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FACULTÉ DES ÉTUDES SUPÉRIEURES
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FACULTY OF GRADUATE AND
POSTDOCTORAL STUDIES

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M. Sc. (Biology)

GRADE - DEGREE

Department of Biology

FACULTÉ, ÉCOLE, DÉPARTEMENT - FACULTY, SCHOOL, DEPARTMENT

TITRE DE LA THÈSE - TITLE OF THE THESIS

Revision of cyclopsetta phylogenetic analysis of cyclopsetta and Syacium
(Pleuronectiformes : Paralichthyidae)

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SUPÉRIEURES ET POSTDOCTORALES

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AND POSTDOCTORAL STUDIES

**Revision of *Cyclopsetta* and phylogenetic analysis of *Cyclopsetta* and
Syacium (Pleuronectiformes: Paralichthyidae)**

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Thesis submitted to the Faculty of Graduate and Postdoctoral Studies in partial fulfilment
of the requirement of the degree of Master of Science.

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Your file *Votre référence*
ISBN: 0-494-01510-1
Our file *Notre référence*
ISBN: 0-494-01510-1

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Abstract

The genus *Cyclopsetta* Gill, 1889 was reviewed and four species were recognised: *C. chittendeni* Bean, 1895 and *C. fimbriata* (Goode and Bean 1886) from the Atlantic coast of North and South America including Gulf of Mexico and the Caribbean Sea; *C. panamensis* (Steindachner 1875) and *C. querna* (Jordan and Bollman 1890) from the Pacific coast of North and South America. A first cladistic analysis of *Cyclopsetta* and *Syacium* was conducted at the species level using morphological data. The result showed that each genus is monophyletic. *Cyclopsetta* is divided into two subgenera: *Cyclopsetta* comprises *C. chittendeni* and *C. fimbriata* and *Azevia* comprises *C. panamensis* and *C. querna*. *Syacium longidorsale* is the first species to branch off the ancestor followed, subsequently, by *S. ovale*, *S. gunteri* and *S. maculiferum*. *S. latifrons* and *S. papillosum* are sister species which together form a trichotomy with *S. guineensis* and *S. micrurum*.

Résumé

La présente étude comprend la révision du genre *Cyclopsetta* Gill, 1889. Quatre espèces furent reconnues: *C. chittendeni* Bean, 1895 et *C. fimbriata* (Goode et Bean 1886) de la côte Atlantique de l'Amérique du Nord et du Sud incluant le Golf du Mexique et la Mer des Caraïbes ; ainsi que *C. panamensis* (Steindachner 1875) et *C. querna* (Jordan et Bollman 1890) de la côte Pacifique de l'Amérique du Nord et du Sud. De plus, une première analyse cladistique de caractères morphologiques de *Cyclopsetta* et *Syacium* au niveau de l'espèces a résolu chaque genre comme étant monophylétique. *Cyclopsetta* était divisé en deux sous-genres, le sous-genre *Cyclopsetta* comprenant *C. chittendeni* et

C. fimbriata, et le sous-genre *Azevia* comprenant *C. panamensis* and *C. querna*. *Syacium longidorsale* est le groupe frère des autres espèces du genre, *S. ovale*, *S. gunteri* et *S. maculiferum* suivent dans l'ordre. *S. latifrons* et *S. papillosum* forment un groupe monophylétique qui forme lui-même une trichotomie avec *S. guineensis* et *S. micrurum*.

To all women in Iraq

Acknowledgements:

I thank my supervisors François Chapleau and Claude Renaud and my committee members Lynn Gillespie and Stewart Peck for their help and guidance.

I thank Dr. Francis Cook for many conversations about science in general and my work in particular. Donna Naughton answered my technical questions. I thank Monique Zaloum for her friendly disposition, suggestions and help with the PCA analysis and during the writing of the thesis.

I thank the following people and institutions for the loan of specimens I used in this study: Susan L. Jewett (USNM), Sylvie Laframboise, Canadian Museum of Nature (CMN) Damaris Rodriguez (AMNH), David Catania (CAS), Christopher P. Kenaley (MCZ), Jessica Rosales (TNHC), Mary Anne Rogers (FMNH) and NMW. William Bussing (UCR) donated three specimens of *Syacium maculiferum* to the Canadian Museum of Nature. Susan L. Jewett (USNM) also provided pictures of type specimens. This work was supported by an operating grant to François Chapleau by the National Sciences and Engineering Research Council of Canada.

Table of Contents

Acknowledgements	iii
List of Figures.....	vi
List of Tables	ix
Abstract.....	1
Résumé.....	2
General Introduction.....	3
References in General Introduction.....	6
Chapter 1: Review of the genus <i>Cyclopsetta</i> (Pleuronectiformes: Paralichthyidae).....	9
Abstract.....	10
Introduction.....	10
Materials and Methods.....	11
Results and Discussion	12
Artificial key to <i>Cyclopsetta</i> species	16
<i>Cyclopsetta chittendeni</i> Bean 1895.....	17
<i>Cyclopsetta fimbriata</i> (Goode and Bean 1886)	19
<i>Cyclopsetta panamensis</i> (Steindachner 1875)	21
<i>Cyclopsetta querna</i> (Jordan and Bollman 1890)	23
References.....	26
Appendix 1.1.....	56
Chapter 2: Phylogenetic relationships of <i>Cyclopsetta</i> and <i>Syacium</i> (Pleuronectiformes: Paralichthyidae)	61
Abstract.....	62

Introduction.....	62
Materials and Methods.....	64
Materials examined.....	65
Results.....	66
Discussion.....	68
References.....	70
Appendix 2.1.....	75
General Conclusion.....	82

List of Figures

Chapter 1

- Fig. 1.1 PC1 vs. PC2 of six meristic and 23 morphometric characters for 94 specimens of the four species of *Cyclopsetta*. 32
- Fig. 1.2 Gill rakers in a. *Cyclopsetta*, b. *Syacium*, c. *Etropus*, d. *Citharichthys gilberti* and *C. spilopterus*, e. *C. gnathus* (from Hoshino and Amaoka, 1999). 33
- Fig. 1.3 First dorsal fin ray position relative to blind side nostrils in a. *Cyclopsetta chittendeni*, b. *C. fimbriata* and c. *C. panamensis* and *C. querna*. 34
- Fig. 1.4 Nostrils and flap of skin on the lower jaw of a. *Cyclopsetta chittendeni*, b. *C. fimbriata*, c. *C. panamensis*, and d. *C. querna*. 35
- Fig. 1.5 *Cyclopsetta chittendeni* holotype, USNM 44100, 170 mm SL. 36
- Fig. 1.6 Geographic distribution of *Cyclopsetta chittendeni*. 37
- Fig. 1.7 *Cyclopsetta fimbriata* holotype USNM 37330, 213.7 mm SL. 38
- Fig. 1.8 Geographic distribution of *Cyclopsetta fimbriata*. 39
- Fig. 1.9 *Cyclopsetta panamensis* syntype USNM 44132, 163.2 mm SL. 40
- Fig. 1.10 Geographic distribution of *Cyclopsetta panamensis*. 41
- Fig. 1.11 *Cyclopsetta querna* syntype USNM 41159, 146.3 mm SL. 42

Fig. 1.12	Geographic distribution of <i>Cyclopsetta querna</i> .	43
Fig. 1.13	Interorbital width vs. standard length in <i>Cyclopsetta</i> species.	44
Fig. 1.14	Upper eye to crest of head depth vs. upper eye diameter in <i>Cyclopsetta</i> species.	45
Chapter 2		
Fig. 2.1	Cladogram from an analysis of 29 characters for 12 ingroup species of <i>Cyclopsetta</i> and <i>Syacium</i> and three outgroup species of <i>Citharichthys</i> and <i>Etropus</i> . Character change is 0→1 except: a: 1→2, b: 2→3, c: 0→2, bold: homoplasy, r: reversal 1→0 except reversal in character 11: 2→1. Bootstrap values are shown as percentages.	72
Fig. 2.2	Lachrymal on ocular side; a: <i>Cyclopsetta chittendeni</i> , AMNH 81153 (118 mm SL); b: <i>Syacium micrurum</i> , USNM 266482 (190.5 mm SL); c: <i>Citharichthys stigmaeus</i> , NMC 74-216 (80 mm SL). Scale bars are 1 mm.	79
Fig. 2.3	Suboperculum on ocular side; a: <i>Cyclopsetta panamensis</i> , USNM 220796 (110 mm SL); b: <i>Syacium micrurum</i> , USNM 266482 (190.5 mm SL); c: <i>Citharichthys stigmaeus</i> , NMC 74-216 (80 mm SL). Scale bars are 1 mm.	80
Fig. 2.4	Suspensorium on ocular side; a: <i>Cyclopsetta chittendeni</i> , AMNH 81153 (118 mm SL); b: <i>Syacium micrurum</i> , USNM 266482 (190 mm SL); c: <i>Citharichthys stigmaeus</i> , NMC 74-216 (80 mm SL). entp: entopterygoid; hyom:	81

hyomandibular; mtp: metapterygoid; pl: palatine; ptr:
pterygoid; qu: quadrate; sym: symplectic. All these
specimens are further identified as 1 with a tag marked 1.
Scale bars are 1 mm.

List of Tables

Chapter1

- Table 1.1 Ranges of meristic characters of the four species of *Cyclopsetta*. Acronyms: D and A: number of dorsal and anal fin rays respectively, vertC: number of caudal vertebrae, rpfo and rpvo: number of ocular side pectoral and pelvic fin rays respectively, lls: number of lateral line scales. 46
- Table 1.2 Character loadings for PC1 and PC2; res is residual, list of acronyms in Tables 1.1 and 1.3. 47
- Table 1.3 Morphometric characters of *Cyclopsetta chittendeni*. Acronyms: SL: Standard length, hl: head length, bd: body depth, llc: curved portion of lateral line, llst: straight portion of lateral line, int: interorbital width, sue: snout to upper eye, sle: snout to lower eye, ued: upper eye diameter, led: lower eye diameter, uc: distance between upper eye and crest of head, ujo: upper jaw on ocular side, ljo: lower jaw on ocular side, ujb: upper jaw on blind side, ljb: lower jaw on blind side, pfo: pectoral fin on ocular side, pfb: pectoral fin on blind side, pvo: pelvic fin on ocular side, pvb: pelvic fin on blind side, b-pvo: base of ocular side pelvic fin, b-pvb: base of blind side pelvic fin, lD: longest dorsal fin ray, lA: longest anal fin ray lC: longest caudal fin ray, cp: depth of caudal

	peduncle.	48
Table 1.4	Morphometric characters of <i>Cyclopsetta fimbriata</i> ; Sample size, when different from 25 is indicated in parentheses. Refer to Table 1 for list of acronyms.	50
Table 1.5	Morphometric characters of <i>Cyclopsetta panamensis</i> ; Sample size, when different from 28 is indicated in parentheses. Refer to Table 1 for list of acronyms.	52
Table 1.6	Morphometric characters of <i>Cyclopsetta querna</i> ; Sample size, when different from 62 is indicated in parentheses. Refer to Table 1 for list of acronyms.	54
Chapter 2		
Table 2.1	Character states of <i>Cyclopsetta</i> and <i>Syacium</i> species; <i>Citharichthys</i> (<i>C. gilberti</i> and <i>C. stigmaeus</i>) and <i>Etropus crossotus</i> are outgroups. Question mark (?) is unknown or uninformative state. List of characters is in Appendix.	74

Abstract

The genus *Cyclopsetta* Gill, 1889 is one of four genera in a monophyletic group within the Paralichthyidae; the others are *Syacium*, *Etropus* and *Citharichthys* (Hensley and Ahlstrom 1984). In this study, *Cyclopsetta* was reviewed and four species were recognised and classified under two new subgenera: *C. chittendeni* Bean, 1895 and *C. fimbriata* (Goode and Bean 1886) from the Atlantic coast of North and South America including Gulf of Mexico and the Caribbean Sea; *C. panamensis* (Steindachner 1875) and *C. querna* (Jordan and Bollman 1890) from the Pacific coast of North and South America. In addition a new key to the species was provided.

Relationships within the Paralichthyidae are poorly understood. This first cladistic study of *Cyclopsetta* and *Syacium* was conducted at the species level using 29 morphological characters. One species of *Etropus* and two species of *Citharichthys* were used as outgroups. The analysis was done using the branch and bound and heuristics searches of PAUP and resulted in one tree with 49 steps and CI= 0.76. The tree showed that each genus was monophyletic. *Cyclopsetta* was divided into two subgenera: *Cyclopsetta* (subg. nov.) comprised *C. chittendeni* and *C. fimbriata* and *Azevia* (subg. nov.) comprised *C. panamensis* and *C. querna*. *Syacium longidorsale* is the most plesiomorphic species of the genus followed, subsequently, by *S. ovale*, *S. gunteri* and *S. maculiferum*. *S. latifrons* and *S. papillosum* were sister species which together formed a trichotomy with *S. guineensis* and *S. micrurum*. Relationships within *Syacium* were not well-supported.

