1967) can be distinguished from *P. lucapensis* in having fewer, broader bands (13), interorbital scales, more pectoral-fin rays (11-14 on ocular side), fewer pelvic-fin rays (4), more lateral-line scales (75-85), and a longer ocular-side pectoral fin (28-48% HL). *Pseudaesopia japonica* (Bleeker, 1860) differs in having a longer ocular-side pectoral fin (25-74% HL), more lateral-line scales (85-103), irregular, thickly demarcated bands, interorbital scales, and more vertical-fin rays (70-82 dorsal-fin rays and 58-71 anal-fin rays). *Pseudaesopia callizona* (Regan, 1903) can be distinguished from *P. lucapensis* by having more lateral-line scales (90-100), fewer, broader bands (14-17), interorbital scales, more vertebrae (44-45), and more vertical-fin rays (77-83 dorsal-fin rays and 62-70 anal-fin rays).

*Pseudaesopia regani* (Gilchrist, 1906)

Figures 2.13-2.17, Table 2.10

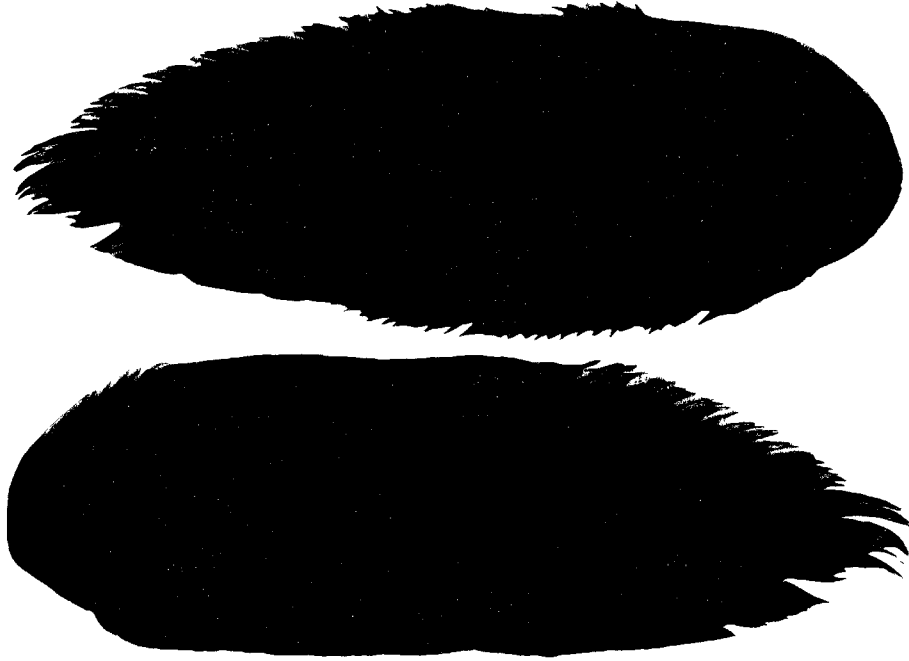


Figure 2.13. Photographs of *Pseudaesopia regani*, syntype, BMNH 1903.12.31.12, 102 mm SL, Western Indian Ocean, South Africa, Natal, depicting the ocular side (above) and blind side (below).

**Synonym(s):** *Synaptura regani* Gilchrist, 1906.

**Common name(s):** South African zebra sole

**Material examined:** 10 specimens (90.75-135.27 mm TL)

**Type material:** Syntype, SAM15424, 1(115.81 mm SL), 2.5 miles off Umhlanga River Mouth, Natal, Sta. No: PF, 26 March 1901; Syntype, BMNH 1903.12.31.12, 1(102.3 mm SL), Western Indian Ocean, South Africa, Natal.

**Non-type material:** SAM15426, 1(110.26 mm SL), Port Natal, Sta. No: Z15426; ANSP145361, 1(109.12 mm SL), Indian Ocean, Mozambique Channel, off Mozambique; SAM16114, 1(79.56 mm SL), Port Natal, Sta No: Z16114; ANSP63893, 1(103.35 mm SL), Indian Ocean, Natal, Durban, South Africa; SAM22357, 2(104.85-118.76 mm SL), Port Natal, Sta No: Z22357; SAM28866, 1(97.28 mm SL), Off Tugela River, Sta No: WT 231, 23 June 1966; ANSP145359, 1(108.78 mm SL), Somali Coast, 10°03'N, 51°15'E.

**Diagnosis:** A species of *Pseudaesopia* with the following combination of characters: 4 pelvic-fin rays; four supracranial pterygiophores on and anterior to first neural spine; interorbital scales absent; ocular-side pectoral-fin length 19-30% HL ( $\bar{x}$  = 24% HL); ocular-side pectoral-fin rays 9-11; 24-25 paired bands across body; 76-84 lateral-line scales.

**Description:** Meristic and morphometric characters are indicated in Table 2.10. Small sole, attaining a total length of 14 cm (Heemstra and Gon, 1986 report 16 cm).

Supracranial pterygiophores typically 4; formula: 1-1-2. Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes contiguous, ocular tentacles absent. Scales absent in interorbital space.

Ocular-side anterior nasal tube reaching as far as posterior nasal tube or anterior margin of ventral eye when flattened. Ocular-side posterior nasal tube approximately half the length of anterior tube. Blind-side anterior nostril a short, uneven tube with higher end folding over to cover nasal aperture. Anterior nostril dorso-anterior to dorsalmost point of mouth. Blind-side posterior nostril a tube of comparable length to ocular-side counterpart; located dorso-posteriorly to anterior nasal tube at vertical through posterior edge of mouth. Posterior margin of ocular-side jaws reaching vertical through midpoint of ventral eye. Ocular-side lips smooth. Blind-side lower lip plicate. Teeth restricted to posterior end of blind-side jaws; teeth minute, difficult to detect. Ocular-side cirri restricted to short fringe along opercular margin. Cirri densely distributed at anterior end of blind-side head, extending along snout, chin and opercular margin. Individual, more sparsely distributed cirri may be present on mid-head region between scales, posterior to dense patch of cirri on anterior region, cirri not extending posterior to opercular margin. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line well developed on both sides of body. Blind-side lateral line not extending anterior to opercular margin. Supraorbital line present on ocular-side head. Lateral-line scales cycloid. Scales on body small, triangular and moderately ctenoid with 6-12 ctenii. Anterior end of dorsal fin at, or slightly anterior to, vertical at anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Caudal fin distinct and squarish or rounded; posteriormost anal-fin ray length 44-61% relative to caudal fin length. Scales present along base of median fins. Pectoral fins short, asymmetrical, ocular-side fin slightly longer than blind-side fin (ocular-side fin 18-30% HL, blind-side fin 12-20% HL). Ocular-side pectoral fin often covered by thick layer of skin. Dorsalmost ray of

pectoral fin longest; more ventral rays decreasing gradually in length. Pelvic fins of comparable length; ocular-side fin sometimes slightly longer. Anus slightly submedian on blind side, just posterior to junction between pelvic fins and slightly anterior to first anal-fin ray. Genital papilla submedian on ocular side. Genital papilla detached from ocular-side pelvic fin.

**Pigmentation of preserved specimens:** Six of nine specimens examined were unpigmented (likely as a result of preservation method used). Ocular side light brown with 24-25 deeper brown, paired bands: body with 9.5 pairs, head with 2.5 pairs and a single band on snout (one pair intersected by opercular margin). Bands narrow, relatively uniform in width across body, those on head becoming narrower. Bands wider than narrow distance separating them in pairs; space between pairs of comparable width to bands. Blind side uniformly pale beige or whitish. Interior of mouth pale, whitish. Bands extending onto dorsal and anal fins, becoming darker. Ocular-side caudal fin darkly pigmented with several oblong, white spots; central spot may be elongate, extending to base of caudal fin. Ocular-side pectoral fin light brown. Blind-side pectoral fin transparent. Pelvic fins whitish.

Table 2.10. Meristic and morphometric characteristics of type and non-type specimens of *Pseudaesopia regani*. Means and standard deviations are shown in parentheses. Measurements and abbreviations are described in Appendix B.

	<i>Synaptura regani</i> syntypes (n=2)	<i>Pseudaesopia regani</i> non-type specimens (n=6)
<b>Standard length (mm)</b>	102.3-115.81 (109.06; 9.6)	79.56-118.76 (104.32; 13.3)
<b>Total length (mm)</b>	119.5-134.49 (127.00; 10.6)	90.75-135.27 (119.37; 15.3)
<b>Counts</b>		
Dorsal-fin rays	68-70	67-72 (69.3; 1.9)
Anal-fin rays	57-59	55-61 (58.5; 2.3)
Caudal-fin rays	18	18 (18; 0)
Precaudal vertebrae	9	9-10 (9.2; 0.4)
Caudal vertebrae	34	33-35 (34; 0.6)
Total vertebrae	43	42-45 (43.2; 1.0)
Haemopophyses	5	5-6 (5.3; 0.5)
Pterygiophores	6-7	5-6 (5.5; 0.6)
Pectoral-fin rays o.s.	10	9-11 (10.2; 0.8)
Pectoral-fin rays b.s.	10-11	9-11 (10.2; 0.8)
Pelvic-fin rays o.s.	4	4-5 (4.2; 0.4)
Pelvic-fin rays b.s.	4	4 (4; 0)
Lateral-line scales	80-84	76-83 (79.2; 3.1)
Number of bands	24	25 <sup>1</sup>
<b>Measurements</b>		
<b>%SL</b>		
Head length	0.18-0.19	0.18-0.19 (0.18; 0.006)
Head depth	0.21-0.22	0.19-0.22 (0.20; 0.01)
Body depth	0.35-0.40	0.30-0.37 (0.34; 0.03)
Caudal fin length	0.16-0.17	0.12-0.17 (0.14; 0.02)
Width caudal peduncle	0.07-0.09	0.06-0.09 (0.075; 0.01)
<b>%HL</b>		
Length of pectoral fin o.s.	0.18-0.21	0.19-0.30 (0.24; 0.04)
Length of pectoral fin b.s.	0.12-0.18	0.12-0.20 (0.17; 0.03)
Length of pelvic fin o.s.	0.29-0.38	0.25-0.34 (0.30; 0.04)
Length of pelvic fin b.s.	0.28	0.26-0.32 (0.29; 0.03)
Pre-orbital head length	0.13-0.19	0.16-0.25 (0.20; 0.04)
Post-orbital head length	0.60-0.66	0.58-0.69 (0.63; 0.04)
Snout length	0.13-0.27	0.22-0.31 (0.26; 0.04)
Nostril to snouth distance	0.036-0.20	0.17-0.23 (0.20; 0.02)
Mouth length o.s.	0.18-0.29	0.27-0.33 (0.30; 0.02)
Mouth length b.s.	0.19-0.25	0.18-0.28 (0.24; 0.04)
Ventral eye diameter	0.22-0.23	0.21-0.25 (0.23; 0.02)
Width of orbits	0.28-0.38	0.27-0.37 (0.33; 0.03)
Longest dorsal ray	0.54-0.56	0.47-0.56 (0.52; 0.03)
Longest anal ray	0.54-0.61	0.47-0.55 (0.51; 0.03)
IOD/V	0	0
BPc/OPc	0.59-0.98	0.59-0.92 (0.72; 0.1)
BPv/OPv	0.75-0.96	0.95-1.05 (1.0; 0.04)

<sup>1</sup>: n=2, other specimens devoid of pigmentation.

**Geographic distribution:** *Pseudaesopia regani* has been reported from the Indian Ocean, along the east coast of Africa, and the Red Sea (Dor, 1984; Goren and Dor, 1994), at depths of 27-30 m.