Résumé

Le genre *Cyclopsetta* Gill 1889 appartient à un groupe monophylétique qui contient trois autres genres : *Syacium*, *Etropus* et *Citharichthys* (Hensley et Ahlstrom 1984). Cette étude contient une révision de *Cyclopsetta*. Quatre espèces ont été validées et classifiées dans deux sous-genres. Ces espèces sont: *C. chittendeni* Bean 1895 et *C. fimbriata* (Goode et Bean 1886) qui sont réparties dans l'Océan Atlantique près des côtes de l'Amérique du Nord et de l'Amérique du Sud, incluant le Golfe du Mexique et la Mer des Caraïbes ainsi que *C. panamensis* (Steindachner 1875) et *C. querna* (Jordan and Bollman 1890) qui vivent dans l'Océan Pacifique près des côtes de l'Amérique du Nord et de l'Amérique du Sud. L'étude contient également une nouvelle clé d'identification des espèces.

On connaît très peu les relations intrafamiliales des Paralichthyidae. Une analyse cladistique des interrelations phylogénétiques des espèces de *Cyclopsetta* et de *Syacium* a été faite en utilisant une matrice 29 caractères morphologiques. Une espèce d'*Etropus* et deux espèces de *Citharichthys* ont été utilisées en tant qu'hors groupe. L'analyse, utilisant les options branch and bound et heuristique, a résulté en un seul cladogramme de 49 pas (IC = 0.76). Les deux genres sont monophylétiques. *Cyclopsetta* se divise en deux sous-genres: *Cyclopsetta* (subg. nov.) incluant *C. chittendeni* et *C. fimbriata* et *Azevia* (subg. nov.) incluant *C. panamensis* and *C. querna*. L'espèce *Syacium longidorsale* est la plus plésiomorphe de son genre suivie de *S. ovale*, *S. gunteri* et *S. maculiferum*. *S. latifrons* and *S. papillosum* sont des espèces sœurs dont le clade forme une trichotomie avec *S. guinensis* and *S. micrurum*. Les interrelations des espèces de *Syacium* sont faiblement corroborées dans le cladogramme.

General Introduction

Cyclopsetta Gill 1889 is a genus of sinistral flatfishes with elongated, moderately deep bodies, large jaws, sharp canine-like teeth, lateral line on both sides of the body and nearly symmetrical pectoral and pelvic fins. Museum specimens indicate that these fishes inhabit the continental shelves of the Atlantic and Pacific coasts of North and South America including the Gulf of Mexico and the Caribbean Sea. There are no commercial species within this genus.

The earliest review of *Cyclopsetta* was by Jordan and Evermann (1898) who examined one specimen each of *Azevia panamensis* (Steindachner 1875), *Cyclopsetta chittendeni* Bean 1895, *C. fimbriata* (Goode and Bean 1886), and *C. querna* (Jordan and Bollman 1890). Meek and Hildebrand (1928) examined eight specimens of *Azevia panamensis* and 11 specimens of *Cyclopsetta querna*. Later, Norman (1934) synonymised *Azevia* with *Cyclopsetta* and based on 13 specimens only, he recognised five species in *Cyclopsetta*: *C. chittendeni*, *C. fimbriata*, *C. panamensis*, *C. querna* and *C. maculifera* (Garman). In 1946, Gunter described a new species of *Cyclopsetta*, *C. decussata*, based on the head and skin of a mounted specimen. Cervigón (1966) examined six specimens of *Cyclopsetta chittendeni* only; Gutherz (1967) placed *C. chittendeni*, *C. fimbriata* and *C. decussata* under *Cyclopsetta* but did not mention the number of specimens he examined. Matsuura et al. (1983) looked at two specimens of *C. chittendeni*.

In their review of *Syacium*, Murakami and Amaoka (1992) transferred *Cyclopsetta maculifera* to *Syacium* based on biserial teeth and shape of gill rakers. The validity of *Syacium maculiferum* was confirmed by van der Heiden and Mitchell (1998) who examined 51 specimens.

Swingle (1971) synonymised *Cyclopsetta decussata* with *C. chittendeni* based on one specimen only. In addition, van der Heiden and Mussot-Pérez (1993) synonymised the monotypic genus *Dorsopsetta* Nielsen 1963 with *Cyclopsetta* and *Dorsopsetta norma* with *Cyclopsetta querna* based on larval characters of eight specimens. However, in their key to the families of fishes of Peru, Chirichigno and Vélez (1998) considered *Dorsopsetta* distinct from *Cyclopsetta*.

Therefore, a review of *Cyclopsetta* was needed to establish exactly how many valid species there were and to assess the work of Gunter (1946) and Swingle (1971) each of which was based on one specimen only. Also, the synonymy of *Dorsopsetta norma* with *Cyclopsetta querna* by van der Heiden and Mussot-Pérez (1993) and the countering position of Chirichigno and Vélez (1998) had to be evaluated.

Moreover, all the above authors reported *Cyclopsetta* as a genus in the family Bothidae. However, the species of *Cyclopsetta* lack the synapomorphies of Bothidae reported by Ahlstrom et al. (1984): ocular side pelvic fin more elongated than the one on the blind side, intermuscular bones and lack of blind-side preorbital. Ahlstrom et al. (1984) placed *Cyclopsetta* along with three more genera, *Citharichthys*, *Etropus* and *Syacium* in the family Paralichthyidae. They proposed that these four genera were monophyletic based on six synapomorphies: urinary papilla on the blind side, base of ocular-side pelvic fin on mid-ventral line of the body, base of the blind-side pelvic fin on the blind side and slightly advanced to that of the ocular side, and 17 caudal fin rays, these caudal rays were not supported by pleural, neural or hemal spines and the fifth hypural was fused to an epural. Berendzen and Dimmick (2002) confirmed that *Citharichthys*, *Etropus* and *Syacium* formed a monophyletic group based on phylogenetic analysis using mitochondrial DNA

extracted from one species per genus. They did not, however, have material for the genus *Cyclopsetta*.

Therefore, it was important to show that each of *Cyclopsetta* and *Syacium* was monophyletic based on data from all the species in the corresponding genus. Furthermore, no cladistic study had been done to show intraspecific relationships within *Cyclopsetta* and *Syacium*. Such a study would provide a hypothesis of interrelationships between these two genera as well as clues to their biogeography.

In chapter 1, the species of *Cyclopsetta* were reviewed based on 180 specimens and a new and improved key to the species of *Cyclopsetta* was provided. Chapter 2, dealt with a cladistic study of interrelationship of *Cyclopsetta* and *Syacium* at the species level. *Syacium* was added to the analysis because it was reviewed relatively recently by Murakami and Amaoka (1992).

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Chapter 1

Review of the genus *Cyclopsetta* (Pleuronectiformes: Paralichthyidae)

Abstract:

The morphology of 180 specimens of *Cyclopsetta* Gill, 1889 from the Atlantic and Pacific coasts of North and South America was examined. Four species of *Cyclopsetta* were recognised: *C. chittendeni* Bean, 1895, *C. fimbriata* (Goode and Bean 1886), *C. panamensis* (Steindachner 1875) and *C. querna* (Jordan and Bollman 1890). A key to the species, with new characters, is provided.

Introduction:

Cyclopsetta Gill, 1889, was placed under the subfamily Paralichthinae, family Bothidae by Norman (1934). Amaoka (1969) defined the family Paralichthyidae but limited it to the sinistral flatfishes of Japan where *Cyclopsetta* does not occur. Hensley and Ahlstrom (1984) expanded the family Paralichthyidae and defined the four genera *Citharichthys*, *Cyclopsetta*, *Etropus* and *Syacium*, as a monophyletic group within Paralichthyidae. The monophyly was based on six synapomorphies: urinary papilla on the blind side, base of ocular-side pelvic fin on mid-ventral line of the body, base of the blind-side pelvic fin on the blind side, slightly advanced to that of the ocular side, 17 caudal fin rays, these caudal rays were not supported by pleural, neural or hemal spines and the fifth hypural was fused to an epural. Berendzen and Dimmick (2002) confirmed that *Citharichthys*, *Etropus* and *Syacium* were a monophyletic group based on a phylogenetic analysis using mitochondrial DNA. They did not, however, have material for the genus *Cyclopsetta*.

Species of *Cyclopsetta* were treated in a number of taxonomic studies (Jordan and Evermann 1898; Norman 1934; Cervigón 1966; Gutherz 1967; Bussing and López 1994). The most complete review of this genus was that of Norman (1934). Based on 13 specimens, Norman (1934) recognised five species in *Cyclopsetta*: *C. chittendeni* Bean, *C.*

fimbriata (Goode and Bean), *C. panamensis* (Steindachner), *C. querna* (Jordan and Bollman) and *C. maculifera* (Garman). Since then, Murakami and Amaoka (1992) transferred *C. maculifera* in *Syacium* based on the shape of gill rakers and the presence of biserial teeth in the upper jaw. The validity of *Syacium maculiferum* was confirmed by van der Heiden and Mitchell (1998) who examined 51 specimens including lectotype and paralectotype material. Murakami and Amaoka (1992) were the first to mention that the diagnostic character of *Cyclopsetta* was shape of gill rakers which they described as palmate; however they neither mentioned the specimens they observed nor their number. In this study, the species of *Cyclopsetta* are re-examined based on 180 specimens and a new improved key to the species is provided.

Materials and Methods:

A total of 180 specimens from nine museums were examined. Museum acronyms follow Leviton *et al.* (1985). Counts and measurements were made according to Hubbs and Lagler (1958). All measurements were made on the ocular side except for the length of the pelvic and pectoral fins which were measured on both sides; measurements were made with an electronic digital caliper (± 0.1 mm). Counts of the dorsal and anal fin rays and vertebrae were made from radiographs. Descriptions of colour are based on formalin fixed and alcohol (70% ethanol) stored specimens.

In order to explore which among the 23 morphometric and six meristic characters (Tables 1.1 and 1.3) may be diagnostic, a principal component analysis (PCA) was performed. The analysis involved 94 of the 180 specimens; these specimens had no missing values in the data and covered the whole latitudinal range of the genus. One character (base of blind side pelvic fin) lacked 18% of the data and was removed to maximize the number of specimens

with complete data for the PCA. Residuals were calculated from log values of the morphometrics to eliminate the effect of size.

Results and Discussion:

The PCA resulted in four separate clusters corresponding to four putative species of *Cyclopsetta*, Fig. 1.1. PC 1 accounted for 35.6% of the variation, PC 2 for 20.3% and the remaining components individually accounted for 7% or less.

PC1 allowed discrimination between *C. chittendeni*, *C. fimbriata* and a third group containing *C. panamensis* and *C. querna*. Nine characters had high loadings in this component: snout to upper eye, snout to lower eye, distance between upper eye and crest of head, curved section of the lateral line, base of ocular side pelvic fin, number of dorsal, anal and ocular side pectoral fin rays, and number of caudal vertebrae.

PC2 allowed distinction between *C. panamensis* and a group containing *C. chittendeni*, *C. fimbriata* and *C. querna*. Five characters had high loading in the second component: interorbital distance, ocular side upper jaw, blind side upper jaw, ocular side pectoral fin and longest dorsal fin ray.

Of the above characters, only two were useful for diagnosis: number of ocular side pectoral fin rays, which separated *C. fimbriata* from the rest of the species, and number of caudal vertebrae, which separated Atlantic species (*C. fimbriata* and *C. chittendeni*) from the Pacific ones (*C. panamensis* and *C. querna*), Table 1.1. None of the remaining characters was diagnostic; nonetheless, PC1 and PC2 together allowed for the distinction of four putative species. In conclusion, when taken together, all characters allowed for separation of the putative species; however, when examined individually none of the characters except

the above two where useful diagnostically. Therefore, the analysis will not be discussed further.

Instead, a total of eight morphological characters proved diagnostic and were used in the artificial key to the species of *Cyclopsetta*. Based on these characters, four species of *Cyclopsetta* were recognised, *C. chittendeni*, *C. fimbriata*, *C. panamensis* and *C. querna*.

Genus *Cyclopsetta* Gill 1889

Cyclopsetta Gill 1889 (type species *Hemirhombus fimbriatus* Goode and Bean 1886)

Azevia Jordan in Jordan and Goss 1889 (type species *Citharichthys panamensis* Steindachner 1875).

Dorsopsetta Nielsen 1963 (type species *D. norma* Nielsen 1963).

Diagnosis: Sinistral fishes, gill rakers short, broad and spinulate (Fig. 1.2a), urinary papilla on the blind side, base of ocular-side pelvic fin on mid-ventral line of body, base of blind-side pelvic fin on blind side and slightly advanced to that of the ocular side, lateral line straight with slight curve above pectoral fin.

Description: Genus *Cyclopsetta* has the following characters: Body long and moderately deep, head profile evenly convex, mouth large, about half of head, upper jaw hooked over lower jaw, posterior end of upper jaw squarely truncated, anterior end of lower jaw vertically truncated with a slight bump on its ventral tip, length of lower jaw almost equal to postorbital distance from lower eye, teeth sharp, pointy and slightly bent inward, uniserial on both jaws with a few canine-like protruding from both jaws. Preoperculum free, margin of operculum fringed with three dark lappets on ocular side, and fimbriated or

scalloped on blind side. Anterior nostrils on both sides surrounded by a tube of skin with a slight tongue-like extension anteriorly and a slender longer flap posteriorly, end of flap rounded, fanned, forked or pointed.