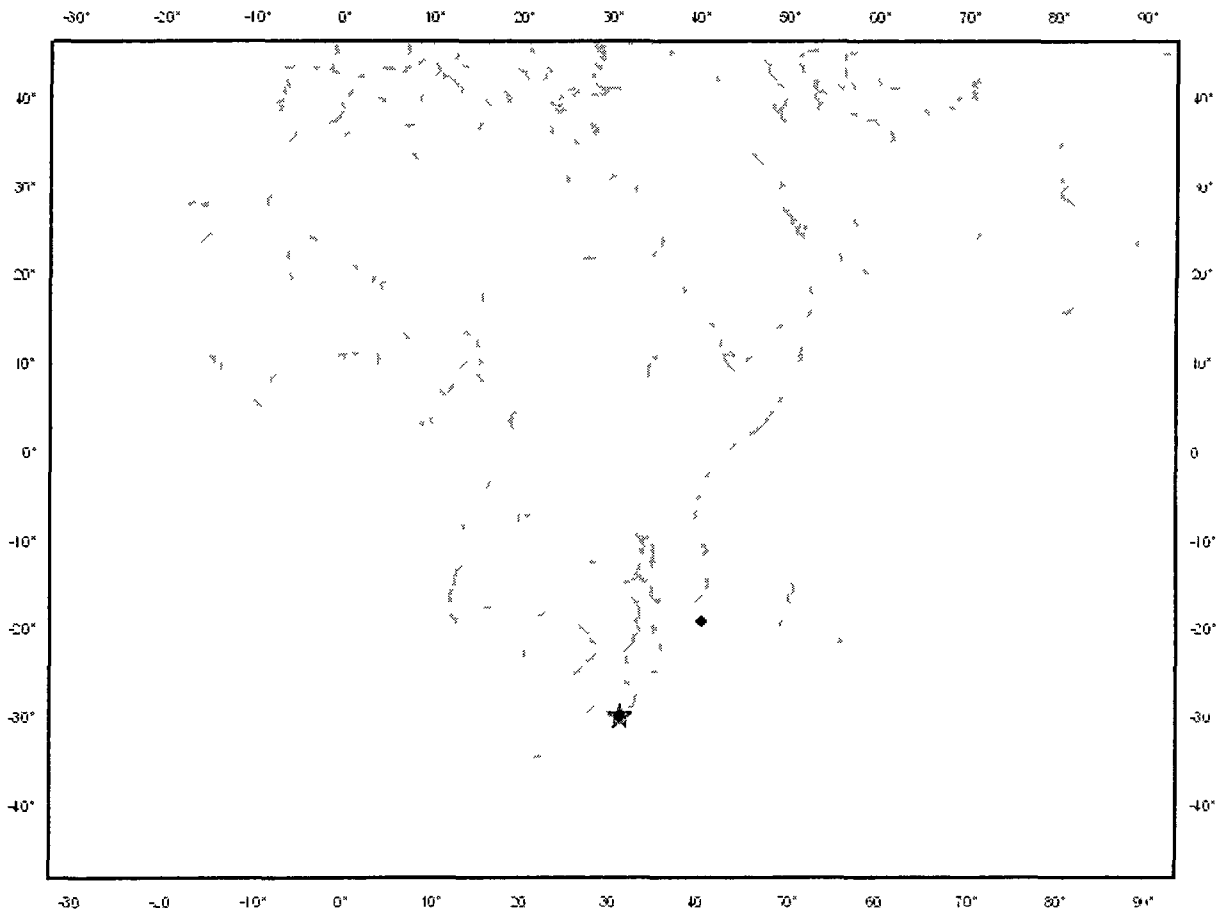


Figure 2.14. Geographic distribution of *Pseudaesopia regani*. Star denotes locality of type material.

**Remarks:** When Chabanaud (1934) established his monospecific subgenus, *Pseudaesopia*, he assigned *P. regani* as the type species. Chabanaud distinguished this subgenus from *Zebrias* by the attachment of the caudal fin to adjacent vertical-fin rays. Although the retention of the genus has been proposed, alternative characters have been used to describe it. As these characters are displayed by *P. regani*, it is proposed that this species be retained as the type species for this genus.

Minor discrepancies exist between the meristics reported in the original description and the present study; Gilchrist (1906) reports 56-59 anal-fin rays, 17 caudal-fin rays, 82-88 lateral-line scales, and 13 pairs of bands. Heemstra and Gon (1986) report 65-70 dorsal-fin rays, 86 scales along the lateral line, and 46 vertebrae for this species.

Among the specimens examined, one stood apart, due to its higher number of scales along the lateral line (102), higher number of supracranial pterygiophores on and anterior to the first neural spine (5 of the formula 1-2-2-), higher number of dorsal-fin rays (74), higher number of ctenii (16), and the presence of scales in the interorbital space. The bands of this specimen, SAM28866 (Figure 2.16), are faded, but there appear to be 13 singular bands across the body. Another specimen from the Somali coast (Figure 2.17), was observed to closely resemble *P. regani* with the exception of a few characters: 12 narrow, singular bands (possibly 13, but scales from posterior end are missing); 12 pectoral-fin rays; meristic values in the low range of *P. regani* (67 dorsal-fin rays, 54 anal-fin rays, 42 vertebrae, 71 lateral-line scales; estimated due to absence of scales at posterior end); and a fanned out caudal fin bearing a dissimilar pattern. It is possible these specimens represent distinct species and may require further examination. Note that these specimens were not included in Table 2.11.

**Comparisons:** *Pseudaesopia japonica* (Bleeker, 1860) and *Pseudaesopia callizona* (Regan, 1903) can be easily distinguished from *P. regani* by their caudal fin pigmentation (absence of light spots), longer pectoral fin ( $\bar{x}$  = 49-71% HL), the presence of interorbital scales, more pelvic-fin rays (5), and a greater number of scales along the lateral line (85-103). In addition, *P. callizona* has 14-17 singular bands, which differs from the band arrangement observed for *P. regani*. *P. lucapensis* (Seigel and Adamson, 1985) and *P. synapturoides* (Jenkins, 1910) differ from *P. regani* in having more pelvic-fin rays (5). In addition, *P. lucapensis* has more numerous, singular bands (24-27), a dusky blind side, fewer lateral-line scales (58-66), and more ocular-side pectoral-fin rays (11-13). *P. synapturoides* also differs in its band morphology and arrangement (*P. regani* with 9.5 pairs on body, 2.5 pairs on head + band on snout; *P. synapturoides* with wider bands, 9 across body, 3 on head, may be singular, paired, or a combination of the two). *P. regani* appears to be most closely allied to *P. cochinchensis* (Rama-Rao, 1967). The latter species can be distinguished by the presence of interorbital scales, a greater number of ocular-side pectoral-fin rays (11-14), a longer ocular-side pectoral fin (28-48% HL), and fewer, singular bands (13).

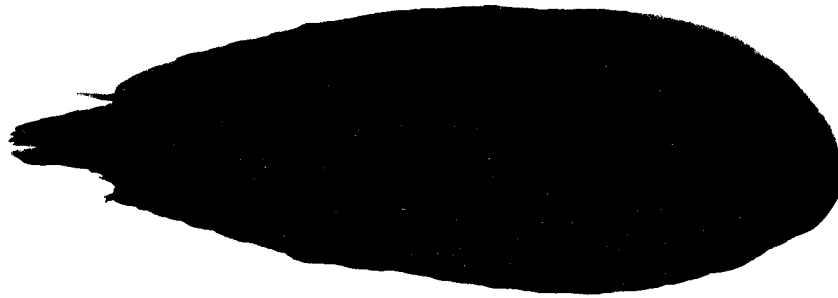


Figure 2.15. Photograph of *Pseudaesopia regani*, SAM15424, syntype, 116 mm SL, 2.5 miles off Umhlanga River Mouth, Natal, Sta. No: PF, 26 March 1901.

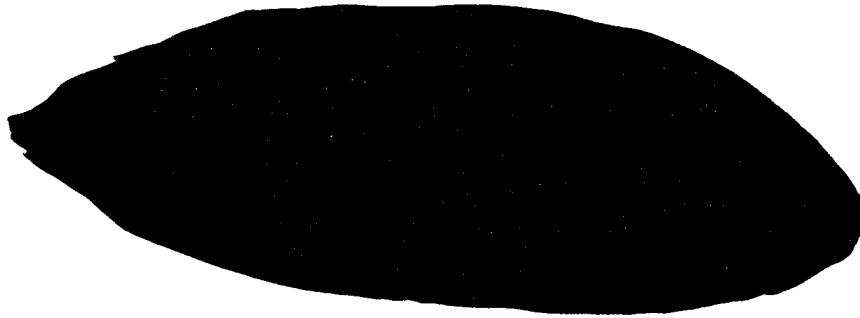


Figure 2.16. Photograph of *Pseudaesopia sp.*, SAM28866, 97 mm SL, Off Tugela River, South Africa, Sta No: WT 231. Specimen displays abnormal meristics for this species. Note that caudal fin appears truncated because it is damaged.

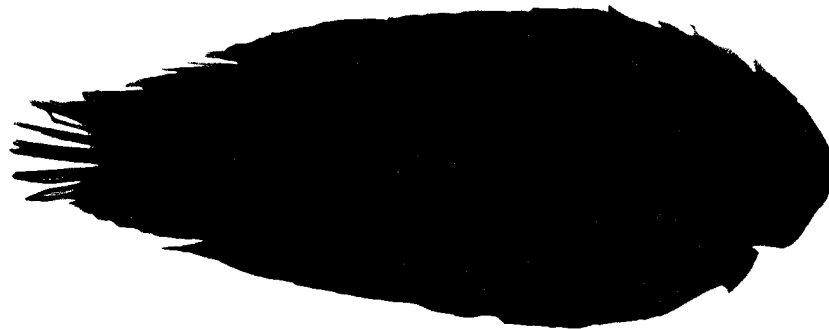


Figure 2.17. Photograph of *Pseudaesopia sp.*, ANSP145359, 109 mm SL, Somali Coast, 10°03'N, 51°15'E.

*Pseudaesopia synapturoides* (Jenkins, 1910)

Figures 2.18-2.24, Table 2.11

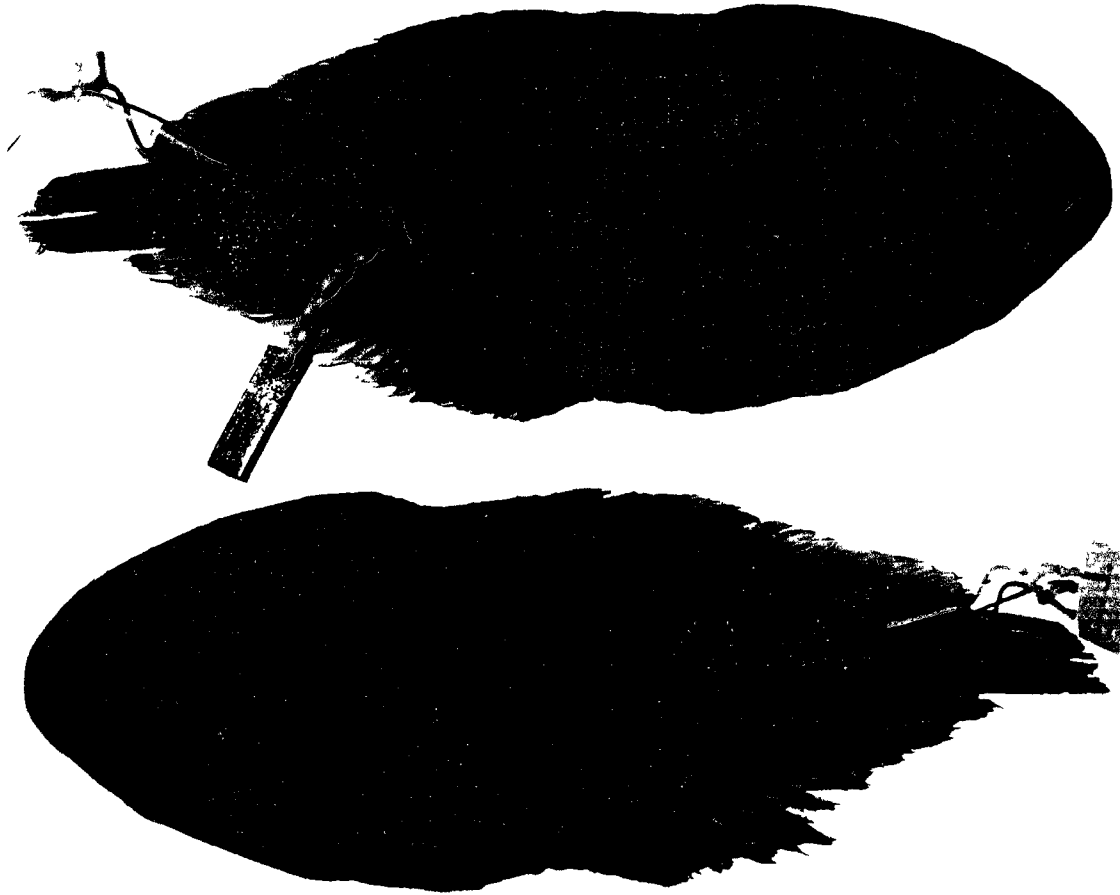


Figure 2.18. Photographs of *Pseudaesopia synapturoides*, syntype, MNHN1976-0380, 106 mm SL, Ganjam, India, 19°28'1"N, 85°4'59"E, 44-55 m depth, depicting ocular (above) and blind (below) sides.

**Synonym(s):** *Solea synapturoides* Jenkins, 1910; *Zebrias crossolepis*, Zheng and Chang, 1965

**Common name(s):** Indian zebra sole, Jenkin's sole

**Material examined:** 24 specimens (89.55-163.3 mm TL)

**Type material:** Only one of the two syntypes could be obtained for examination

ZSI F 3230/1 (not examined); MNHN1976-0380, 1(105.5 mm SL), Ganjam, India, 19°28'1"N, 85°4'59"E, 44-55 m depth.