Lateral line on both sides, almost straight with slight curve above pectoral fin, ocular side lateral line forms a network of tubules in supraorbital area, behind eyes, along preoperculum margin, along lower jaw and on snout. On blind side, network less intricate than on ocular side.

Six pelvic fin rays on each side, rarely five (3 of 180), membrane connecting pelvic fins to body, that of blind side extended to vent. Pectoral fins on both sides, that of blind side shorter than one on ocular side, 17 caudal fin rays, rarely 16 (2 of 180), caudal fin convex or double truncate, vent on blind side near origin of anal fin.

Scales cycloid or ctenoid on ocular side and only cycloid on blind side, premaxillary not scaled, maxillary and lower jaw scaled, a few imbedded scales on snout. Dorsal and anal fin rays scaled, longest caudal ray entirely scaled by continuation of lateral line, rest of rays are almost entirely scaled.

Based on the depth of capture of material examined, species of *Cyclopsetta* occur at 0-158 m, with *C. fimbriata* being the only species recorded below 80 m depth.

Comparison: *Cyclopsetta* is the only genus, in the monophyletic group comprising *Cyclopsetta*, *Syacium*, *Etropus* and *Citharichthys*, with short broad and spinulate gill rakers (Fig. 1.2a). In *Syacium*, gill rakers are short, stout and serrated posteriorly (Murakami and Amaoka 1992) (Fig. 1.2b); in *Etropus crossotus*, *E. cyclosquamus*, *E. microstomus* and *E. rimosus*, gill rakers are short and stout (Leslie and Stewart 1986); in *E. ectenes*, also, short and stout (personal observation) (Fig. 1.2c) In *Citharichthys mariajoriseae*, gill rakers are

long and slender (van der Heiden and Mussot-Pérez 1995); *C. gilberti* and *C. spilopterus*, long and slender (personal observation) (Fig. 1.2d). In *C. gnathus*, gill rakers are long, slender and serrated posteriorly (Hoshino and Amaoka 1999) (Fig. 1.2e); and in *C. stigmaeus*, gill rakers are similar to those in *C. gnathus* (personal observation).

Artificial key to *Cyclopsetta* species:

1- Caudal vertebrae 26-27; first dorsal ray above blind side anterior nostril (Fig. 1.3a) or in advance of blind side nostrils (Fig. 1.3b)-----2

Caudal vertebrae 28-31; first dorsal ray between blind side nostrils (Fig. 1.3c) -----3

2- First dorsal ray above blind side anterior nostril; all scales on ocular side cycloid; 2/3 of ocular side lower jaw fringed with scalloped flap of skin; anterior nostril of ocular side slightly dorsal to posterior nostril (Fig. 1.4a); 13-16 ocular side pectoral fin rays; no dark band on posterior part of ocular side pectoral fin; no ocular papilla

.....*C. chittendeni* (western central Atlantic Ocean)

First dorsal ray in advance of blind side nostrils; weakly ctenoid scales dispersed among cycloid ones on ocular side; all of ocular side lower jaw fringed with scalloped flap of skin; ocular side nostrils both on a horizontal line parallel to long axis of eyes (Fig. 1.4b); 9-11 ocular side pectoral fin rays, dark band on posterior part of ocular side pectoral fin; papilla on one or both eyes.....*C. fimbriata* (western central Atlantic Ocean)

3- Ocular side scales strongly ctenoid except on caudal peduncle and caudal fin; ventro-posterior angle of ocular side lower jaw fringed with scalloped flap of skin; ocular side nostrils both on a horizontal line parallel to long axis of eyes (Fig. 1.4c); anterior margin of both eyes in line with each other; posterior margin of maxillary in line with posterior margin of lower eye.....*C. panamensis* (eastern central Pacific Ocean)

Scales on ocular side cycloid; ocular side lower jaw not fringed with scalloped flap of skin; anterior nostril of ocular side slightly dorsal to posterior nostril (Fig. 1.4d); anterior margin of upper eye slightly advanced relative to that of lower eye; posterior margin of maxillary exceeds posterior margin of lower eye

.....*C. querna* (eastern central Pacific Ocean)

***Cyclopsetta chittendeni* Bean 1895 (Fig. 1.5)**

Cyclopsetta decussata Gunter 1946, (junior synonym, suggested by Swingle 1971)

Common name: Mexican flounder (Robins and Ray 1986).

Diagnosis: First dorsal ray above anterior blind side nostril (Fig. 1.3a), scales on ocular side cycloid, about 2/3 of ocular side lower jaw fringed with scalloped flap of skin, anterior nostril of ocular side slightly dorsal to posterior nostril (Fig. 1.4a), interorbital scaled either entirely (6 of 54) or half way (5 of 54, scales may have fallen in rest of specimens).

Description: Dorsal fin rays 75-90, anal fin rays 62-69, pectoral fin rays on ocular side 13-16, caudal vertebrae 26-27, number of gill rakers on lower limb 6-9 and on upper limb 2-5 (53 of 54), lateral line scales 71-96 (44 of 54). No papillae on eyes, anterior margin of eyes at the same level, posterior edge of pectoral fin oblique, caudal fin double truncate, rarely convex (2 of 54). Morphometrics are shown in Table 1.3.

Colour in alcohol: Dark to light brown on ocular side, dark brown to yellow on blind side. Posterior halves of dorsal and anal fins each with 1-4 ocelli; anterior part of dorsal fin with

0-2 small dark spots, anal fin with 0-1 dark spot. Posterior margin of caudal fin with three dark spots. In some specimens, skin under ocular side pectoral fin with dark blotch (24 of 54), also, some specimens (20 of 54) body with 3-5 bands of slightly darker brown. Ocular side pectoral fin dark brown mottled with small lighter brown patches.

Geographic distribution: Gulf of Mexico, Caribbean Sea and Atlantic coast of South America to Rio de Janeiro, Brazil, (Fig. 1.6). Further sampling may fill in the distribution gap.

Comparison: *C. chittendeni* and *C. fimbriata* had similar morphometrics and colour, however, *C. chittendeni* could be distinguished from *C. fimbriata* in number of pectoral fin rays (13-16 vs. 9-11), type of scales on ocular side (all cycloid vs. cycloid and weakly ctenoid), papillae on either eye (absence vs. presence), and length of scalloped flap of skin on ventral margin of lower jaw ($2/3$ vs. entire distance).

Remarks: Swingle (1971) synonymised *C. decussata* Gunter (1946) with *C. chittendeni* based on overlapping morphometric characters and colour including presence of bands. An examination of the holotype of *C. decussata* confirmed this assessment as its morphometric values fell within the ranges of *C. chittendeni* (Table 1.3). The holotype of *C. decussata* had 85 dorsal fin rays, 65 anal fin rays, 15 pectoral fin rays and 77 lateral line scales, all within the corresponding ranges of *C. chittendeni* (Table 1.1). Number of gill rakers and vertebrae were not available as they were removed by a taxidermist (Gunter 1946).

Dawson (1963) suggested that *C. chittendeni* spawned in fall or winter, and Topp and Hoff (1972) suggested that *C. fimbriata* spawned in late spring, and therefore they inferred that

these two species were reproductively isolated. Moreover, in fall and winter, the Gulf Stream circulates near the centre of the Gulf of Mexico away from the continental shelf (Briggs 1974) and therefore, would not carry the larvae of *C. chittendeni* towards Atlantic Florida. In spring and summer the Gulf Stream circulates near the continental shelf (Briggs 1974) and would probably carry the larvae to the Atlantic Ocean. In support of this, one larva of *C. fimbriata* was collected on June 19th from the Atlantic Ocean in Georges Bank, off New England, USA (Scott and Scott 1988). This might explain why adult *C. chittendeni* were restricted to the Gulf of Mexico while those of *C. fimbriata* were also found in the Atlantic Ocean from Florida up to North Carolina.

Evseenko (2000) gave the range of caudal vertebrae as 27-28 for 3 larvae and /or juveniles; as opposed to 26-27, the range observed in this study (n=54). It is possible that one or more of the larvae and/or juveniles examined by Evseenko were misidentified.

***Cyclopsetta fimbriata* (Goode and Bean 1886) (Fig. 1.7)**

Hemirhombus fimbriatus Goode and Bean 1886

Common name: Spotfin flounder (Robins and Ray 1986)

Diagnosis: First dorsal ray anterior to blind side nostrils (Fig. 1.3b), weakly ctenoid scales dispersed among cycloid ones on ocular side, all of ocular side lower jaw fringed with scalloped flap of skin, ocular side nostrils both on a horizontal line parallel to long diameter of eyes (Fig. 1.4b), papilla on lower eye or on both eyes, anterior margin of eyes at the same level, interorbital not scaled, dark spot in centre of caudal fin.

Description: Dorsal fin rays 80-85, anal fin rays 60-67, ocular side pectoral fin rays 9-11, caudal vertebrae 26-27, gill rakers on lower limb 8-11, on upper limb 3-5, lateral line scales 73-87 (n=22). Posterior edge of pectoral fin ray of ocular side truncated (12 of 20) or oblique, caudal fin convex (13 of 23) or double truncate. Morphometrics are shown in Table 1.4.

Colour in alcohol: Grey brown, yellowish brown to dark brown on ocular side, dark brown to yellow on blind side. Posterior halves of dorsal and anal fins each with two large ocelli; anterior part of dorsal fin had 0-3 small dark spots, that of anal fin had one similar spot, caudal fin had one large dark spot in the middle, 0-5 small dark spots irregularly spaced on posterior margin, ocular side pectoral fin with a narrow dark band near its base, followed by a cream coloured section with dark specs on fin rays, posterior part marked with dark band or an incomplete dark oval spot.

Geographic distribution: coast of North Carolina to Florida, Gulf of Mexico and Caribbean Sea, (Fig. 1.8).

Comparison: *C. fimbriata* can be distinguished from all *Cyclopsetta* species by the presence of a papilla on lower or both eyes, dark band on posterior part of pectoral fin, number of pectoral fin rays (9-11), flap of skin on ventral margin of ocular side lower jaw, weakly ctenoid scales among cycloid scales on ocular side.

Remarks: Goode and Bean (1886) reported that, in the holotype, dorsal and anal fins were not scaled and the number of caudal rays was 16. This was incorrect; dorsal and anal fins in the holotype were found to be scaled and number of caudal fin rays was found to be 17. In addition, it was found that 15 of the 16 specimens from Gulf of Mexico had 10 pectoral fin rays on the ocular side, one had 9. On the other hand, the 10 specimens from the Caribbean Sea had 11 pectoral fin rays on the ocular side. With respect to vertebrae, 15 of the 16 specimens from the Gulf of Mexico had 26 caudal vertebrae, while one had 27, and 7 of the 10 specimens from the Caribbean Sea had 27 caudal vertebrae and three had 26. More specimens are required to see if these observed patterns are consistent and if they warrant the description of a new species.

Cyclopsetta panamensis (Steindachner 1875) (Fig. 1.9)

Citharichthys panamensis Steindachner 1875

Azevia panamensis (new combination) Jordan and Goss 1889

Common names: Panamanian flounder (Allen and Robertson 1994), God's flounder (Chirichigno and Vélez 1998), Southern flounder (Bussing and López 1994).

Diagnosis: First dorsal ray between nostrils of blind side (Fig. 1.3c), ocular side scales strongly ctenoid except on caudal peduncle and caudal fin, only ventro-posterior angle of ocular side lower jaw fringed with a scalloped flap of skin, ocular side nostrils on a horizontal line parallel to long diameter of eyes (Fig. 1.4c), interorbital not scaled, no papillae on eyes except, rarely, the lower eye has a bump-like structure (2 out of 35 specimens).

Description: Dorsal fin rays 90-99, anal fin rays 73-77 (n=34), ocular side pectoral fin rays 14-16, caudal vertebrae 28-30 (n=32), gill rakers on lower limb 8-10, on upper limb 3-5 (n=32), lateral line scales 74-85 (n=30), anterior margin of eyes at the same level, first dorsal fin ray between nostrils of blind side (Fig. 1.4c), posterior edge of pectoral fin oblique, caudal fin double truncate. Morphometrics are shown in Table 1.5.

Colour in alcohol: Brown to white on ocular side, light brown to white on blind side, 1-3 ocelli on dorsal fin (27 of 35), 1-2 ocelli on anal fin (28 of 35), 1 dark spot mottled with lighter patches in the middle of caudal fin (21 out of 35). Some specimens (5 of 35) had dark spots in vague circles and dark specs on head, body and fins. Pectoral fin on ocular side, darker than body and slightly mottled with lighter patches.

Geographic distribution: Pacific Ocean, from tip of Baja California to Pacific coast of Ecuador (Fig. 1.10). According to Jordan and Evermann (1898), *C. panamensis* is abundant along the coast of Mazatlan (Mexico) and Panama.

Comparison: Only species in *Cyclopsetta* with strong ctenoid scales on ocular side and with posterior angle of ocular side lower jaw fringed with a scalloped flap of skin.

Remarks: Only one specimen, FMNH 93698, had 16 caudal fin rays; possibly an abnormality. Meek and Hildebrand (1928) reported 76-91 lateral line scales and 68-78 anal fin rays (8 specimens), both wider ranges than observed in this study, 74-85 and 73-77 respectively.

***Cyclopsetta querna* (Jordan and Bollman 1890) (Fig. 1.11)**

Azevia querna Jordan and Bollman, 1890.