**Non-type material:** CAS34230, 1(80.39 mm SL), Indo-West Pacific, Taiwan, Southwest of Kao-Hsiung into South China Sea; LACM42293-1, 2(110.9-112.34 mm SL), Hainan Is., Baimajing, China; ASIZP0054562, 1(90.19 mm SL), Penghu, off Taiwan, 23.57°N, 119.56°E; MNHN1976-382, 1(94.53 mm SL), India, 18°30'0"N, 84°46'1"E; ANSP145382, 10(92.56 -110.75 mm SL), Indian Ocean, 09°13'N, 97°51'E; ASIZP0064793, 1(139.57 mm SL), Tongkang, Pingtung, Taiwan, 22.47°N, 120.43°E; ASIZP0064772, 1(134.37 mm SL), Tongkang, Pingtung, Taiwan, 22.47°N, 120.43°E; BPBM20519, 1(106.05 mm SL), India, off Madras; ANSP145253, 1(91.57 mm SL), Indian Ocean, 14°07'N, 97°05'E; ANSP145358, 1(93.45 mm SL), Indian Ocean, 14°07'N, 97°05'E; ASIZP0060303, 1(84.74 mm SL), Dahsi, Ylian, 24.94°N, 121.9°E; USNM Uncatalogued, 2(88.09-97.82 mm SL), India.

**Diagnosis:** A species of *Pseudaesopia* with the following combination of characters: more or less symmetrical, rudimentary pectorals, none of the rays of which are elongate (length 18-31% HL,  $\bar{x}$  = 24% HL); 62-82 lateral-line scales; 5 pelvic-fin rays; 42-44 vertebrae; minute, dark spots on blind side; caudal fin dark with light spots at distal end; strongly ctenoid scales on both sides; interorbital scales absent; genital papilla free from pelvic fin; 9 bands on body, 3 on head, bands may be singular, split into pairs, or a combination of the two.

**Description:** Meristic and morphometric characters are indicated in Table 2.11. Small sole, attaining a total length of 17 cm. Supracranial pterygiophores 4-6; formula: 1-1-(1-4) (typically 1-1-3). Body oblong with greatest depth just posterior to opercular margin; body tapering at posterior end. Head slightly wider than long. Eyes contiguous or nearly so. Interorbital scales absent. Ocular tentacles absent. Ocular-side anterior nasal tube just reaching posterior nasal tube when flattened or slightly surpassing anterior margin of ventral eye. Ocular-side posterior nasal tube approximately half the length of anterior tube. Blind-side anterior nostril inconspicuous; a short, uneven tube. Anterior nostril slightly dorso-anterior to dorsalmost point of mouth. Blind-side posterior nasal tube dorso-posterior to anterior nasal tube, at a vertical through posterior edge of mouth and at posterior margin of dense cirri on anterior region of head. Posterior tube very short, of comparable length to ocular-side counterpart. Posterior margin of ocular-side jaws reaching vertical through anterior third to half of ventral eye. Ocular-side lips smooth. Blind-side lower lip plicate. Teeth minute, restricted to blind-side jaws. Ocular-side cirri restricted to opercular margin. Cirri densely-distributed at anterior end of blind-side head, extending along snout, chin and opercular margin. More sparsely distributed cirri may be present on mid-head region between scales posterior to dense patch of cirri on anterior region, cirri not extending posterior to opercular margin. Branchiostegal membrane attached to upper rays of pectoral fin on both sides. Lateral line extending horizontally from operculum to caudal peduncle on both blind and ocular sides, not extending anterior to opercular margin on blind side. Supraorbital line present on ocular-side head. Lateral-line scales cycloid. Scales on body strongly ctenoid on blind and ocular sides with 6-13 ctenii. Anterior end of dorsal fin at, or slightly anterior to, vertical

at anterior margin of dorsal eye. Anterior end of anal fin just posterior to anus. Vertical-fin rays increasing in length toward posterior end of body; longest fin rays in proximity to caudal fin, but not directly adjacent to it. Vertical-fin rays bifurcating at their distal ends. Caudal fin rounded and distinct, posteriormost anal-fin ray length 30%-62% ( $\bar{x}$  = 47%) relative to length of caudal fin. Scales extending onto median fins. Pectoral fins symmetrical, rudimentary, rays of comparable length (ocular-side fin length 18-31% HL, blind-side fin length 13-25% HL). Pelvic fins of comparable length; ocular-side fin typically slightly longer than blind-side fin. Anus submedian on blind side. Genital papilla submedian on ocular side, free from ocular-side pelvic fin.

**Pigmentation of preserved specimens:** Ocular side light brown or grey with bands of a darker hue. Body with 9 bands from opercular margin to base of caudal fin, head with 3; bands may be singular, paired, or a combination of the two (Figure 2.21). Bands relatively uniform in width across body, those on head becoming considerably narrower. Bands may appear paired with inter-band space darker than body, but lighter than bands. Inter-band space may be darker, making demarcation between bands almost inconspicuous and giving illusion of a singular band with a faint hint of splitting in center. Blind side pale with a dusting of minute, dark spots concentrated along posterior median-fin margins; spots may extend anteriorly along median-fin margins, on head, and on skin beneath operculum. Mouth pale with dark spots on tongue and floor of mouth. Bands extending onto dorsal and anal fins, becoming darker. Ocular-side caudal fin dark at its distal end with light spots. Ocular-side pectoral fin light brown, grey or black. Blind-side pectoral fin mostly transparent with minute, dark spots. Pelvic fins whitish.

Table 2.11. Meristic and morphometric characteristics of type and non-type specimens of *Pseudaesopia synapturoides*. Means and standard deviations are shown in parentheses. Measurements and abbreviations are described in Appendix B.

	<i>Solea synapturoides</i> syntype (n=1)	<i>P. synapturoides</i> non-type specimens (n=23)	<i>Zebrias crossolepis</i> <sup>1</sup> holotype and paratypes (n=25)
<b>Standard length (mm)</b>	105.5	80.39-139.57 (101.27; 14.1)	-
<b>Total length (mm)</b>	122.8	89.55-163.30 (118.39; 16.6)	77-127
<b>Counts</b>			
Dorsal-fin rays	79	69-78 (74.1; 2.2)	65-76
Anal-fin rays	63	56-64 (59.8; 2.0)	54-63
Caudal-fin rays	18	17-18 (18.0; 0.2) <sup>2</sup>	18
Precaudal vertebrae	9	8-9 (9.0; 0.2)	9
Caudal vertebrae	34	32-34 (33.3; 1.0)	34-36
Total vertebrae	43	42-44 (42.8; 0.5) <sup>3</sup>	-
Haemopophyses	5	5-6 (5.0; 0.2)	-
Pterygiophores	7	6-8 (6.7; 0.6)	-
Pectoral-fin rays o.s.	10	9-12 (10.9; 1.1)	(8)9-11
Pectoral-fin rays b.s.	11	9-13 (11.0; 1.0)	10-11
Pelvic-fin rays o.s.	5	4-5 (4.8; 0.4)	(4)5
Pelvic-fin rays b.s.	5	4-5 (4.8; 0.4)	(4)5
Lateral-line scales	70	62-82 (68.7; 5.8)	60-80
Number of bands	12	12-24 (16.0; 3.6) <sup>4</sup>	-
<b>Measurements</b>			
<b>%SL</b>			
Head length	0.20	0.17-0.21 (0.20; 0.01)	-
Head depth	0.23	0.19-0.27 (0.23; 0.02)	-
Body depth	0.37	0.32-0.42 (0.36; 0.02)	-
Caudal fin length	0.16	0.11-0.21 (0.17; 0.02)	-
Width caudal peduncle	0.09	0.05-0.09 (0.07; 0.008)	-
<b>%HL</b>			
Length of pectoral fin o.s.	0.15	0.18-0.31 (0.24; 0.03)	-
Length of pectoral fin b.s.	0.16	0.13-0.25 (0.18; 0.04)	-
Length of pelvic fin o.s.	0.32	0.17-0.41 (0.31; 0.05)	-
Length of pelvic fin b.s.	0.28	0.23-0.38 (0.28; 0.04)	-
Pre-orbital head length	0.14	0.18-0.30 (0.23; 0.03)	-
Post-orbital head length	0.56	0.52-0.64 (0.58; 0.03)	-
Snout length	0.23	0.21-0.33 (0.29; 0.03)	-
Nostril to snouth distance	0.12	0.15-0.66 (0.25; 0.1)	-
Mouth length o.s.	0.29	0.31-0.41 (0.36; 0.02)	-
Mouth length b.s.	0.25	0.26-0.36 (0.30; 0.03)	-
Ventral eye diameter	0.26	0.19-0.28 (0.23; 0.02)	-
Width of orbits	0.34	0.26-0.39 (0.34; 0.04)	-
Longest dorsal ray	0.46	0.39-0.66 (0.52; 0.05)	-
Longest anal ray	0.44	0.39-0.66 (0.52; 0.05)	-
IOD/V	0	0-0.15 (0.02; 0.04)	-
BPc/OPc	1.09	0.54-1.08 (0.78; 0.2)	-
BPv/OPv	0.87	0.80-1.62 (0.93; 0.2)	-

<sup>1</sup>: Data obtained from original description (Zheng and Chang, 1965); <sup>2</sup>: n=22; <sup>3</sup>: n=21; <sup>4</sup>: n=20.

**Geographic distribution:** *Pseudaesopia synapturoides* has been reported from the coasts of India, the Bay of Bengal, the Andaman Sea, the South China Sea and Taiwan. This species has also been reported from the Persian Gulf, the Arabian Gulf (Carpenter et al., 1997), and Pakistan (Hussain and Khan, 1981), although no representative specimens were examined in the present study. Reported from depths of 44-73 m.

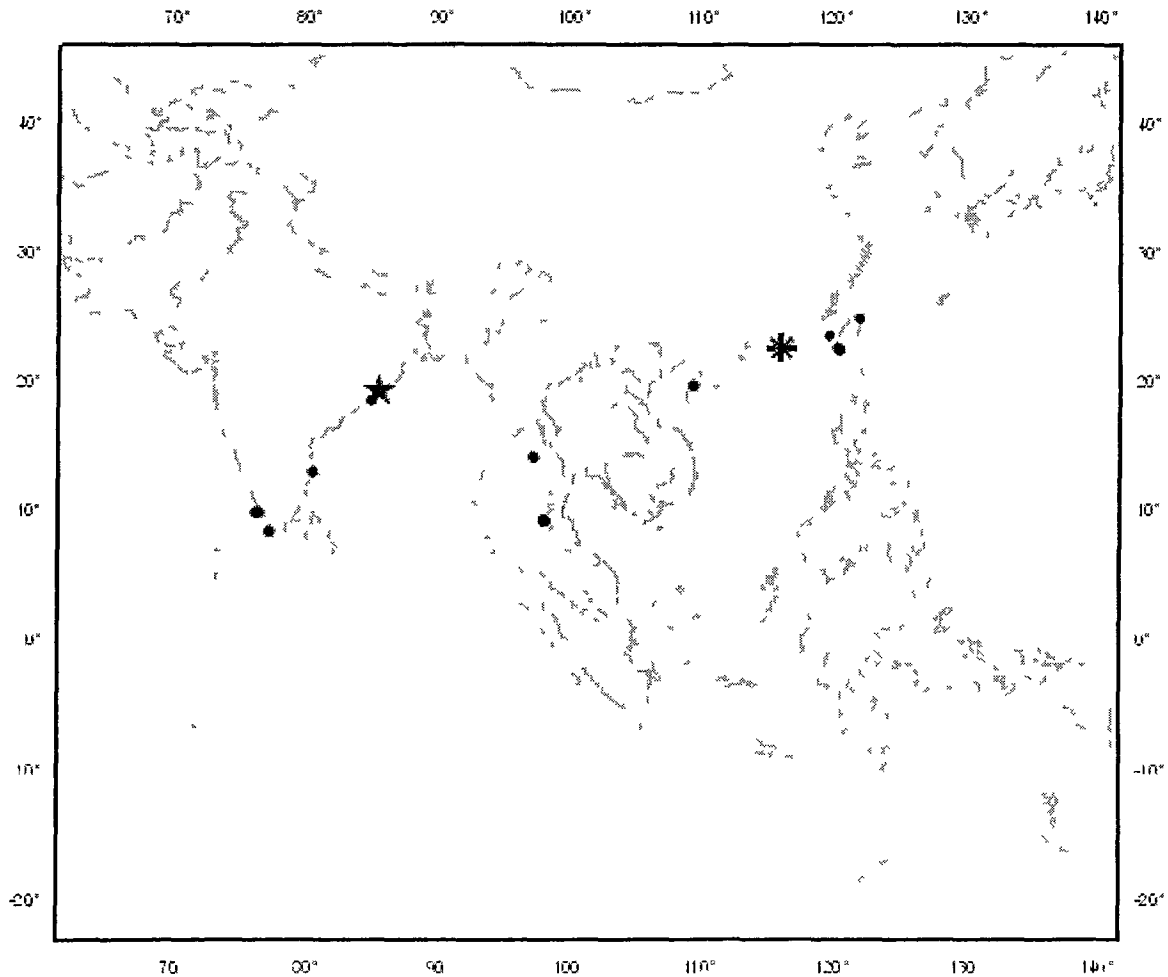


Figure 2.19. Geographic distribution of *Pseudaesopia synapturoides*. Star denotes locality of a syntype for *P. synapturoides*. Asterisk denotes locality of holotype for *Z. crossolepis*, according to Zheng and Chang (1965).