Dorsopsetta norma Nielsen, 1963, (junior synonym, suggested by van der Heiden and Mussot-Pérez 1993)

Common name: Toothed flounder (Bussing and López 1994), Chocolate flounder (Allen and Robertson 1994).

Diagnosis: First dorsal ray between nostrils of blind side (Fig. 1.3c), scales on ocular side cycloid, ocular side lower jaw not fringed with a scalloped flap of skin, anterior nostril of ocular side slightly dorsal to posterior nostril (Fig. 1.4d), upper eye slightly anterior to lower eye, maxillary extends posteriad to lower eye.

Description: Dorsal fin rays 86-96, anal fin rays 69-77, ocular side pectoral fin rays 13-18, caudal vertebrae 28-31 (n=62), gill rakers on lower limb 8-10, upper limb 4-9 (n=62), lateral line scales 90-103 (n=49), anterior margin of upper eye slightly advanced to that of lower eye, posterior edge of pectoral fin oblique, caudal fin double truncate.

Morphometrics are shown in Table 1.6.

Colour in alcohol: Chocolate brown to pale brown on ocular side, chocolate brown to yellow on blind side. Sometimes 1-2 dark spots each on dorsal (17 of 65) and anal (19 of 65) fins. Allen and Robertson (1994) reported faint indications of lighter bands on body; these were not observed in this study, perhaps because they faded with time.

Geographic distribution: Pacific Ocean, from coast of Chiapas, Mexico, down to Peru (Fig. 1.12). Allen and Robertson (1994) reported a range from Gulf of California to Peru but they did not mention specific specimens from these areas.

Comparison: *C. querna* is the only *Cyclopsetta* species where anterior margin of upper eye is slightly advanced to that of lower eye and posterior margin of maxillary exceeds posterior margin of lower eye. Also, interorbital width tends to be wider (Fig. 1.13) while the upper eye tends to be closer to the crest of head (Fig. 1.14) than in the rest of species in *Cyclopsetta*.

Remarks: Syntype SU 478, shows a faint dark spot on caudal fin; perhaps a juvenile coloration. Also, only this specimen, in a sample of 65, had 16 caudal fin rays and 13 pectoral fin rays; possibly teratology.

The locality of one specimen, USNM 282978 (collected in 1890) was recorded as the Bering Sea, off Russia, an area outside (5080 Km) the known geographic range of *C. querna*. Since no extra specimens of this species were found from the Bering Sea, it is highly unlikely that *C. querna* is actually found in the Bering Sea; instead this could be an error in data records.

Nielsen (1963) described a new genus, *Dorsopsetta*, and a new species, *D. norma*, based on prolonged anterior dorsal and pelvic fin rays and presence of ocelli on dorsal and anal fins of two specimens, a holotype (33 mm SL) and a paratype (36 mm SL). Nielsen (1963) indicated that the absence of teeth on the upper jaw of the holotype might have been because it was a larva. Ahlstrom *et al.* (1984) suggested that these two specimens were

metamorphosing larvae of *Cyclopsetta* because they were similar to the larvae of this genus. van der Heiden and Mussot-Pérez (1993) found eight *C. querna* larvae with ocelli and elongated dorsal fin rays similar to those in *D. norma* (Nielsen, 1963). They showed that the morphometrics and meristics of the *C. querna* larvae and those reported for *D. norma* by Nielsen (1963) completely overlapped; therefore, van der Heiden and Mussot-Pérez (1993) synonymised *Dorsopsetta* with *Cyclopsetta* and *D. norma* with *C. querna*. Observation of ten small specimens of *C. querna*, USNM 236111, 53-62 mm SL, showed that the gill rakers on the upper limb were longer than wide, similar to those in *D. norma* (Nielsen 1963). These observations further supported Ahlstrom *et al.*'s (1984) claim that the holotype and paratype of *D. norma* were actually metamorphosing larvae of *Cyclopsetta*, and the synonymy of *D. norma* with *C. querna* by van der Heiden and Mussot-Pérez (1993).

Acknowledgements: We thank the following people and institutions for loan of specimens: Susan L. Jewett (USNM), Sylvie Laframboise, Canadian Museum of Nature (CMN), Damaris Rodriguez (AMNH), David Catania (CAS), Christopher P. Kenaley (MCZ), Jessica Rosales (TNHC), Mary Anne Rogers (FMNH) and NMW. Susan L. Jewett (USNM) also provided pictures of type specimens; Andrew Cooper hand carried the type specimens from the USNM, Washington, D.C. to the University of Ottawa; Reinhard Pienitz (Université Laval) translated old German text. This work was supported by an operating grant to François Chapleau by the National Sciences and Engineering Research Council of Canada.

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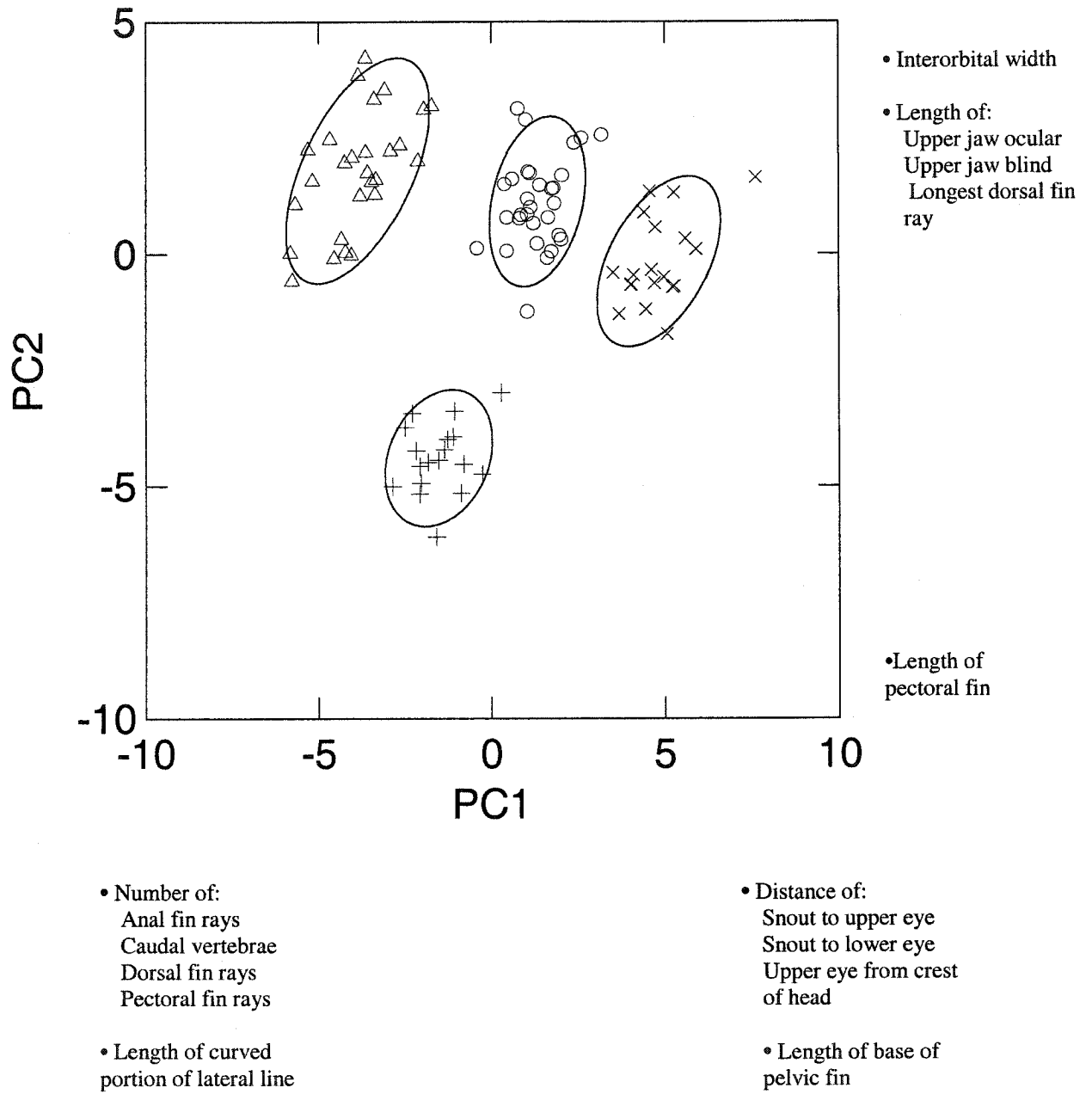


Fig. 1.1: PC1 vs. PC2 using six meristic and 23 morphometric characters of four putative species of *Cyclosetta*; o: *C. Chittendeni*, x: *C. fimbriata*, + : *C. panamensis*, Δ: *C. querna*.

Ellipses contain 80% of the data per each species.

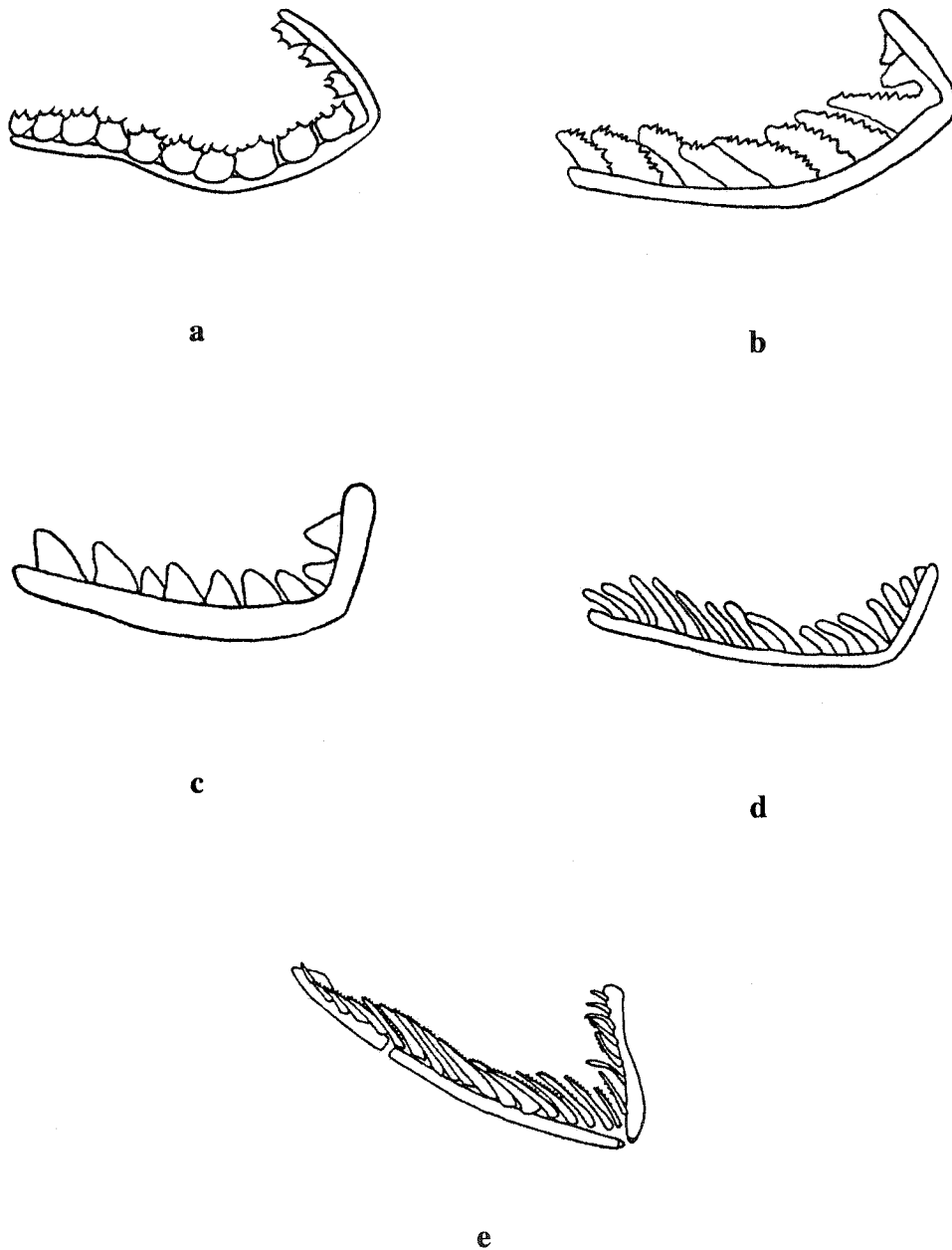


Fig. 1.2: Gill rakers in a. *Cyclopsetta*, b. *Syacium*, c. *Etropus*, d. *Citharichthys gilberti* and *C. spilopterus*, e. *C. gnathus* (from Hoshino and Amaoka, 1999). Drawings are for illustration purposes only, not drawn to scale.