**Remarks:** When Zheng and Chang (1965) first described *Zebrias crossolepis*, they distinguished it from *Pseudaesopia synapturoides* on the basis of several characters, including the presence of teeth on the blind side (in the original description, *P. synapturoides* was described as being edentate), a urohyal having a larger angle ( $54^{\circ}$ - $64^{\circ}$  compared with  $30^{\circ}$ ), the absence of scales in the interorbital space, and nine pairs of cross-bands on the ocular side (body bands said to be singular in *P. synapturoides*).

Although the syntype examined (MNHN1976-0380; the other syntype, ZSI F3430/1 was unavailable for examination) was determined to be edentate, minute teeth were present on the blind-side jaw of all non-type material. It is possible the teeth were absent from the syntype as a result of damage.

The angle of the urohyal of the *P. synapturoides* syntype was found to be considerably greater than  $30^{\circ}$ . As shown by Figure 2.20, the angle is in accordance with the range reported for *Zebrias crossolepis*. The angle of the urohyal was found to be somewhat variable across all nominal specimens examined.

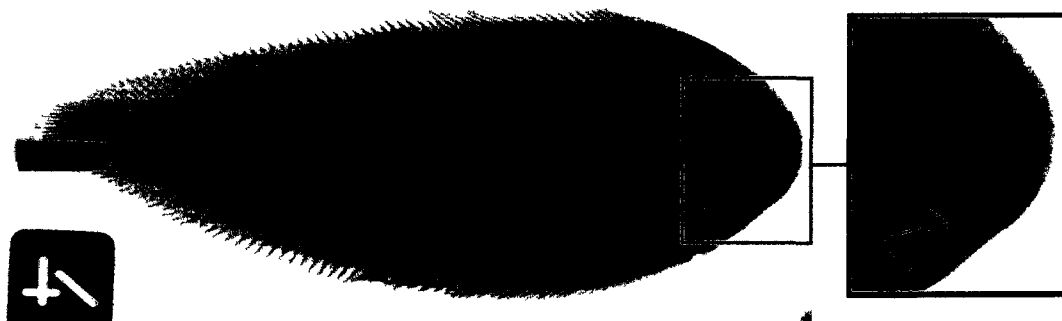


Figure 2.20. Radiograph showing the anterior region of the syntype *Solea synapturoides*, Jenkins, 1910, MNHN1976-0380, 106 mm SL, Ganjon Port, Calcutta, India. Urohyal is circled and denoted by a dotted line for enhanced visibility.

Interorbital scales were absent on the *P. synapturoides* syntype examined, in addition to all non-type material observed. Interorbital scales were only observed in one non-type specimen from Dahsi, Ylian which was identified as *Z. crossolepis*. The bands at the posterior end of this specimen appear to be singular, while the anterior body bands appear to be paired.

As with other species within *Pseudaesopia* and *Zebrias*, the banding pattern among non-type material was found to be somewhat variable. Within the same lot, there were specimens with paired body bands, some with singular body bands, and some with a mixture of the two (Figure 2.21). This variability precludes the use of paired or singular bands as a diagnostic character for this species.

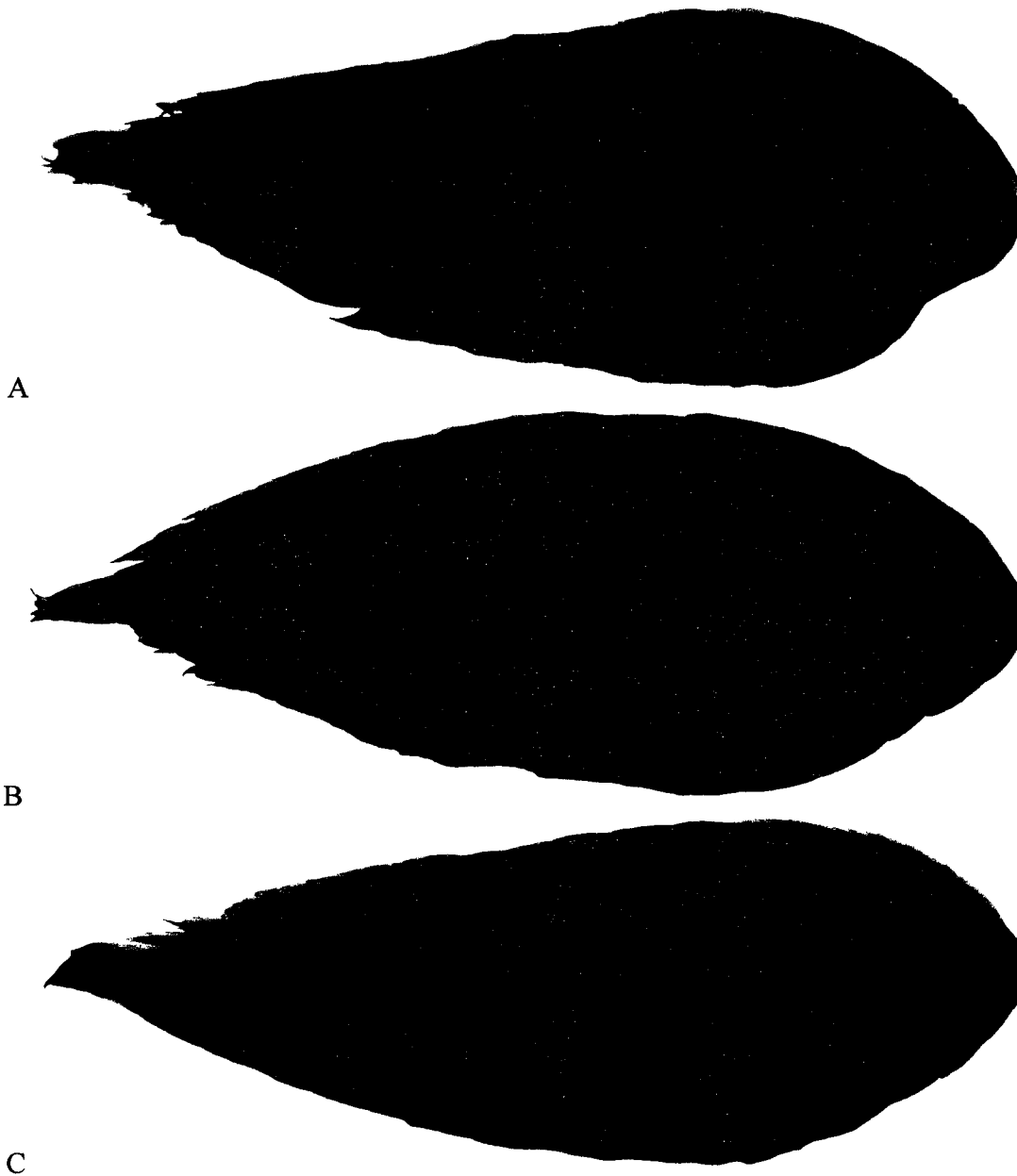


Figure 2.21. Photographs showing variation in banding pattern among a lot of *Pseudaesopia synapturoides* specimens from the Indian Ocean, ANSP145382, 10(93 - 111 mm SL), 9°13'N, 97°51'E. Photograph A shows a specimen having paired body bands; Photograph B shows a specimen with a mixture of paired and singular bands; Photograph C shows a specimen with singular body bands.

The type material for *Zebrias crossolepis* could not be obtained for examination. An examination of this material is required to confirm that *Z. crossolepis* is synonymous with *Pseudaesopia synapturoides*. A scan of the illustration depicting the holotype from the original description is provided below (Figure 2.22).

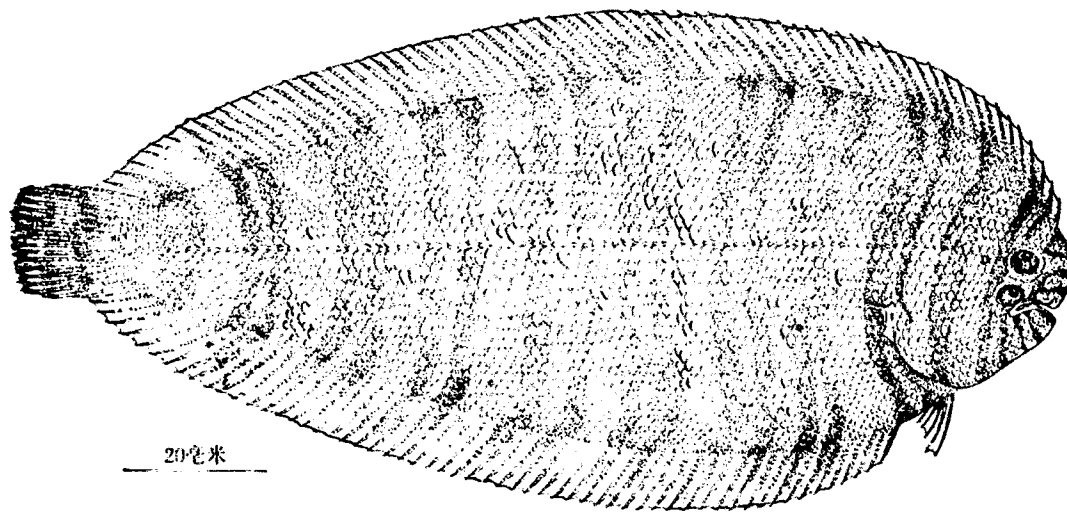


Figure 2.22. Scan of the illustration of the holotype of *Zebrias crossolepis* (Zheng and Chang, 1965) as presented in the original description, ASIZB 29861, 127 mm SL, Jieshi Harbor, Guangdong, China.

It is of note that in the original description of *P. synapturoides*, the number of lateral line scales is recorded as 90-93. It was not explicitly stated how the longitudinal scale measurement was obtained, so it is possible the reported count refers to the number of scales extending from the base of the caudal peduncle to the anterior margin of the snout. In the present study, 70 scales were counted from the base of the caudal peduncle to the opercular margin, which is consistent with Norman's (1928) findings. Moreover, in Jenkins' description, the dorsal- and anal-fin rays were said to be unbranched;

however, an examination of radiographs in the present study suggests the rays are bifurcate. Jenkins also reports 14 rays for the caudal fin, while the present authors observed 18 caudal-fin rays for this species (including the syntype), as did Norman.

Among the specimens examined, one Indonesian specimen stood out as having the general attributes of *P. synapturoides* but differing in its small size (67.04 mm TL), eyes separated by a scaly interorbital space, fanned caudal fin, lower number of pectoral-fin rays (8 on ocular side, 9 on blind side), and reddish pigmentation. It is possible this specimen represents a distinct species and may require further examination. Note that this specimen, shown in Figure 2.23, is not included in the data set presented in Table 2.11.

Also noted were 26 specimens (not included in data set) from Western Australia and the Gulf of Carpentaria. These specimens also appear to be closely-related to *P. synapturoides*, but differ in their band arrangement and caudal fin pattern. The common caudal fin pattern observed among all of these specimens consists of a white distal end with numerous black spots (Figure 2.24). The specimens from the Gulf of Carpentaria and the proximate Arnhem Bay have 18-19 bands (13 behind the operculum, the posterior 5/6 and 7/8 bands appear to be paired, the rest are singular), and the blind side is covered in minute dark spots, giving the body a dusky appearance. The specimens from Western Australia have 20-24 paired bands and the blind side is pale with minute, inconspicuous dark spots. These specimens may represent undescribed *Pseudaesopia* species, and warrant further investigation.

**Comparisons:** *P. japonica* (Bleeker, 1860) and *P. callizona* (Regan, 1903) are easily distinguished from *P. synapturoides* by their caudal fin pigmentation (solid black or pale with 4-5 oblong black spots at distal end; light spots absent), pectoral fin morphology (upper two rays elongate, mean length 49-71% HL), higher number of scales along the lateral line (85-103), and attachment of the genital papilla to the ocular-side pelvic fin. *P. cochinensis* (Rama-Rao, 1967) differs in having fewer pelvic-fin rays (4), a longer ocular-side pectoral fin (28-48% HL), banding pattern (13 singular, darkly-demarcated bands), and the presence of scales in the interorbital space. *P. lucapensis* (Seigel and Adamson, 1985) is easily distinguished by its banding pattern (24-27 singular bands), generally fewer scales along the lateral line (58-66), and dusky blind side. *P. regani* (Gilchrist, 1906) differs from *P. synapturoides* in its banding pattern (24-25 bands in pairs with 9.5 pairs on body), and fewer pelvic-fin rays (4).



Figure 2.23. Photograph of *Pseudaesopia* sp., BPBM38806, 56 mm SL, Indonesia, Sulawesi, Lembeh Strait, “Hairball” dive site, 56 feet. Note: the membrane attaching the posteriormost vertical-fin rays to the caudal fin appears to be damaged, giving the caudal fin the illusion of being connected to the vertical-fin rays at its base.