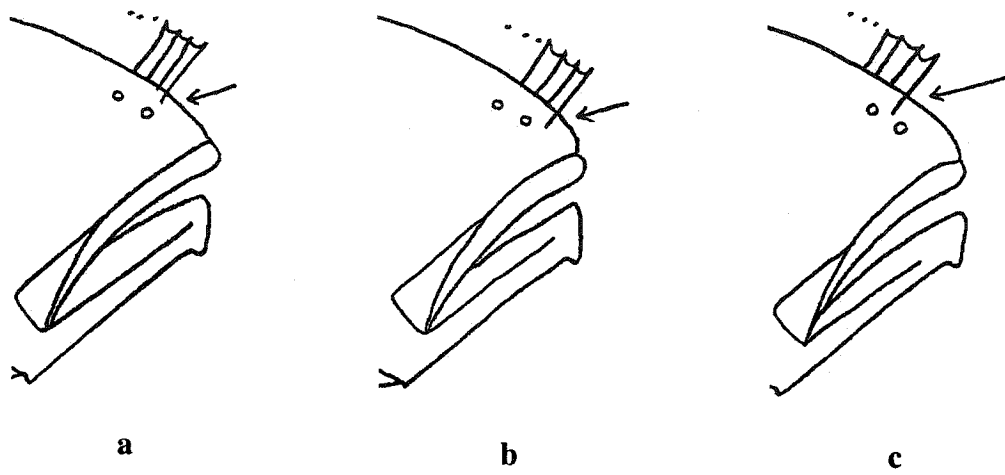


Fig. 1.3: First dorsal fin ray position relative to blind side nostrils in a. *Cyclopsetta chittendeni*, b. *C. fimbriata* and c. *C. panamensis* and *C. querna*. Drawings are for illustration purposes only, not drawn to scale.

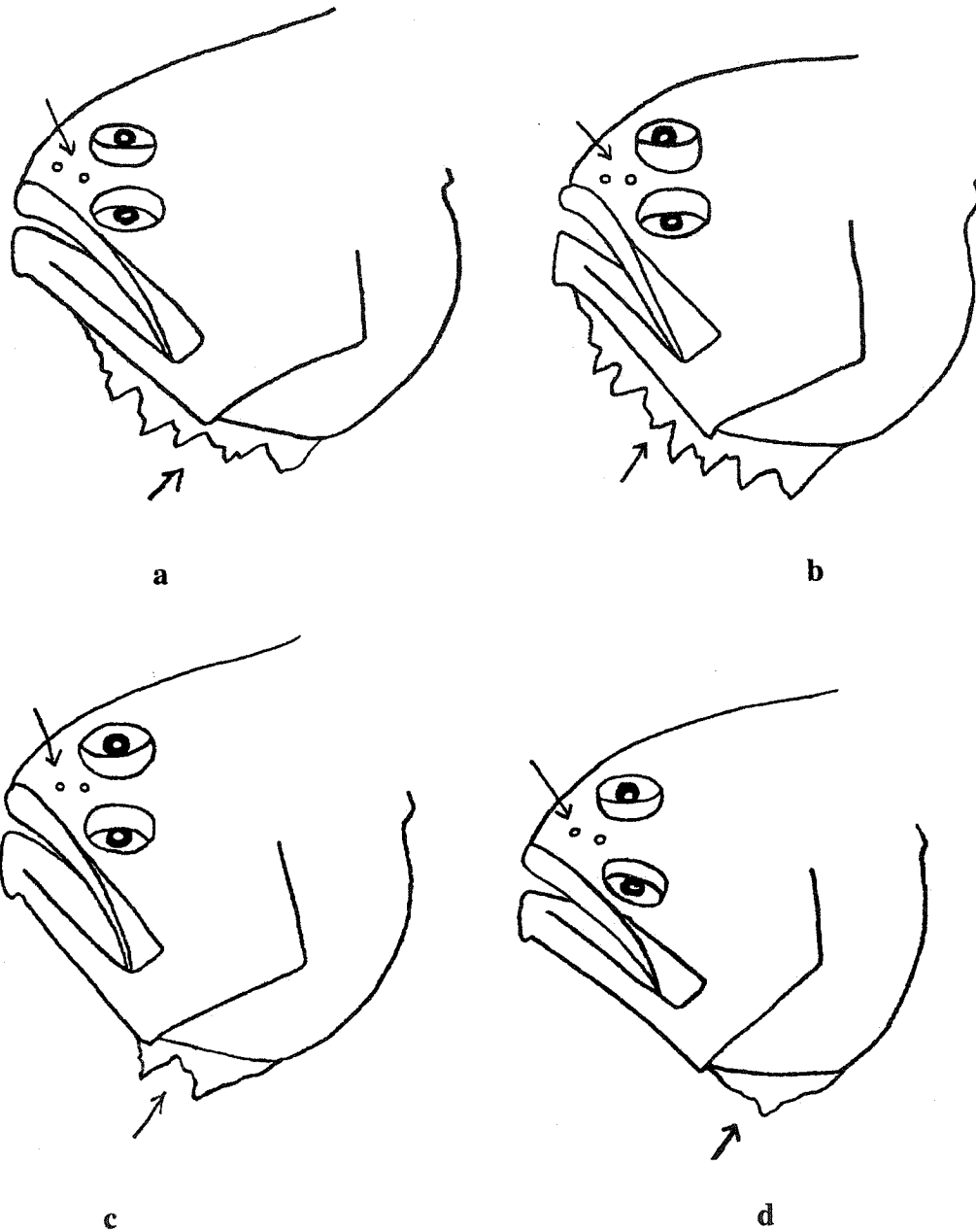


Fig. 1.4: Nostrils and flap of skin on the lower jaw of a. *Cyclopsetta chittendeni*, b. *C. fimbriata*, c. *C. panamensis*, and d. *C. querna*. Drawings are for illustration purposes only, not drawn to scale.

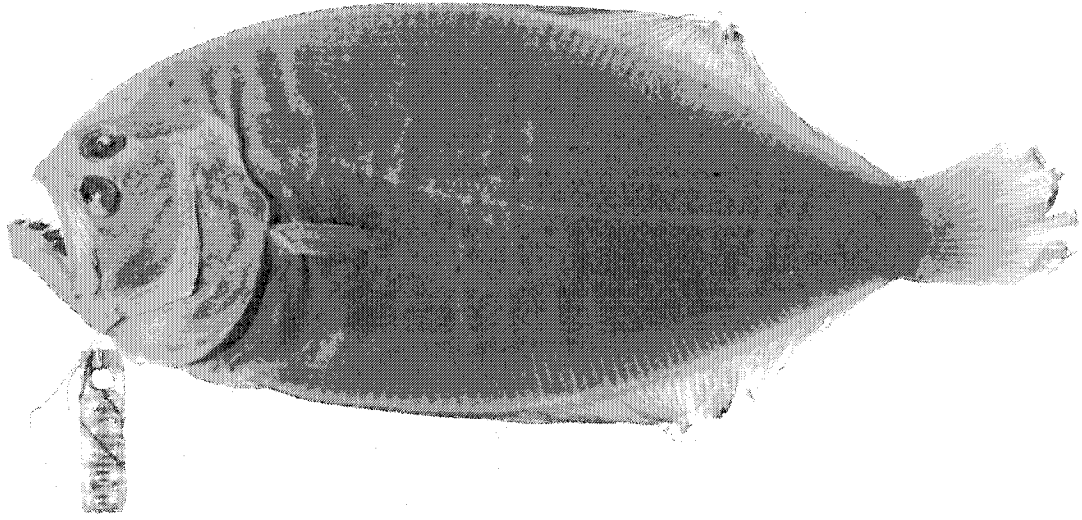


Fig. 1.5: *Cyclopsetta chittendeni* holotype, USNM 44100, 170 mm SL.

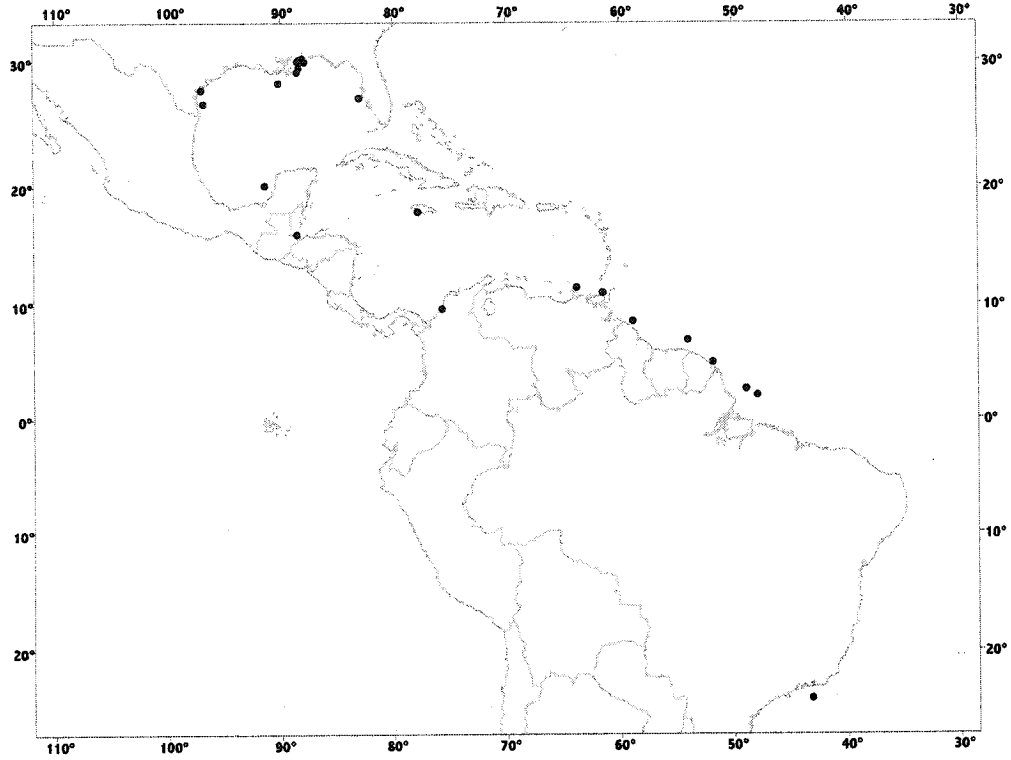


Fig. 1.6: Geographic distribution of *Cyclopsetta chittendeni*.

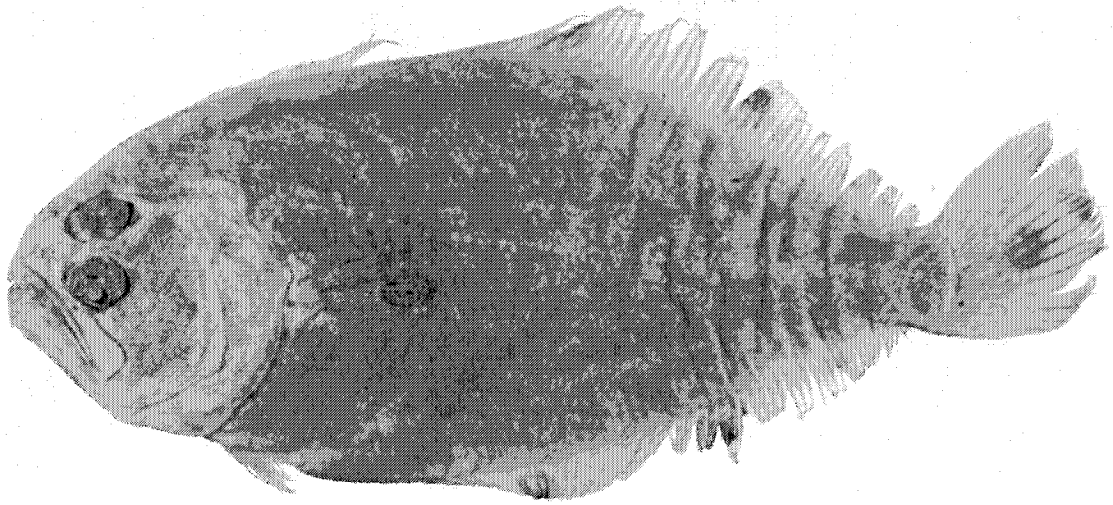


Fig. 1.7: *Cyclopsetta fimbriata* holotype USNM 37330, 213.7 mm SL.

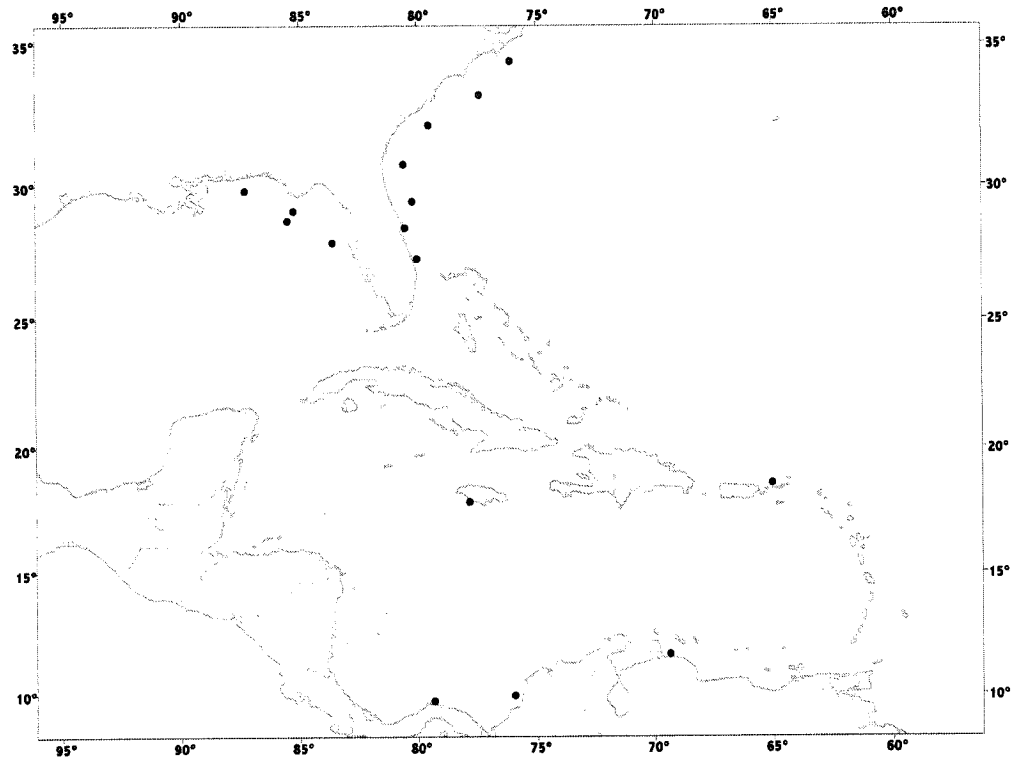


Fig. 1.8: Geographic distribution of *Cyclopsetta fimbriata*.