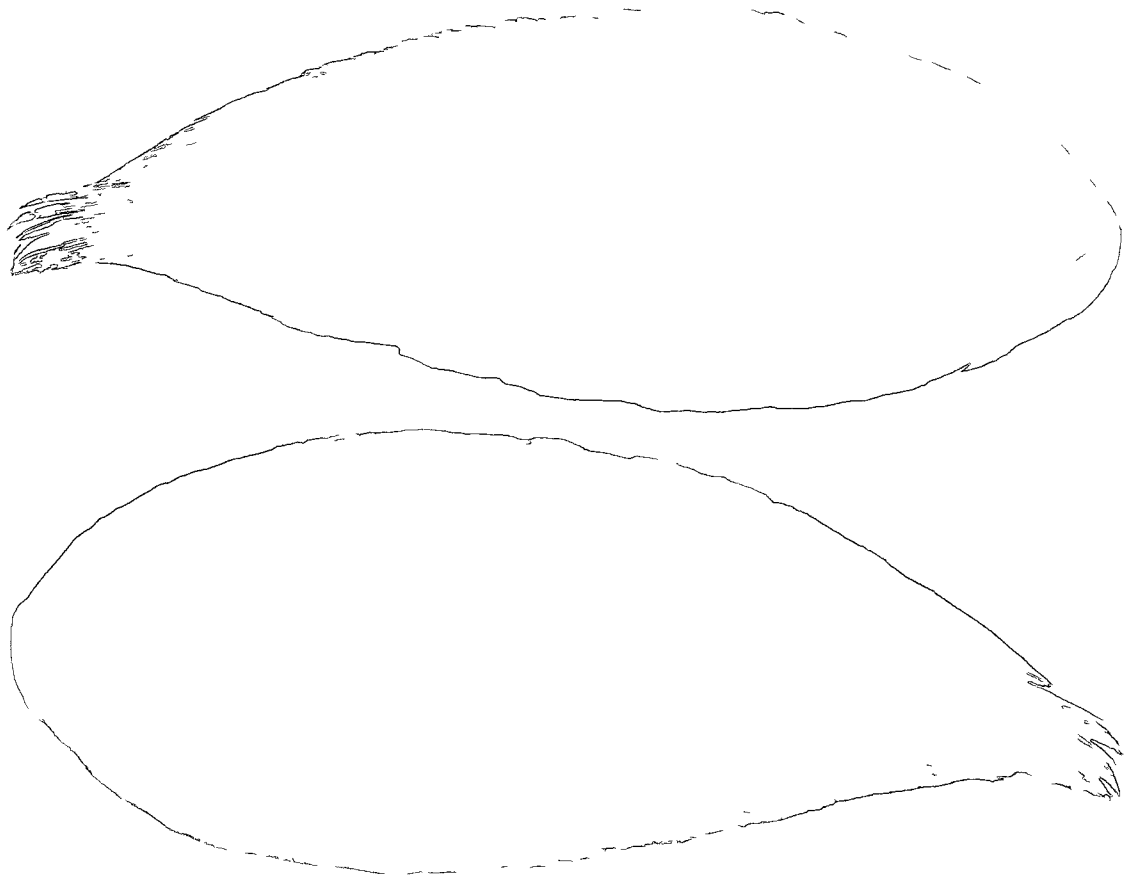


Figure 2.24. Photographs depicting *Pseudaesopia sp.*, QMI.28792, 131 mm SL, Gulf of Carpentaria, Australia, 11.26°S, 137.09°E, 47 m depth.

**KEY TO SPECIES OF *PSEUDAESOPIA***

- 1      Upper two rays of ocular-side pectoral fin elongate (Figure 2.1); ocular-side pectoral fin length 49-71% HL (average); 85-103 scales along the lateral line; genital papilla attached to ocular-side pelvic fin..... 2
- Upper two rays of ocular-side pectoral fin not elongate (Figure 2.8); ocular-side pectoral fin length 14-39% HL (average); 58-85 scales along the lateral line; genital papilla free from ocular-side pelvic fin..... 3
- 2      40-44 vertebrae; ocular-side pectoral fin length 49% HL (average); 10-26 thickly-demarcated bands in pairs, singular, or a combination of the two; caudal fin solid black at its distal end; blind side pale, devoid of conspicuous pigmentation.....*P. japonica* p. 224
- 44-45 vertebrae; ocular-side pectoral fin length 71% HL (average); 14-17 thinly-demarcated, singular bands; caudal fin solid black at its distal end, or pale with 4-5 oblong black spots at its distal end; blind side with minute dark spots around head and median fin margins.....*P. callizona* p.208
- 3      4 pelvic-fin rays; average 4 supracranial pterygiophores on and anterior to the first neural spine..... 4
- 5 pelvic-fin rays; average 5 supracranial pterygiophores on and anterior to the first neural spine..... 5

- 4 Interorbital scales present; ocular-side pectoral fin length 28-48% HL (average 39% HL); ocular-side pectoral-fin rays 11-14; 13 singular, darkly-demarcated bands; ocular-side anterior nasal tube just reaches posterior nostril when flattened.....*P. cochinensis* p.215
- Interorbital scales absent; ocular-side pectoral fin length 19-30% HL (average 24% HL); ocular-side pectoral-fin rays 9-11; 24-25 paired bands across body; ocular-side anterior nasal tube extends as far as the anterior margin of the ventral eye when flattened.....*P. regani* p.242
- 5 24-27 narrow, singular bands across body; 11-13 ocular-side pectoral-fin rays; ocular-side pectoral fin length 13-15% HL (average 14% HL); 58-66 scales along lateral line; 41-42 vertebrae; caudal fin dark brown or black at its distal end, spots absent.....*P. lucapensis* p.235
- 9 bands on body, 3 on head, bands may be singular, paired, or a combination of the two; 9-12 ocular-side pectoral-fin rays; ocular-side pectoral fin length 18-31% HL (average 24% HL); 62-82 scales along lateral line; 42-44 vertebrae; caudal fin dark with light spots.....*P. synapturoides* p.251

## REFERENCES

Alcock, A. W. 1890. Natural history notes from H. M. Indian marine survey steamer 'Investigator,' Commander R. F. Hoskyn, R. N., commanding.--No. 20. On some undescribed shore-fishes from the Bay of Bengal. *Annals and Magazine of Natural History (Series 6)* v. 6 (no. 36): 425-443.

Bleeker, P. 1856. Beschrijvingen van nieuwe en weinig bekende vischsoorten van Amboina, verzameld op eene reis door den Molukschen Archipel gedaan in het gevolg van den Gouverneur Generaal Duymaer van Twist, in September en Oktober 1855. *Acta Societatis Regiae Scientiarum Indo-Neêrlandicae*. 1: 1-76.

Bleeker, P. 1860. Zesde bijdrage tot de kennis der vischfauna van Japan. *Acta Societatis Regiae Scientiarum Indo-Neêrlandicae* v. 8: 1-104.

Bloch, M. E. 1787. *Naturgeschichte der ausländischen Fische*. Berlin. *Naturgeschichte der Ausländischen Fische*. 3: i-xii + 1-146, Pls. 181-216.

Carpenter, K. E., F. Krupp, D. A. Jones and U. Zajonz. 1997. *FAO species identification guide for fishery purposes. The living marine resources of Kuwait, eastern Saudi Arabia, Bahrain, Qatar, and the United Arab Emirates*. FAO Rome. 1-293, Pls. 1-17.

Chabanaud, P. 1934. Les soléidés du groupe *Zebrias*. Définition d'un sous-genre nouveau et description d'une sous-espèce nouvelle. Bulletin de la Société Zoologique de France **59**: 420-436.

Chabanaud, P. 1936. Sur divers soléidés apparentés au genre *Zebrias*. Bulletin de la Société Zoologique de France. **61**: 382-404, Pl. 6.

Dor, M. 1984. Checklist of the fishes of the Red Sea. CLOFRES. Israel Academy of Sciences and Humanities. Checklist of the fishes of the Red Sea. CLOFRES.: i-xxii, map + 1-437.

Gilchrist, J. D. F. 1906. Descriptions of fifteen new South African fishes, with notes on other species. Marine Investigations in South Africa. **4**: 143-171, Pls. 37-51.

Goren, M. and M. Dor. 1994. An updated checklist of the fishes of the Red Sea - CLOFRES II. Israel Academy for Sciences and Humanities. The Israel Academy of Sciences and Humanities. Jerusalem, 120 pp.

Heemstra, P. C. and O. Gon. 1986. Family No. 262: Soleidae (pp. 868-874). *In*:

Smith, M. M. and P. C. Heemstra (eds.). 1986. Smiths' Sea Fishes. Macmillan South Africa, Johannesburg. i-xx + 1-1047, Pls. 1-144.

Hoese, D. F. and D. J. Bray. 2006. Families and subfamilies: p. 88, 113-115, 116-117, 188-189, 675-685, 1000-1001, 1029-1030, 1031-1033, 1047, 1073-1077, 1176-1182, 1212-1217, 1264-1274, 1280, 1317-1327, 1350-1352, 1363-1365, 1476-1478, 1495-1496, 1497-1499, 1500-1504, 1505-1506, 1507-1508, 1540-1566, 1568-1576, 1578-1592, 1711-1712, 1729, 1787-1792, 1793-1797, 1800-1801, 1804-1805, 1807-1809, 1810-1823, 1824-1825, 1826-1830, 1831-1837, 1838-1840, 1841-1852, 1853-1858. In: Zoological Catalogue of Australia. Volume 35. Fishes.

Hussain, S.M. and J.A. Khan. 1981. Species of family Soleidae (Pleuronectiformes) from Pakistan. *Biologia*. **27**(1): 19-32.

Jenkins, J. T. 1910. Report on the fishes taken by the Bengal Fisheries Steamer "Golden Crown" Part IV. Pleuronectidae. *Memoirs of the Indian Museum*. **3**(no. 1): 23-31.

Joglekar, A. 1976. On a new species of the genus *Zebrias* Jordan and Snyder, 1900 (Pisces: Soleidae) from Kerala coast (India). *Zoologischer Anzeiger* v. 197 (no. 1-2): 67-70.

Jordan, D. S. and J. O. Snyder. 1900. A list of fishes collected in Japan by Keinosuke Otaki, and by the United States steamer Albatross, with descriptions of fourteen new species. *Proceedings of the United States National Museum*. **23**(no. 1213): 335-380, Pls. 9-20.

Kamohara, T. 1964. Revised catalogue of fishes of Kochi Prefecture, Japan. *Rep. Usa Mar. Biol. Sta.* **11**: 1-99.

Kaup, J. 1858. Uebersicht der Soleinae, der vierten Subfamilie der Pleuronectidae. Archiv für Naturgeschichte. **24** (no. 1): 94-104.

Lindberg, G. U. and V. V. Fedorov. 1993. Fishes of the Sea of Japan and the adjacent parts of the Sea of Okhotsk and the Yellow Sea. Part 6. Teleostomi. Osteichthyes. Actinopterygii. XXI. Pleuronectiformes (Fam. CXCIV. Psettodidae -- Fam. CCI. Cynoglossidae). Handbook on the Identification of Animals, Zoological Institute of the Russian Academy No. 166: 1-271.

Manilo, L.G., and Bogorodsky, S.V. 2003. Taxonomic composition, diversity and distribution of coastal fishes of the Arabian Sea. Journal of Ichthyology. 43(1): S75-S149.

McCulloch, A. R. 1916. Ichthyological items. Memoirs of the Queensland Museum v. 5: 58-69, Pls. 7-9.

Munroe, T.A. in Randall, J. E. and K. K. P. Lim. 2000. A checklist of the fishes of the South China Sea. The Raffles Bulletin of Zoology Supplement No. 8: 569-667.

Nakabo, T. (Ed.). 2002. Fishes of Japan with pictorial keys to the species, English edition. Tokai University Press. Fishes of Japan with pictorial keys to the species. Second edition. **2**: i-vii + 867-1749.

Norman, J. R. 1928. The flatfishes (Heterosomata) of India, with a list of the specimens in the Indian Museum. Part II. Records of the Indian Museum (Calcutta). **30** (pt 2): 173-215, Pls. 4-7.

Ochiai, A. 1963. Fauna Japonica. Soleina (Pisces). Biogeographical Society of Japan (Tokyo) 1963: i-vi + 1-114, Pls. 1-24.

Rama-Rao, K. V. 1967. A new sole *Zebrias cochinensis* from India. Journal of the Zoological Society of India. 19(nos. 1-2): 99-100.

Rao, K.S., and M.R. Murty. 1981. Occurrence of *Zebrias japonicus* (Bleeker) (Soleidae: Pisces) in the Bay of Bengal, off Visakhapatnam. Journal Bombay Natural Hist. Society. 78(3): 614-615.

Regan, C.T. 1903. Notes on the genus *Synaptura* Cantor, with descriptions of two new species. Annals and Magazine of Natural History (Series 7). 11(61): 56-58, Pl. 6.

Sakamoto, K. 1997. Pleuronectidae, Soleidae and Cynoglossidae. In Okamura, O. and K. Amaoka (eds.). Sea fishes of Japan, Yama-Kei Publ. Co., Ltd., Tokyo, pp. 672-684.

Schwarzhan, W. 1999. *Piscium Catalogus: Part Otolithi piscium*, Vol. 2, A comparative morphological treatise of recent and fossil otoliths of the order Pleuronectiformes. Verlag Dr Friedrich Pfeil, München.

Seigel, Jeffrey A. and Adamson, Thomas A. 1985. First record of the genus *Zebrias* (Pisces: Pleuronectiformes: Soleidae) from the Philippine Islands, with the description of a new species. Proc. Biol. Soc. Wash. 98(1): 13-16.

Shinohara, G., H. Endo, K. Matsuura, Y. Machida and H. Honda. 2001. Annotated Checklist of the Deepwater Fishes from Fishes from Tosa Bay, Japan. Monographs of the National Science Museum Tokyo No. 20: 283-343.

Taki, I. 1938. On the abnormal arrangement of scales and colour bands in a sole (*Zebrias*), with special reference to its adverse scales. Journal of Science of the Hiroshima University. Series B, Div. 1, Vol. 6, Art. 3, pp.1-14, Pls. I-II.

Talwar, P. K. and S. Chakrapany. 1967. A new flatfish of the genus *Zebrias* Jordan and Snyder [Soleidae] from the Orissa coast, India. Proceedings of the Zoological Society of Calcutta. v. 20 (no. 2): 119-121.

Talwar, P.K. and R.K. Kacker. 1984. Commercial sea fishes of India. Zoological Survey of India, Calcutta. 997pp.

Temminck, C. J. and H. Schlegel. 1846. Fauna Japonica, sive descriptio animalium quae in itinere per Japoniam suscepto annis 1823-30 collegit, notis observationibus et adumbrationibus illustravit P. F. de Siebold. Parts 10-14: 173-269.

Zheng, P.-S. and Y.-W. Chang. 1965. Studies on the Chinese soleoid fishes of the genus *Zebrias*, with description of a new species from the South China Sea. Acta Zoologica Sinica. 2(no. 4): 267-278.

## GENERAL CONCLUSION

Results of the present taxonomic study show that of the 25 nominal species associated with the genus, *Zebrias*, 16 were found to be valid. Ten of these species have been assigned to *Zebrias* with the remaining six being placed in the genus *Pseudaesopia*. Both *Zebrias* and *Pseudaesopia* were re-described to encompass all presently recognized valid species assigned to each genus. The latter genus closely resembles *Zebrias*, but the posteriormost vertical fin rays are only confluent with the caudal fin along the proximal half of its length, at most, leaving the caudal fin quite rounded and distinct. Moreover, the species of this genus generally have a higher number of pectoral-fin rays.

Species keys incorporating all valid species were presented for both genera. The revision of *Pseudaesopia* suggests a need for additional research due to the possibility of several undescribed species, found primarily around Australia and Indonesia. Based on several potential synapomorphies found in the present study, *Zebrias* and *Pseudaesopia* are hypothesized to form a monophyletic group characterized by the structure of the supracranial complex, the broad interconnection of the caudal fin to the adjacent vertical-fin rays, the attachment of the upper pectoral-fin rays to the opercular membrane, the separation of the anal fin and ocular-side pelvic fin, the presence of moderately to strongly ctenoid scales, and by the presence of irregular spots or transverse bands.

Following the taxonomic revision of *Zebrias*, several synonyms were established. *Solea zebrina*, *Solea fasciata*, and *Solea ommatura* were synonymised under the senior synonym *Z. zebra*, which was confirmed to be the type species anchoring the genus. It is strongly suspected that *Z. maculosus* represents a synonym of *Z. annularis*; however, in the absence of type and non-type material, it has been tentatively recognized as a valid species pending further review.

The description presented for this species in the current study is a summary of the original description. *Synaptura fasciata* Macleay, 1882, which is secondarily preoccupied in *Zebrias* by *Solea fasciata* Basilewsky, 1855, was synonymised under its replacement name, *Zebrias scalaris* Gomon, 1987. It was determined that *Strabozebrias munroi* would be better placed in the genus, *Phyllichthys*, due to its confluent ocular-side pelvic and anal fins.

Following the taxonomic revision of *Pseudaesopia*, *Zebrias annandalei* and *Synaptura smithii* were synonymised under the senior synonym *P. japonica*. *Z. crossolepis* was synonymised under the senior synonym *P. synapturoides*. *Z. keralensis* was synonymised under the senior synonym *P. cochinensis*, the holotype of the latter species displaying an abnormal band arrangement.

The taxonomy of the soles is in great need of revision. The known biodiversity present within this family continues to increase and through taxonomic revisions of its various genera, a greater understanding of the composition of the family and the interrelationships present therein can be achieved. This improved understanding is important when considering the proper management of fisheries dealing with this important resource, in addition to conservation issues dealing with individual species.

## PHYLOGENETIC OBSERVATIONS

A phylogenetic study is necessary to more accurately assess the monophyletic status of both genera as well as determine interspecific and intergeneric relationships; both genera present a challenge in obtaining an adequate sample size of fresh material for most species, potentially making such a study unfeasible at the present time. A preliminary hypothesis of phylogenetic relationships based on morphological data is presented herein.

As previously discussed, *Zebrias* and *Pseudaesopia* are hypothesized to form a monophyletic group. The closely-related genus, *Soleichthys*, would be an appropriate sister group in a formal phylogenetic analysis. In particular, the species *Soleichthys microcephalus* (Günther, 1862) bears a strong resemblance to *Pseudaesopia japonica*, except for its distinct caudal fin, joined basally to the adjacent vertical-fin rays (Figure 2.25).

### Generic Relationships:

In the absence of a formal phylogenetic analysis, it is difficult to place *Zebrias* and *Pseudaesopia* among closely-related genera. *Pseudaesopia*, *Soleichthys*, *Aesopia* and *Phyllichthys* appear to form a monophyletic group based on several shared characters, including the attachment of the opercular membrane to the upper pectoral-fin rays; the attachment (at least basally) of the caudal fin to the adjacent vertical-fin rays; and a comparable supracranial morphology. Chabanaud (1930a) also distinguished these genera (excluding *Pseudaesopia*) by the absence of the hypocoracoid bone, the presence of simple, parallel pectoral-fin rays (fanned out in other genera), the location of the longest vertical-fin rays at the posterior end of the body, and a short blind anterior nasal tube not surrounded by a naked furrow.

*Phyllichthys*, *Aesopia*, *Zebrias* and *Pseudaesopia* are all characterized by having broadly interconnected caudal and vertical fins, while *Soleichthys* is characterized by its distinct caudal fin, joined only at its base to adjacent vertical-fin rays. The posteriormost vertical-fin rays of *Pseudaesopia* species only extend along the proximal half of the caudal fin, giving the fin a distinct appearance; the corresponding rays of *Aesopia*, *Phyllichthys*, and *Zebrias* species extend nearly the length of the caudal fin, giving the illusion of a more or less continuous fin. Given the close relationship between *Zebrias* and *Pseudaesopia*, the latter genus may actually represent an intermediate form between *Soleichthys* and *Zebrias*. *Aesopia* bears a superficially strong resemblance to *Zebrias*, making it likely the two are closely-related; however, *Aesopia* has several unique and presumably derived characters including a modified first dorsal-fin ray, weakly ctenoid scales, a greater number of pectoral-fin rays (12-19), and a blind-side anterior nasal tube of comparable length to the posterior tube. Transverse bands are absent from the majority of species belonging to *Phyllichthys*, most of which exhibit spots; moreover, this genus is characterized by the confluence of the ocular-side pelvic and anal fins. *Phyllichthys munroi* exhibits transverse bands, but these are wavy and highly irregular; some of the bands are broken up, with some pieces resembling irregular spots, similar to those observed in *Z. annularis*. The irregular bands are similar to those observed among multiple species of *Soleichthys*. Schwarzahns (1999) proposed that *Phyllichthys* could represent the most plesiomorphic genus with respect to *Zebrias*, *Pseudaesopia*, *Aesopia* and *Soleichthys*, based on otolith morphology. The primitive banding observed in only one or two *Phyllichthys* species seems to support this theory. A phylogenetic study is required to fully resolve the inter-generic relationships present within this group. A key to the aforementioned genera is provided below.

## KEY TO GENERA

- 1      Posteriormost vertical-fin rays attached along their entire length to adjacent caudal-fin rays; ocular-side anterior nasal tube reaching as far as anterior margin of ventral eye when flattened..... 2
- Posteriormost vertical-fin rays attached at their base to adjacent caudal-fin rays; ocular-side anterior nasal tube reaching at least midpoint of ventral eye when flattened.....*Soleichthys*
- 2      Anal fin broadly attached to ocular-side pelvic fin; body without regular transverse bands (*Phyllichthys munroi* with highly irregular, wavy bands; Figure 1.5).....*Phyllichthys*
- Anal fin free from ocular-side pelvic fin; body with regular transverse bands or large spots..... 3
- 3      Caudal fin more or less completely confluent with vertical fins..... 4
- Posteriormost vertical-fin rays attached to basal half of caudal fin.....*Pseudaesopia* p. 196
- 4      Anteriormost dorsal-fin ray enlarged and free (Figure 1.45); scales very weakly ctenoid; pectoral-fin rays 10-19; blind-side anterior nostril a tube of comparable length to blind-side posterior nasal tube; haemapophyses and precaudal vertebrae usually 6 and 10, respectively.....*Aesopia* p. 151
- Anteriormost dorsal-fin ray not enlarged or free; scales moderately to strongly ctenoid; pectoral-fin rays 4-10 (*Zebrias altipinnis* with 9-12); blind-side anterior nostril a short, uneven tube; haemapophyses and

precaudal vertebrae usually 5 and 9, respectively.....*Zebrias* p. 38

### **Interspecific Relationships:**

Within *Zebrias* and *Pseudaesopia* some shared characters might define possible clades.

*Zebrias quagga* and *Z. captivus* share the unique character of ocular tentacles, in addition to a unique pectoral fin morphology in which the upper two ocular-side pectoral-fin rays are tightly joined by a thin membrane with the second ray being the longest.

*Z. annularis* and *Z. maculosus* are unique in having irregular, darkly-demarcated spots in lieu of transverse bands. If these spots represent the precursor to transverse bands, then these two species could represent the most plesiomorphic species within the genus. Alternatively, the spots could represent modified bands, in which case the two species may be the most derived.

*Z. penescalaris* and *Z. scalaris* are nearly indistinguishable, both species having poorly-defined, narrow transverse bands and the genital papilla situated at the base of the posteriormost ocular-side pelvic-fin ray, as opposed to directly adjacent the anus. Moreover, *Z. penescalaris* and *Z. scalaris* have 4-5 supracranial pterygiophores (pattern 1-1-2/1-1-3), while other species in the genus typically have 3-4 (pattern 1-1-1/1-1-2).

*Zebrias zebra*, *Z. cancellatus* and *Z. altipinnis* all have high meristic values (90-133 lateral-line scales, 45-53 vertebrae; *Z. altipinnis* and *Z. zebra* with >79 dorsal-fin rays) and attain a relatively large size when compared to other species in the genus (23-33cm).

*Zebrias zebra*, *Z. penescalaris*, and *Z. scalaris* are all characterized by having eyes separated by scales and 16 caudal-fin rays, as opposed to 18.

*Z. altipinnis*, *Z. annularis*, and *Z. maculosus* also have separate eyes, but they possess 18 caudal-fin rays.

*Z. craticula*, *Z. altipinnis*, *Z. annularis*, and *Z. cancellatus* all have the genital papilla free from the ocular-side pelvic fin. In other *Zebrias* species, these two structures are attached by a thin membrane.

*Z. altipinnis* and *Z. annularis* are the only species in *Zebrias* having 5 pelvic-fin rays (*Z. maculosus* likely shares this character, but data are unavailable); in addition, they both have 5-6 supracranial pterygiophores (pattern 1-1-3/1-1-4).

The species of *Pseudaesopia* all bear a strong resemblance, making monophyletic units more difficult to define. *P. japonica* and *P. callizona* appear to be closely-related and share numerous characters absent from all other species in the genus, including their ocular-side pectoral fin morphology and length, a high number of scales along the lateral line (85-103), the attachment of the genital papilla to the ocular-side pelvic fin, and the absence of light spots from the caudal fin. In addition, these species share similar meristics with *Soleichthys microcephalus* (43-45 vertebrae, 76-80 dorsal-fin rays, 64-68 anal-fin rays, 16-18 caudal-fin rays, 4-5 supracranial pterygiophores; n=7), which bears a strong resemblance to *Pseudaesopia japonica*.

*Pseudaesopia cochinchensis* and *P. regani* have a comparable range of lateral-line scale counts as well as 4 pelvic-fin rays, while the remaining species in the genus have 5.