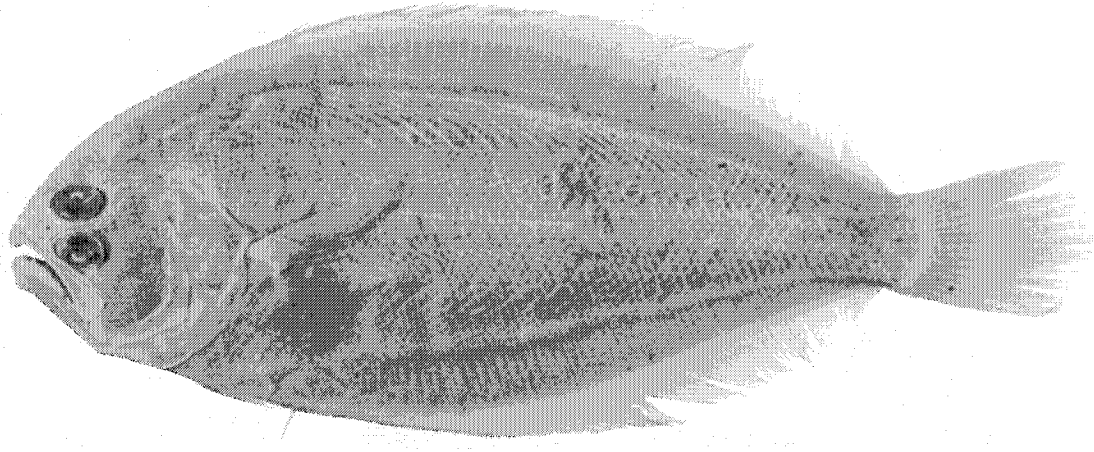


Fig. 1.9: *Cyclopsetta panamensis* syntype USNM 44132, 163.2 mm SL.

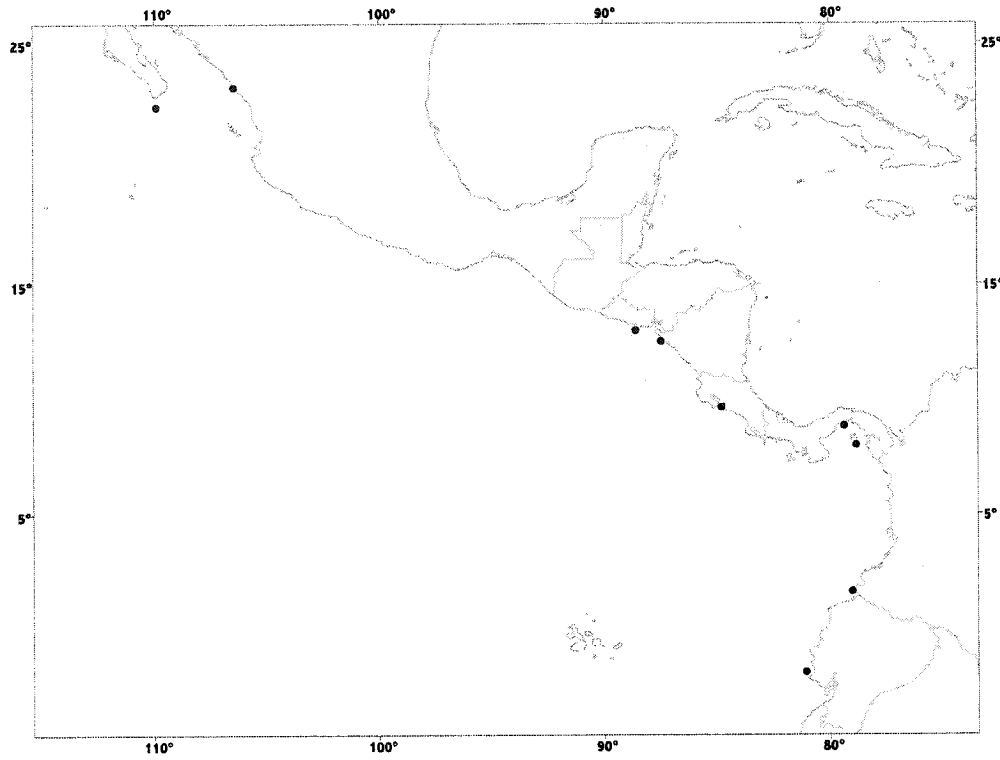


Fig. 1.10: Geographic distribution of *Cyclopsetta panamensis*.

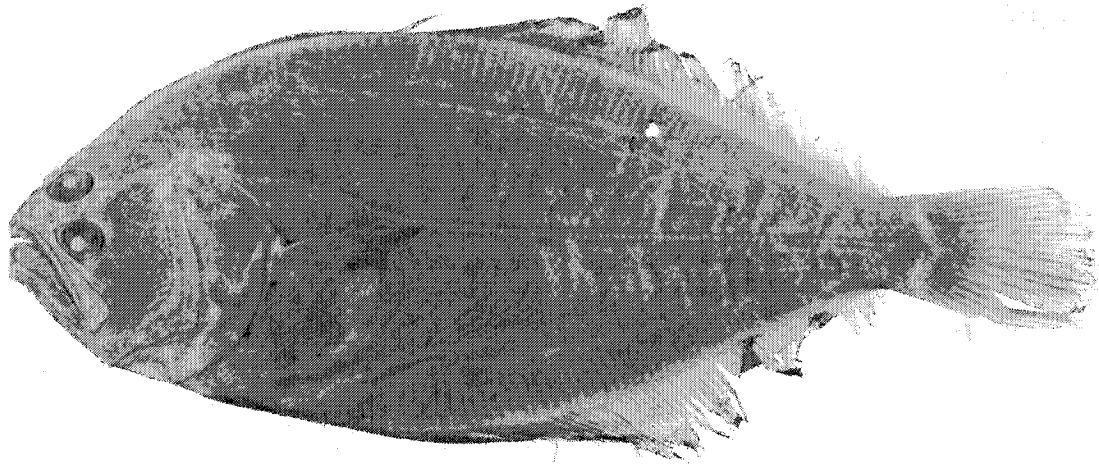


Fig. 1.11: *Cyclopsetta querna* syntype USNM 41159, 146.3 mm SL.

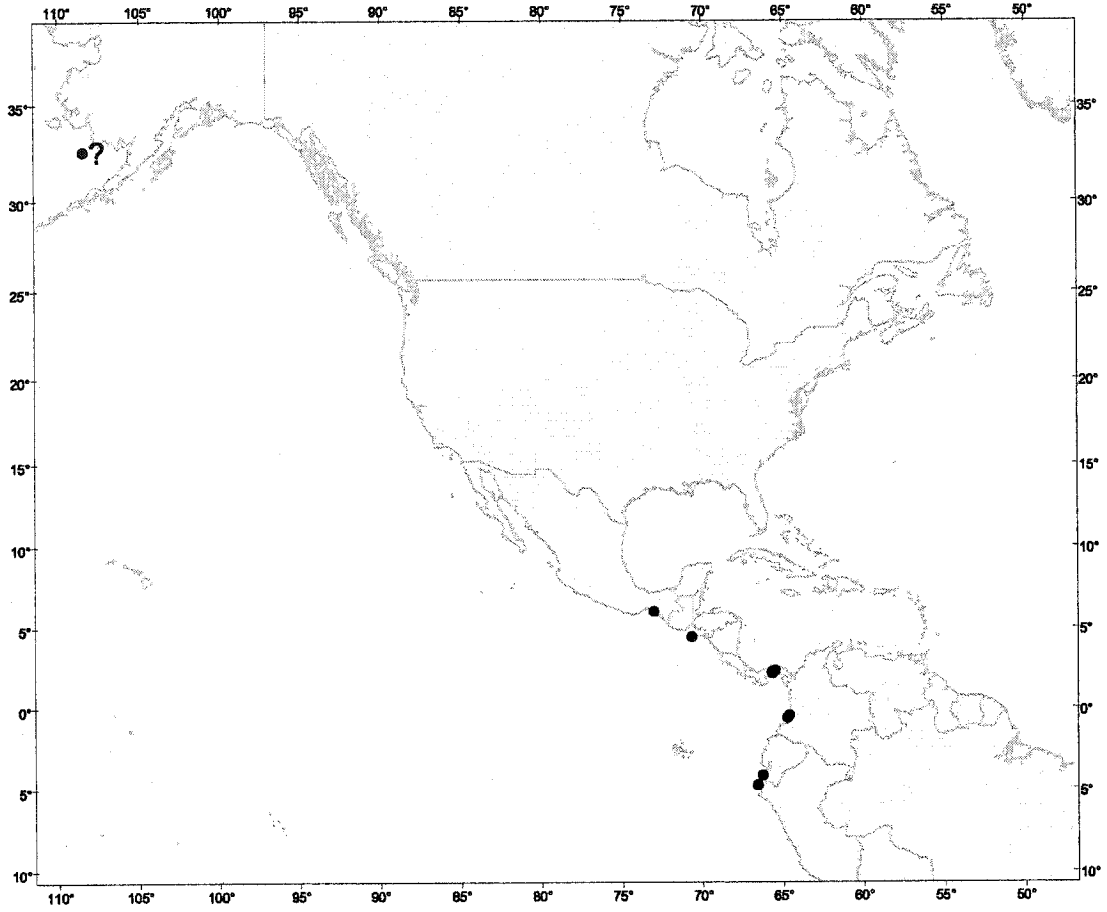


Fig. 1.12: Geographic distribution of *Cyclopsetta querna*.

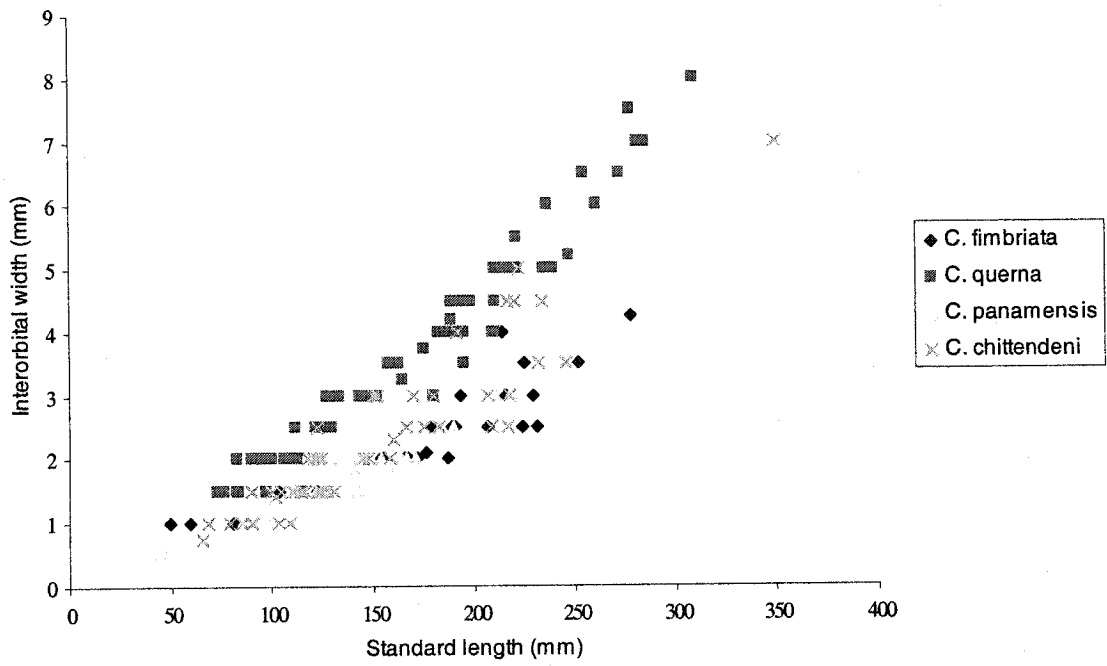


Fig. 1.13: Interorbital width vs. standard length in *Cyclopsetta* species.

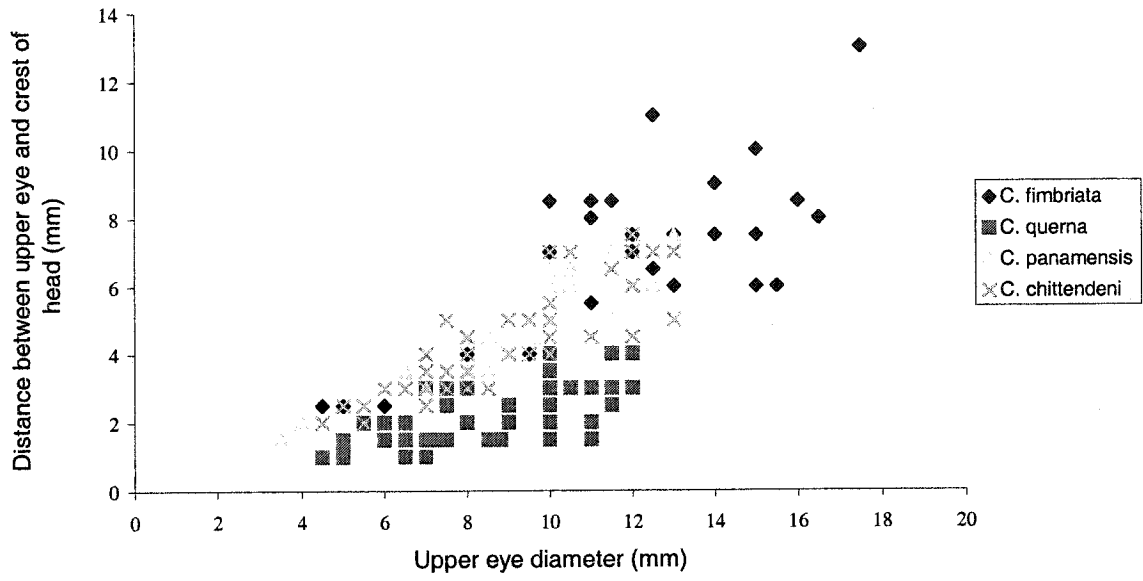


Fig. 1.14: Distance between upper eye and crest of in *Cyclopsetta* species.

Table 1.1: Ranges of meristic characters of the four species of *Cyclopsetta*. Acronyms: D and A: number of dorsal and anal fin rays respectively, vertC: number of caudal vertebrae, rpfo and rpvo: number of ocular side pectoral and pelvic fin rays respectively, IIs: number of lateral line scales. Sample size when different from n is indicated in parentheses.

Species	n	D	A	vertC	rpfo	rpvo	IIs
<i>C. chittendeni</i>	56	75-90	62-69	26-27	13-16	6	71-96
<i>C. fimbriata</i>	26	80-85	60-67	26-27	9-11	5-6	73-87 (22)
<i>C. panamensis</i>	35	90-99	73-77 (34)	28-30 (32)	14-16	6	74-85 (30)
<i>C. querna</i>	65	86-96	69-77	28-31 (62)	13-18	6	90-103 (49)

Table 1.2: Character loadings for PC1 and PC2; list of acronyms in Tables 1.1 and 1.3.

Character	A	vertC	sue	D	rpfo	sle	uc	bpvo	llc	lls	ued	led	pvo	ljo
PC1	-0.914	-0.887	0.885	-0.875	-0.828	0.806	0.767	0.737	0.711	-0.689	-0.686	0.662	0.652	0.631
PC2	-0.190	-0.043	-0.228	-0.282	0.159	-0.016	-0.444	-0.245	-0.261	0.495	-0.589	-0.493	-0.111	0.665

	ljb	int	ujo	ujb	pfo	ID	IA	bd	IC	cp	pvb	llst	pfb	hl	rpvo
0.575	-0.534	0.520	0.511	0.503	0.076	0.098	0.341	0.021	0.148	0.192	0.376	0.272	0.369	-0.150	
0.693	0.703	0.755	0.794	-0.701	0.706	0.623	0.138	0.131	-0.330	0.152	0.184	0.307	0.456	-0.087	

Table 1.3: Morphometric characters of *Cyclopsetta chittendeni*. Acronyms: SL:

Standard length, hl: head length, bd: body depth, llc: curved portion of lateral line, llst: straight portion of lateral line, int: interorbital width, sue: snout to upper eye, sle: snout to lower eye, ued: upper eye diameter, led: lower eye diameter, uc: distance between upper eye and crest of head, ujo: upper jaw on ocular side, ljo: lower jaw on ocular side, ujb: upper jaw on blind side, ljb: lower jaw on blind side, pfo: pectoral fin on ocular side, pfb: pectoral fin on blind side, pvo: pelvic fin on ocular side, pvb: pelvic fin on blind side, b-pvo: base of ocular side pelvic fin, b-pvb: base of blind side pelvic fin, LD: longest dorsal fin ray, LA: longest anal fin ray LC: longest caudal fin ray, cp: depth of caudal peduncle.

Character	<i>C. chittendeni</i>	<i>C. decussata</i>	Non-type specimens	SD
	Holotype	Holotype	n=52	
	USNM 44100	USNM 123802	Mean (Range)	
SL (mm)	170	191.7	148.9 (66-350)	56.3
In SL				
hl	3.5	3.5	3.5 (3.2-3.9)	0.1
bd	2.2	2.2	2.2 (2.1-2.4)	0.1
In llst				
llc	2.9	3.1	3 (2.6-3.6)	0.2
In hl				
int	16.3	18.2	20 (12.8-31.5)	4.3
sue	4.5	5	4.8 (4.4-5.5)	0.2

sle	4.9	5.2	5 (4.5-5.5)	0.2
ued	4.9	4.5	4.7 (4.2-6.1)	0.4
led	4.9	5	4.8 (4.2-6)	0.4
uc	8.9	13.6	9.9 (7.1-12.5)	1.4
ujo	1.8	1.9	1.9 (1.7-2)	0.1
ljo	1.7	1.8	1.7 (1.6-1.8)	0.1
ujb	1.7	1.8	1.7 (1.6-1.8)	0.1
ljb	1.6	1.6	1.6 (1.5-1.7)	0.0
pfo	-	1.8	1.9 (1.6-2.1)	0.1
pfb	2.5	-	2.3 (1.9-2.6)	0.2
pvo	-	2.9	2.5 (2.2-3.2)	0.2
pvb	2.6	2.9	2.7 (2.3-3.2)	0.2
b-pvo	4.1	4	4.1 (3.5-5.2)	0.4
b-pvb	-	-	3.9 (3.3-4.7)	0.4
ID	2.9	2.9	2.4 (2.1-2.9)	0.2
IA	2.2	2.4	2.2 (2-2.5)	0.1
IC	1.6	1.5	1.4 (1.2-1.8)	0.2
cp	2.7	2.7	2.8 (2.4-3.2)	0.2

Table 1.4: Morphometric characters of *Cyclopsetta fimbriata*; Sample size, when different from 25 is indicated in parentheses. Refer to Table 1.3 for list of acronyms.

Character	<i>C. fimbriata</i>	Non-type specimens	SD
	Holotype	n=25	
	USNM 37330	Mean (Range)	
SL(mm)	213.7	175.2 (49-278.2)	57.1
In SL			
hl	3.3	3.4 (3.1-3.7)	0.2
bd	2.3	2.2 (2.1-2.5)	0.1
In llst			
llc	3	2.8 (2.1-3.5)	0.3
In hl			
int	16.3	22.0 (16.0-26.9)	2.7
sue	4.1	4.0 (3.7-4.6)	0.2
sle	4.6	4.7 (4.0-5.2)	0.3
ued	3.9	4.2 (3.5-4.7)	0.4
led	4.2	4.4 (3.6-5.2)	0.5
uc	8.1	7.5 (5.3-10.1)	1.4
ujo	1.9	1.9 (1.8-2.1)	0.1
ljo	1.7	1.7 (1.7-1.9)	0.1
ujb	1.7	1.8 (1.7-1.9)	0.1

ljb	1.6	1.6 (1.6-1.7)	0.0
pfo	-	1.6 (1.5-1.9) (24)	0.1
pfb	2.8	2.5 (2.2-2.7)	0.2
pvo	2.8	2.5 (2.0-2.9) (24)	0.3
pvb	2.8	2.7 (2.3-3.1) (23)	0.2
b-pvo	-	4.0 (3.4-5.0) (24)	0.4
b-pvb	3.6	3.7 (2.9-5.4) (21)	0.5
lD	3	2.6 (2.2-3.0) (23)	0.2
lA	2.8	2.3 (2.0-3.3) (22)	0.3
lC	1.7	1.5 (1.3-1.7) (24)	0.1
cp	2.9	2.9 (2.5-3.5) (24)	0.3

Table 1.5: Morphometric characters of *Cyclopsetta panamensis*; Sample size, when different from 28 is indicated in parentheses. Refer to Table 1.3 for list of acronyms.

Character	<i>C. panamensis</i> Syntypes: MCZ 24981, USNM 44132, NMW 9132-9136 (5), n=7	SD	Non-type specimens n=28 Mean (Range)	SD
SL (mm)	166.4 (140.1-197.7)	20.6	148.1 (44-218.6)	47.5
In SL				
hl	3.8 (3.6-3.9)	0.1	3.7 (3.1-3.9)	0.2
bd	2.3(2.2-2.5)	0.1	2.3(2.1-2.4)	0.1
In llst				
llc	3.4 (3.2-3.5) (4)	0.1	3.2 (2.8-3.7)	0.3
In hl				
int	19.5 (13.2-23.1)	3.6	22.8 (17.9-34.0)	3.9
sue	4.8 (4.2-5.4)	0.4	4.6 (4.0-5.0)	0.3
sle	5.0 (4.6-5.3) (4)	0.3	4.9 (4.0-5.3)	0.3
ued	4.2 (4-4.5)	0.2	4.1 (3.5-4.8)	0.3
led	4.4 (4.2-4.6)	0.1	4.3 (3.6-5.5)	0.4
uc	7.5 (5.6-9.2)	1.6	8 (5.6-9.5)	1.1
ujo	2.1 (2.0-2.1)	0.0	2.1 (1.9-2.2)	0.1

ljo	1.9 (1.8-1.9)	0.0	1.9 (1.8-1.9)	0.0
ujb	2.0 (1.9-2.1)	0.1	2.0 (1.9-2.0)	0.0
ljb	1.9 (1.7-2.0)	0.2	1.8 (1.6-2.0)	0.1
pfo	1.7 (1.5-1.9)	0.1	1.6 (1.5-1.7)	0.1
pfb	2.4 (2.2-2.5)	0.1	2.4 (2.1-2.8)	0.2
pvo	2.5 (2.3-2.7) (4)	0.2	2.4 (2.1-2.9)	0.2
pvb	2.6 (2.5-2.7) (3)	0.1	2.5 (2.2-2.7) (24)	0.1
b-pvo	4.3 (4.0-4.5) (3)	0.2	4.2 (3.4-5.1) (27)	0.5
b-pvb	4.2 (3.9-4.7) (3)	0.5	3.8 (3.3-5.4) (22)	0.5
ID	2.5 (2.5-2.7) (4)	0.1	2.5 (2.2-3.0)	0.2
IA	2.2 (2.1-2.4) (4)	0.1	2.3 (2.0-2.6)	0.1
IC	1.4 (1.3-1.4) (3)	0.0	1.4 (1.1-1.5) (21)	0.2
cp	2.5 (2.4-2.7) (6)	0.3	2.6 (2.3-3.1)	0.2

Table 1.6: Morphometric characters of *Cyclopsetta querna*; Sample size, when different from 62, it is indicated in parentheses. Refer to Table 1.3 for list of acronyms.

Character	<i>C. querna</i> Syntypes: SU 478, USNM 41159 (2), n=3	SD	Non-type specimens n=62 Mean (Range)	SD
SL(mm)	131.6 (84-164.4)	42.2	171.4 (72.5-309)	61.7
In SL				
hl	3.3 (3.2-3.4)	0.1	3.6 (2.9-4) (61)	0.2
bd	2.4 (2.4-2.5)	0.1	2.3 (1.8-2.6) (61)	0.1
In llst				
llc	3.2 (2.9-3.4)	0.3	3 (2.7-3.5)	0.2
In hl				
int	15.4 (14.2-17.3)	1.7	13 (10.1-21.3)	1.9
sue	5.3 (5.2-5.5)	0.1	5.3 (4.5-6.6)	0.4
sle	5.2 (5-5.3)	0.2	5.3 (4.7-6.6)	0.3
ued	5.4 (5.2-5.7)	0.3	5.6 (4.2-6.6)	0.5
led	5.4 (5.2-5.7)	0.3	5.6 (4.2-6.8)	0.5
uc	28.8 (26-32)	3.0	21.1 (10.4-33.4)	4.7
ujo	2	0.1	1.9 (1.8-2.1)	0.1
ljo	1.8 (1.7-1.8)	0.1	1.7 (1.7-1.9)	0.1
ujb	1.8 (1.7-1.8)	0.1	1.8 (1.7-1.9) (61)	0.1

ljb	1.7 (1.6-1.7)	0.1	1.7 (1.5-1.9)	0.1
pfo	-	-	1.9 (1.7-2.4) (57)	0.2
pfb	2.6 (2.4-2.9)	0.3	2.4 (2.1-3.8) (59)	0.3
pvo	2.7 (2.2-3)	0.4	2.6 (2.1-3.2) (52)	0.3
pvb	2.6 (2.4-2.7)	0.2	2.5 (2-2.9) (52)	0.2
b-pvo	6.5 (5.6-6.5) (2)	0.6	5.4 (4-6.7) (50)	0.6
b-pvb	4.4 (3.6-4.8)	0.7	4.2 (3.4-5.3) (51)	0.4
ID	-	-	2.3 (1.6-2.9) (61)	0.3
IA	1.7 (1)	-	2.1 (1.6-2.6) (58)	0.2
IC	1.4 (2)	0.0	1.4 (1.2-1.8) (55)	0.1
cp	3.3 (3-3.7)	0.4	3 (2.5-3.7) (54)	0.3

Appendix 1.1

Materials examined:

Cyclopsetta chittendeni, 54 specimens (66-350 mm SL).