*P. synapturoides* and *P. regani* are both characterized by the absence of scales in the interorbital space. *P. lucapensis*, *P. synapturoides*, and *P. regani* all have rudimentary pectoral fins (mean length = 14-25% HL), having a comb-like appearance. A similar pectoral fin morphology is observed in *Zebrias scalaris*, *Z. penescalaris*, *Z. cancellatus*, *Z. altipinnis* and *Z. craticula* (mean length = 7-24% HL).

*Pseudaesopia synapturoides*, *P. regani*, and *P. keralensis* all have dark caudal fins with numerous light spots. The caudal fin pigmentation of *P. lucapensis* is similar to that of *P. japonica*.

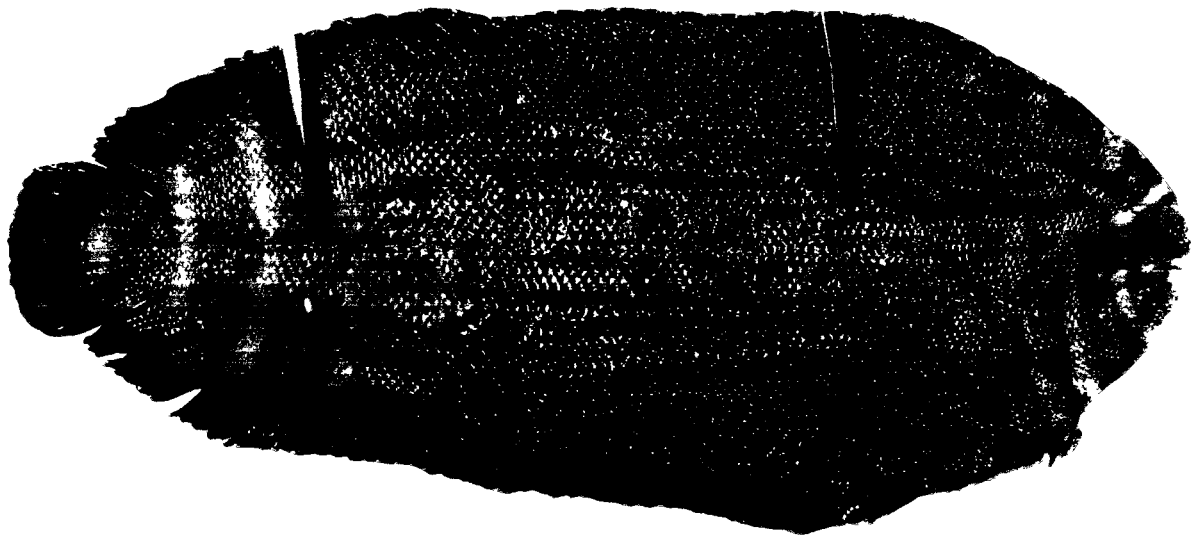


Figure 2.25. Photograph of *Soleichthys microcephalus*, AMSI.40868-015, 135 mm TL, NSW, Chowder Bay, end of fuel wharf, east side, 33°51.58'S, 151°12.01'E, 14.4 m depth.

APPENDIX A

Status of the nominal species of *Zebrias* and *Pseudaesopia*.

Nominal Species Author/Year	Current Status	Nominal Reference	Type Specimen (s)	Comments
<i>Synaptura altipinnis</i> Alcock 1890	Valid as <i>Zebrias</i> <i>altipinnis</i>	Alcock, A. W. 1890. Natural history notes from H. M. Indian marine survey steamer 'Investigator,' Commander R. F. Hoskyn, R. N., commanding.--No. 20. On some undescribed shore-fishes from the Bay of Bengal. Ann. Mag. Nat. Hist. (Ser. 6) 6 (36): 425-443.	Holotype: ZSI F12917	Type material unavailable for examination
<i>Zebrias annandalei</i> Talwar & Chakrapany 1967	Synonym of <i>Pseudaesopia</i> <i>japonica</i>	Talwar & Chakrapany. 1967. A new flatfish of the genus <i>Zebrias</i> Jordan and Snyder [Soleidae] from the Orissa coast, India. Proc. Zool. Soc. (Calcutta) 20 (2): 119-121.	Holotypes: ZSI F5011/2; Paratypes: ZSI F5012/2	Type material unavailable for examination
<i>Brachirus annularis</i> Fowler 1934	Valid as <i>Zebrias</i> <i>annularis</i>	Fowler, H. W. 1934. Descriptions of new fishes obtained 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. Proc. Acad. Nat. Sci. Phila. 85 (for 1933): 233-367.	Holotype: USNM 93095; Paratype: USNM 93206	Examined
<i>Synaptura callizona</i> Regan 1903	Valid as <i>Pseudaesopia</i> <i>callizona</i>	Regan, C.T. 1903. Notes on the genus <i>Synaptura</i> Cantor, with descriptions of two new species. Annals and Magazine of Natural History (Series 7). 11 (61): 56-58, Pl. 6.	Holotype: BMNH 1879.5.14.68	Examined
<i>Synaptura cancellata</i> McCulloch 1916	Valid as <i>Zebrias</i> <i>cancellatus</i>	McCulloch, A. R. 1916. Ichthyological items. Mem. Queensl. Mus. 5: 58-69, Pls. 7-9.	Holotype: AMS I.13199; Paratype: AMS E.2486	Examined

<i>Zebrias captivus</i> Randall 1995	Valid as <i>Zebrias captivus</i>	Randall, J. E. 1995. <i>Zebrias captivus</i> , a new species of sole (Pleuronectiformes: Soleidae) from the Persian Gulf. J. South Asian Nat. Hist. 2 (2): 241-246.	Holotype: BPBM 29478; Paratype: USNM 334423	Examined
<i>Zebrias cochinensis</i> Rama-Rao 1967	Valid as <i>Pseudaesopia cochinensis</i>	Rama-Rao, K. V. 1967. A new sole <i>Zebrias cochinensis</i> from India. J. Zool. Soc. India 19 (1-2): 99-100.	Holotype: Whereabouts unknown	Unable to examine: location of holotype unknown Examined
<i>Synaptura craticula</i> McCulloch 1916	Valid as <i>Zebrias craticula</i>	McCulloch, A. R. 1916. Ichthyological items. Mem. Queensl. Mus. 5: 58-69, Pls. 7-9.	Holotype: AMS E.2700; Paratype: AMS I.13616	Examined
<i>Zebrias crossolepis</i> Zheng & Chang 1965	Synonym of <i>Pseudaesopia synapturoides</i>	Zheng, P.S. and Y.W. Chang. 1965. Studies on the Chinese soleoid fishes of the genus <i>Zebrias</i> , with description of a new species from the South China Sea. Acta Zool. Sin 2 (4): 267-278. [In Chinese. First author's name spelled "Cheng" in English summary].	Holotype: ASIZB 29861; Paratypes: ASIO(?), ASIZB(9)	Unable to examine: type material only available for examination at the Chinese Academy of Sciences (Beijing, China) Unable to examine: no type material
<i>Solea fasciata</i> Basilewsky 1855	Synonym of <i>Zebrias zebra</i>	Basilewsky, S. 1855. Ichthyographia Chinae Borealis. Nouv. Mém. Soc. Imp. Natur. Moscou 10: 215-263, Pls. 1-9. [Apparently published in 1855, 1852 on cover. Plates cites in text do not agree with the actual plates].	No types at ZIN	Unable to examine: no type material
<i>Synaptura fasciata</i> Macleay 1882	Objective synonym of <i>Zebrias scalaris</i>	Macleay, W. 1882. Notes on the Pleuronectidae of Port Jackson, with descriptions of two hitherto unobserved species. Proc. Linn. Soc. N. S. W. 7 (pt 1): 11-15.	Holotype: AMS I.16281-001 [ex MAMU F1168]	Examined

<i>Aesopia japonica</i> Bleeker 1860	Valid as <i>Pseudaesopia</i> <i>japonica</i>	Bleeker, P.1860. Zesde bijdrage tot de kennis der vischfauna van Japan. Acta Soc. Sci. Indo-Neerl. 8: 1-104.	Holotype: Whereabouts unknown	Unable to examine: location of holotype unknown
<i>Zebrias</i> ( <i>Nematozebras</i> ) <i>keralensis</i> Joglekar 1976	Synonym of <i>Pseudaesopia</i> <i>cochinensis</i>	Joglekar, A. 1976. On a new species of the genus <i>Zebrias</i> Jordan and Snyder, 1900 (Pisces: Soleidae) from Kerala coast (India). Zool. Anz. 197 (1-2): 67-70.	Holotype: ZSI F6822/2; Paratypes: ZSI F6823/2	Type material unavailable for examination
<i>Zebrias lucapensis</i> Seigel & Adamson 1985	Valid as <i>Pseudaesopia</i> <i>lucapensis</i>	Seigel, J. A. and T. A. Adamson. 1985. First record of the genus <i>Zebrias</i> (Pisces: Pleuronectiformes: Soleidae) from the Philippine Islands, with the description of a new species. Proc. Biol. Soc. Wash. 98 (1): 13-16.	Holotype: LACM 37436-6; Paratype: LACM 37346-8	Examined
<i>Zebrias maculosus</i> Oommen 1977	Valid as <i>Zebrias</i> <i>maculosus</i>	Oommen, V. P. 1977. New records of bathypelagic fishes from the Arabian Sea with description of a new species. J. Bombay Nat. Hist. Soc. 74 (2): 282-287.	Holotype: Mus. Mar. Res. Integrated. Fish. Proj. F55a; Paratypes: Mus. Mar. Res. Integrated. Fish. Proj. F55b-c	Not examined: unable to obtain type material
<i>Zebrias munroi</i> Whitley 1966	Valid as <i>Phyllichthys</i> <i>munroi</i>	Whitley, G.P. 1966. Notes on some Queensland fishes. Australian Zoologist. 13(pt 3): 235-243, Pls. 13-14.	Holotype: AMS IB.7210; Paratypes: AMS 15557-063 (3)	Examined
<i>Solea ommatura</i> Richardson 1846	Synonym of <i>Zebrias zebra</i>	Richardson, J. 1846. Report on the ichthyology of the seas of China and Japan. Rep. Brit. Assoc. Adv. Sci. 15th meeting [1845]: 187-320.	Syntypes: Cambridge Philosophical Soc. (2, whereabouts unknown)	Unable to examine: location of type material unknown

<i>Zebrias penescalaris</i> Gomon 1987	Valid as <i>Zebrias penescalaris</i>	Gomon, M. F. 1987. New Australian fishes. Part 6. New species of <i>Lepidotrigla</i> (Triglidae), <i>Choerodon</i> (Labridae) and <i>Zebrias</i> (Soleidae). Mem. Mus. Victoria 48 (1): 17-23.	Holotype: SAMA A96; Paratypes: AMS I.20194-029 (7), CSIRO H572-03, SAMA A1085, A1662, A1697, A6554	Examined: AMS I.20194-029 (7), CSIRO H572-03
<i>Aesopia quagga</i> Kaup 1858	Valid as <i>Zebrias quagga</i>	Kaup, J. J. 1858. Uebersicht der Soleinae, der vierten Subfamilie der Pleuronectidae. Arch. Naturgeschichte 24 (1): 94-104.	Holotype: MNHN 1998-1307	Examined
<i>Synaptura regani</i> Gilchrist 1906	Valid as <i>Pseudaesopia regani</i>	Gilchrist, J. D. F. 1906. Descriptions of fifteen new South African fishes, with notes on other species. Mar. Invest. S. Africa 4: 143-171, Pls. 37-51.	Syntypes: BMNH 1903.12.31.12, SAM 15424	Examined
<i>Zebrias scalaris</i> Gomon 1987	Valid as <i>Zebrias scalaris</i>	Gomon, M. F. 1987. New Australian fishes. Part 6. New species of <i>Lepidotrigla</i> (Triglidae), <i>Choerodon</i> (Labridae) and <i>Zebrias</i> (Soleidae). Mem. Mus. Victoria 48 (1): 17-23.	Holotype: AMS I.16281-001 [ex MAMU F1168]	Examined
<i>Synaptura smithii</i> Regan 1903	Synonym of <i>Pseudaesopia japonica</i>	Regan, C. T. 1903. Notes on the genus <i>Synaptura</i> Cantor, with descriptions of two new species. Ann. Mag. Nat. Hist. (Ser. 7) 11 (61): 56-58, Pl. 6.	Holotype: BMNH 1902.10.31.152	Examined
<i>Solea synapturoides</i> Jenkins 1910	Valid as <i>Pseudaesopia synapturoides</i>	Jenkins, J. T. 1910. Report on the fishes taken by the Bengal Fisheries Steamer "Golden Crown" Part IV. Pleuronectidae. Mem. Indian Mus 3 (1): 23-31.	Syntypes: MNHN 1976-0380, ZSI F3430/1	Examined: MNHN 1976-0380

<i>Pleuronectes zebra</i> Bloch 1787	Valid as <i>Zebrias zebra</i>	Bloch, M. E. 1787. Naturgeschichte der ausländischen Fische. Berlin. Naturg. Ausl. Fische v. 3: i-xii + 1-146, Pls. 181-216. [Also a French edition, Ichthyologie, ou Histoire naturelle des Poissons, v. 6, published 1788.]	Lectotype: ZMB 2423; Paralectotypes: ZMB 7406 (1 dry, missing)	Examined
<i>Solea zebrina</i> Temminck & Schlegel 1846	Synonym of <i>Zebrias zebra</i>	Temminck, C. J. and H. Schlegel. 1846. Pisces. In: Fauna Japonica, sive descriptio animalium quae in itinere per Japoniam suscepto annis 1823-30 collegit, notis observationibus et adumbrationibus illustravit P. F. de Siebold. Pisces, Fauna Japonica Parts 10-14: 173-269	Lectotype: RMNH D1308 (stuffed); Paralectotypes: RMNH D1306-07 (2, stuffed), 3580 (3)	Examined

---

## APPENDIX B:

### Description of Measurements and Qualitative Observations

#### Morphological measurements

**Blind-side pectoral fin length (BPc):** Length of the blind-side pectoral fin from the base of the central fin ray to the tip of the longest ray.

**Blind-side pelvic fin length (BPv):** Length of the blind-side pelvic fin from the base of the central fin ray to the tip of the longest ray.

**Body depth (BD):** Largest distance between base of dorsal- and anal-fin rays.

**Caudal fin length:** Horizontal distance from the caudal peduncle to the distal end of the longest caudal-fin ray. Caudal fin length was also measured in relation to the length of the posteriormost anal-fin ray.

**Depth of the caudal peduncle:** Smallest vertical distance of the juncture where the caudal fin and body meet.

**Head depth:** Depth of the head at the posterior edge of the ventral eye.

**Head length (HL):** Distance from tip of snout to posterior edge of operculum.

**Interorbital distance (IOD):** Distance between dorsal and ventral eyes.

**Longest dorsal- and anal-fin ray:** Longest distance from the base of the dorsal- or anal-fin ray to its distal end.

**Mouth length (Moc):** Linear distance from posterior corner of mouth to anteriormost point of mouth.

**Nostril to snout distance:** Distance from tip of snout to most anterior ocular-side nostril.

**Ocular distance:** Shortest distance between the edge of the dorsal eye and base of the dorsal fin rays.

**Ocular-side pectoral fin length (OPc):** Length of the ocular-side pectoral fin from the base of the central fin ray to the tip of the longest ray.

**Ocular-side pelvic fin length (OPv):** Length of the ocular-side pelvic fin from the base of the central fin ray to the tip of the longest ray.

**Postorbital head length:** Horizontal distance from posterior margin of posteriormost eye to posterior edge of operculum.

**Predorsal distance:** Distance between the edge of upper lip and first dorsal-fin ray.

**Preorbital head length:** Distance from anterior margin of anteriormost eye to anterior edge of head.

**Snouth length:** Distance from snout tip to most anterior edge of ventral eye.

**Standard length:** Distance from tip of snout to caudal peduncle.

**Thickness:** Thickness of the body measured just posterior to the operculum.

**Total length (TL):** Distance from tip of snout to end of longest caudal-fin ray.

**Width of dorsal eye:** Horizontal distance from posterior margin of dorsal eye to anterior margin.

**Width of orbits:** Horizontal distance from posterior margin of ventral eye to anterior margin of dorsal eye.

**Width of ventral eye (V):** Horizontal distance from posterior margin of ventral eye to anterior margin.

### **Meristic counts**

**Anal-fin rays:** Number of anal-fin rays.

**Band Count:** Number of transverse bands across the body.

**Caudal-fin rays:** Number of caudal-fin rays.

**Caudal vertebrae:** Number of caudal vertebrae.

**Ctenii:** Number of ctenii on scales present at the posterior end of the fish, ventral to the lateral line.

**Dorsal-fin rays:** Number of dorsal-fin rays.

**Haemapophyses:** Number of haemapophyses.

**Lateral-line scales:** Number of scales along the lateral line from the caudal peduncle to the posterior edge of the opercular margin.

**Pectoral-fin rays:** Number of pectoral-fin rays.

**Pelvic-fin rays:** Number of pelvic-fin rays.

**Precaudal vertebrae:** Number of precaudal vertebrae.

**Pterygiophores:** Number of pterygiophores in contact with the first haemal spine.

**Supracranial Complex Pattern:** A detailed explanation of how to derive this pattern can be found in the Methods section. In addition, the number of pterygiophores anterior to the second neural spine were counted.

**Urohyal:** Angle of the urohyal.

### **Qualitative Characters**

**Anterior nasal tube (blind):** Location and state (simple nostril or a short, uneven tube).

**Anterior nasal tube (ocular):** Length in relation to which structure it reaches when flattened, pigmentation, morphology.

**Anus:** Location relative to pelvic fins, first anal-fin ray and mid-ventral line.

**Bands:** Banding pattern (singular, paired, or a combination of the two), relative width of bands, presence of incomplete or irregular bands, presence or absence of bands on vertical fins, band demarcation (thick or thin).

**Barbels:** Presence or absence, location and number.

**Caudal fin:** Pattern, shape and attachment to the adjacent vertical-fin rays.

**Cirri:** Presence or absence from ocular-side opercular margin, arrangement on blind side, presence or absence from blind-side pelvic fin.

**Dorsal fin insertion point:** Location of the insertion of the dorsal fin in relation to the dorsal eye.

**Eyes:** Contiguous or separate, scales present or absent from interorbital space, ocular tentacles present or absent, positioning of dorsal eye in relation to ventral eye.

**Genital papilla:** Location relative to anus, attachment to ocular-side pelvic fin.

**Lateral line:** Shape of the lateral line, presence or absence on the blind side, association with cirri, and the type of scales found along it.

**Longest dorsal- and anal-fin ray:** Location of longest dorsal- and anal-fin ray.

**Mouth:** Length of the mouth in relation to the ventral eye, pigmentation of its interior, curvature, presence or absence of plicate lips on the blind side, presence or absence of extension of lower lip on ocular side, and the location of teeth.

**Pectoral fin:** Morphology and pigmentation.

**Pigmentation:** Presence or absence of minute dark spots on blind side (and arrangement, if present), colour of body and bands (or blotches) on ocular side.

**Posterior nasal tube (blind):** Location and length, relative to the ocular-side nasal tubes.

**Posterior nasal tube (ocular):** Length in relation to anterior nasal tube, orientation.

**Scales:** Presence or absence of scales on median fins, degree of spinulation (assessed as “moderately” to “strongly” ctenoid).

## APPENDIX C:

### Glossary<sup>1</sup>

**Anal fin** (Figure 1.4): The median, unpaired, ventrally located fin that extends from the anus to the base of the caudal fin.

**Apomorphy:** A derived character state.

**Autapomorphy:** A derived trait that is unique to a given taxon.

**Barbels** (Figure 1.39): Fleshy projection near mouth, chin or snout; slender tentacle-like protuberance generally used for locating food.

**Benthic:** Dwelling on, or relating to, the bottom of a body of water.

**Blind side (b.s.):** Side of the body without eyes.

**Branchiostegal membrane** (Figure 1.4): The membrane below the operculum, often attached to the isthmus, supported by branchiostegals and helping to enclose the gill chamber ventrolaterally. (FB)

**Caudal fin** (Figure 1.4): Also referred to as the tail fin, it provides the main power for forward movement in fish.

**Caudal peduncle** (Figure 1.4): The wrist-like portion of the posterior part of the body between the end of the anal fin and the base of the caudal fin.

---

<sup>1</sup> Definitions obtained from [www.fishbase.org](http://www.fishbase.org)

**Caudal vertebrae** (Figure 1.3): Vertebrae that bear a haemal spine ventral to the vertebral centrum (central portion of the vertebra).

**Cirri (plural of cirrus)**: Hair-like structures in animals and plants; small, slender, flexible fleshy protuberances.

**Congener**: A member of the same genus.

**Ctenii**: The teeth or spinules characteristic of ctenoid scales.

**Ctenoid**: Having the margin toothed like a comb; used to describe the free margins of the scales of some fishes, as in perciforms.

**Cycloid**: Having a smooth free margin; used to describe the scales of some fishes.

**Dextral**: Eyes located on the right side of the body. Antonym: sinistral.

**Dorsal fin** (Figure 1.4): The median, unpaired, dorsally located fin that extends from just anterior to the dorsal eye to the base of the caudal fin.

**Erisma** (Figure 1.3): A modified structure in the supracranial region resulting from the coalescence of two anteriormost dorsal-fin pterygiophores.

**Etymology**: Used in taxonomy for the derivation and meaning of a scientific name.

**Fin rays**: The supporting bony elements of fins (pectoral, pelvic, anal, dorsal, caudal).

**Geminate species**: Scarcely differentiated species that have evolved from a close common ancestor.

**Genital papilla:** A small, fleshy tube behind the anus in some fishes, from which the sperm or eggs are released.

**Haemal spine** (Figure 1.3): The ventral spine on the caudal vertebra.

**Haemapophysis (pl. Haemapophyses)** (Figure 1.3): Ventral projection of the centrum (central portion of the vertebra) of a precaudal vertebra; fused in the caudal region to form a haemal arch bearing a spine.

**Holotype:** The single specimen selected by the original describer of a species to be the standard-bearer for the new name.

**Lamellose:** The body (or lamellose portion) of the scale, excluding the ctenii.

**Lateral line** (Figure 1.4): A sensory organ of fishes which consists of a canal running along the side of the body and communicating via sensory pores through scales to the exterior; functions in perceiving low frequency vibrations and pressure differences in general.

**Lectotype:** A syntype designated as the single name-bearing type specimen subsequent to the establishment of a nominal species or subspecies.

**Median fins:** Refers to dorsal, anal and caudal fins, collectively.

**Monophyletic:** Refers to a group of species that all have a single common ancestral species. A monophyletic taxon includes all and only the descendants from the common ancestor of its members.

**Nasal tube** (Figure 1.4): Fleshy, tube-like structure that encircles the anterior and posterior nostrils on both the ocular and blind sides. Tube tapers toward its distal end.

**Neural spine** (Figure 1.3): The dorsalmost spine of a vertebra.

**Nominal species:** A name used in an original description, which may be valid or synonymous; A nomenclatural concept denoted by an available name, and based, actually or potentially, upon its name-bearing type but having no defined taxonomic boundaries.

**Ocular side (o.s.):** Side of the body where the eyes are located.

**Operculum** (Figure 1.4): Bony gill cover; comprised of four bones: opercle, preopercle, interopercle and subopercle.

**Paralectotype:** Each specimen of a former syntype series remaining after the designation of a lectotype.

**Paratype:** one of any number of specimens, in addition to the holotype, used by the original namer of a species in formulating his or her description of it; a specimen, other than the holotype, on which the description of a new species is based.

**Pectoral fin** (Figure 1.4): The paired fin born by the pectoral girdle, located just posterior to the gill opening. It functions to steer, brake and propel the fish.

**Pelvic fin:** The paired fin which is located ventral to the pectoral fins, slightly anterior to the insertion of the anal fin (abdominal, thoracic or jugular in position). It functions to steer, brake and propel the fish.

**Plesiomorphic:** Ancestral character state.

**Plicate:** With accordion pleats; when folds of skin are arranged to form a fan-shaped structure.

**Precaudal vertebrae** (Figure 1.3): All vertebrae anterior to the first vertebra bearing a haemal spine.

**Preorbital region** (Figure 1.4): Region of the head anterior to the dorsal eye.

**Protusible:** Capable of being protruded, extended or thrust out.

**Postorbital region** (Figure 1.4): Region of the head posterior to the ventral eye.

**Pterygiophore** (Figure 1.3): The bones that support the dorsal fin; bones on the distal end of which sit the median-fin rays and to which are attached erector and depressor fin muscles.

**Rudimentary:** Very small and poorly formed; undeveloped; imperfectly developed.

**Sinistral:** Eyes located on the left side of the body. Antonym: dextral.

**Snout** (Figure 1.4): The part of the head anterior to the eye; the distance from the eye to the anterior tip of the head above the upper jaw (normally the upper lip).

**Squamation:** Arrangement of scales.

**Supracranial Complex Pattern:** The pattern derived from the number of pterygiophores in the region of the cranium. For a detailed explanation of how to derive the supracranial complex pattern, see Methods.

**Synonym:** An invalid scientific name of an organism proposed after the accepted name; each of two or more scientific names of the same rank used to denote the same taxon.

**Syntype:** One of the specimens on which a species description is based if no holotype was designated.

**Tentacles (ocular)** (Figure 1.21): A short fleshy appendage.

**Transverse band** (Figure 1.4): Bands of pigment that extend vertically across the body, usually extending onto the vertical fins.

**Type species:** The species of a genus with which the generic name is permanently associated; the description of a genus is based primarily on its type species, being modified and expanded by the features of other included species.

**Type material:** A collective term for all type specimens.

**Type specimen:** Specimen used in the original description of a given species; this specimen fixes a name to a taxon.

**Urohyal** (Figure 1.3): U-shaped bone in the hyoid arch (The second of seven bony V-shaped arches that support the gills of fish).

**Vertical fins:** Refers to the dorsal and anal fins, collectively.