Holotypes: *C. chittendeni* USNM44100; Caribbean Sea, Trinidad, West Indies; 2 April 1892; 170 mm SL. *C. decussata* USNM123802; Gulf of Mexico, Texas, about 64 Km south of Port Aransas, USA; 46.8 m; 12 August 1945; 191.7 mm SL.

Other material: Gulf of Mexico: AMNH 83559; south of Santa Rosa County, off Florida, USA; 30° 4' 30" N, 86° 48' W; 29 August 1976; 245.3 mm SL. AMNH 80229; off Alabama, USA; 29° 30' 30" N, 88° 23' 15" W; 7 October 1972; 6; 66-123 mm SL. AMNH 81750; south of Mobile Bay, off Alabama, USA; 29° 57' N, 87° 54' W; 20 April 1975; 182.8 mm SL. USNM 205273; Alabama, Mobile County, Dauphin Island Bay Channel, USA; 3 October 1969; 111 mm SL. USNM 286002; Louisiana, USA; 28° 20' N, 90° 12' W; 69-73 m; 20 February 1964; 2; 208.6-216.2 mm SL. AMNH 81153; south of Pascagoula, Mississippi, USA; 30° N, 88°30' W; 24 October 1974; 10 of 12; 109-124 mm SL. USNM 282990; Mississippi, USA; 29° 11' 18" N, 88° 34' W; 77 m; 14 December 1959; 207 mm SL. AMNH 84175; Gulf of Mexico, about 24 Km south of the west end of Dauphin Island, USA; 19 November 1973; 101.8 mm SL. SU 40544; Texas, USA; 11 August 1940; 3; 68-89.5 mm SL. TNHC 23838; Gulf Coast between Port Aransas and Corpus Christi, Texas, USA; 1993; 166.6 mm SL. TNHC 20678; off Port Aransas, Texas, USA; 24 July 1962; 2; 158.6-159.6 mm SL. USNM 155615; Port Aransas, Texas, USA; 24 October 1946; 130.7 mm SL. USNM 156194; off Brownsville, Texas, USA; 26° 43' N 96° 51' W; 45 m; 4 February 1939; 3; 114.2-120 mm SL. USNM 158334; off Campeche, Mexico; 20° 5' N, 91° 28' W; 16 m; 26 August 1951; 6; 144.4-231.5 mm SL.

Caribbean Sea: AMNH 84475; Bahia de Amatique, near Puerto Barrios, Guatemala; 3 June 1974; 122.3 mm SL. USNM 266479; Jamaica; 17° 53' N 77° 50' W; 40-47 m; 18 May 1968; 2; 191.5-221-7 mm SL. USNM 282995; Panama; 9° 35' N, 75° 44' W; 33 m; 28 November 1968; 179.5 mm SL. USNM 282986; Venezuela; 11° 24' N, 63° 52' W; 49 m; 24 September 1965; 152 mm SL.

Atlantic Ocean: USNM 282989; British Guyana; 8° 3' N 58 56' W; 67.6 m; 28 August 1958; 2; 150-216.7 mm SL. USNM 159505; Surinam; 6° 51' N, 54° 3' W; 51 m, 15 June 1957; 2; 100-122 mm SL. USNM 283000; French Guiana ; 4° 57' N, 51° 49' W; 0-36 m; 5 May 1975; 216.5 mm SL. SU 61518; SW, Rio de Janeiro, Brazil; 8 June 1944; 350 mm SL. USNM 286003; Brazil; 2° 36' N, 48° 54' W; 60-64 m; 10 May 1975; 234 mm SL. USNM 282994; Brazil; 2° 3' N, 47° 55' W; 47-56 m; 11 May 1975; 220 mm SL.

Cyclopsetta fimbriata, 26 specimens (49-278.2 mm SL).

Holotype: Gulf of Mexico: USNM 37330; off Florida, USA; 28° 42' 30" N, 85° 29' W; 158 m; 213.7 mm SL.

Other material: Atlantic Ocean: USNM 152052; North Carolina, USA; 34° 23' 30" N, 76° 3' 30" W; 61 m; 19 January 1950; 178.2 mm SL. AMNH 74240; off South Carolina, USA; 32° 10' N, 79° 30' W; 13 December 1967; 215.6 mm SL. USNM 151943; off South Carolina, USA; 33° 13' 30" N, 77° 21' W; 72 m; 1 February 1950; 176.5 mm SL. AMNH 76358; off Florida, USA; 29° 25' 6" N, 80° 12' W; 30 October 1973; 3; 166.8-178 mm SL. NMC 87-54; Port Canaveral area, Florida, USA; 28° 26' N, 80° 30' W; 30 March 1987; 278.2 mm SL. NMC 80-483; Port Canaveral area, Florida, USA; 30° 46' 2" N, 80 34 W; 69 m; 15 September 1978; 252 mm SL. USNM 266486; Florida, USA; 27° 16' 30" N, 80° 1' W; 54 m; 15 March 1965; 206.8 mm SL.

Gulf of Mexico: AMNH 82180; off Florida, USA; 29° 4' N, 85° 14' W; 25 July 1975; 3; 59-230 mm SL. AMNH 83219; south of Santa Rosa Island, Florida, USA; 29° 48' N, 87° 17' W; 28 August 1976; 223.4 mm SL. AMNH 85840; USA; 27° 52' 48" N, 83° 34' 12" W; 5 February 1978; 224.5 mm SL. TNHC 2087; Texas, USA; 24 June 1950; 193.7 mm SL.

Caribbean Sea: USNM 261535; Panama; 9° 43' N, 79° 20' W; 94 m; 19 October 1965; 2; 49-103.4 mm SL. USNM 266484; Colombia; 9° 56' N, 75° 56' W; 126 m; 25 November 1968; 5; 154.1-190.6 mm SL. USNM 261355; Venezuela; 11° 39' N, 69° 22' W; 99 m; 1 October 1965; 229.6 mm SL. USNM 261599; Jamaica; 17° 51' N, 77° 49' 30" W; 50 m; 18 May 1965; 121.7 mm SL. USNM 286007; Virgin Islands; 18° 35' N, 65° 3' W; 75 m; 26 September 1959; 81.3 mm SL.

Cyclopsetta panamensis, 35 specimens (44-218.6 mm SL).

Syntypes: Pacific Ocean: MCZ 24981; Gulf of Panama, Panama, 140.4 mm SL.

NMW 9132-9136; unknown locality; 5; 140.1-197.7 mm SL. USNM 44132; unknown locality, 163.2 mm SL.

Other material: Pacific Ocean: CAS 3439; Baja California, Cabo San Lucas, Mexico; 8 June 1932; 44 mm SL. SU 3029; Mazatlan, Mexico; 7; 85-209 mm SL. USNM 47483; Mazatlan, Mexico; 1895; 210.6 mm SL. FMNH 61557; El Salvador; 128 mm SL. FMNH 93697; El Salvador; 3; 176.2-181 mm SL. FMNH 93698; Punta San Juan, Jiquilisco Bay, station 1, El Salvador; 1976; 134.2 mm SL. USNM 220796; Punta San Juan, Jiquilisco Bay, El Salvador; 29 September 1976; 5; 93.6-143.1 mm SL. SU 46199; Nicaragua; 180 mm SL. FMNH 61556; Costa Rica; 149 mm SL. USNM 92167; Puntarenas, Costa Rica; 154 mm SL. USNM 81040; Panama Market, Panama; 8 February 1912; 218.6 mm SL.

USNM 321717; Panama; 8° 17' 30" N 78° 52' 30" W; 4 May 1990; 17 m; 48 mm SL.

USNM 286010; off Cape Manglares, south of Tumaco, Colombia; 1° 35' 5" N, 79° 3' W to 1° 37' N 79° 4' W; 9 m; 3; 123.8-210.5 mm SL. USNM 362494; Ecuador; 2° 43' S, 8° 33' W; 11 September 1966; 0-20 m; 217.8 mm SL.

Cyclopsetta querna, 65 specimens (72.5-309 mm SL).

Syntypes: Pacific Ocean: *Azevia querna* USNM 41159; Gulf of Panama, Panama; 8° 51' N, 79° 31' 30" W; vessel Albatross, Station 2800; 30 March 1888; 2; 146.3-164.4 mm SL. SU 478; Gulf of Panama, Panama; 8° 38' N, 79° 31' 30" W; 28.8 m; vessel Albatross, Station 2802; 30 March 1888; 84 mm SL.

Other material: USNM 282978; Bering Sea, off Russia; Albatross; Station 3250; 58° 11' 30" N, 163° 2' 45" W; 32 m; 13 June 1890; 210.2 mm SL. NMC 68-1110; Chiapas Strait at Puerto Arista, Mexico; 16° N, 93° 55' W; 21 August 1959; 5; 184.4-234 mm SL. USNM 286021; Pacific Ocean, El Salvador; 29 October 1975; 25.6 m; 8; 76.7-162.8 mm SL. NMC 68-1187; Tobago Island, north of Panama City, Panama; 8° 48' N, 79° 34' W; 3 June 1959; 3; 254.3-281.7 mm SL. USNM 236111; Gulf of Panama, Panama; 8° 57' N, 79° 9' 10" W; 11 m; 23 March 1967; 10 of 44; 72.5-146 mm SL. USNM 362497; Colombia; 3° 20' N, 77° 40' W; 52-60 m; 16 September 1966; 2; 125.7-217.4 mm SL. USNM 282979; Colombia; 3° 36' N, 77° 28' W; 38 m; 19 September 1969; 26; 112.7-309 mm SL. USNM 362496; Ecuador; 3° 39' S, 80° 41' W; 13 m; 10 September 1966; 5; 121.8-150 mm SL. USNM 362495; Peru; 4° 48' S, 81° 17' W; 16-37 m; 2 June 1966; 2; 83-126.4 mm SL.

Additional material:

The following specimens were examined for the shape of gill rakers: *Citharichthys gilberti*: NMC 68-1930; Punta Island, Ecuador; October 1968; 2; 107.6-121.2 mm SL. *Citharichthys spilopterus*: NMC 67-0213; Lake Maracai, Venezuela; August 1977; 3; 53.2-89.8 mm SL. *Citharichthys stigmaeus*: NMC 85-0049; Fulford Harbour, near Jackson Rock, south east Vancouver Island, Victoria District, British Colombia, Canada; 48° 45' 5" N, 123° 25' 35" W; 27 July 1982; 2; 126.3-129.2 mm SL. *Etropus crossotus*: NMC 68-1930; Punta Island; interior lagoon, Ecuador; October 1968; 114 mm SL. *Etropus ectenes*: NMC 68-1959; Posorja, Ecuador; January 1977; 65 mm SL.

Chapter 2:

Phylogenetic relationships of *Cyclosetta* and *Syacium* (Pleuronectiformes:

Paralichthyidae)

Abstract: Phylogenetic relationships among four species of *Cyclopsetta* and eight species of *Syacium* were examined based on a total of 29 morphological, meristic and osteological characters; *Citharichthys* and *Etropus* were designated as the outgroup. *Cyclopsetta* was strongly supported as monophyletic by eleven synapomorphies. This genus was divided into two new subgenera, *Cyclopsetta* (subg. nov.) comprised *C. chittendeni* and *C. fimbriata* and *Azevia* (subg. nov.) comprised *C. panamensis* and *C. querna*.

Syacium was also found to be monophyletic based on five synapomorphies. *S. longidorsale* was the first extant species to evolve followed subsequently by *S. ovale*, *S. gunteri* and *S. maculiferum*. The remaining four species were grouped in a trichotomy of *S. guineensis*, *S. micrurum* and the sister species *S. latifrons* and *S. papillosum*.

Key words: *Cyclopsetta*, *Syacium*, *Citharichthys*, *Etropus*, phylogenetic analysis, cladogram.

Introduction: *Cyclopsetta* and *Syacium* are sinistral flatfishes inhabiting the continental shelves of the Atlantic and Pacific coasts of North and South America. *Cyclopsetta* comprises four species; *C. chittendeni* and *C. fimbriata* are found on the Atlantic coast from North Carolina, USA, to Rio de Janeiro, Brazil, and *C. panamensis* and *C. querna* are found on the Pacific coast from Baja California, Mexico to Peru (Chapter1).

Syacium comprises eight species (Murakami and Amaoka 1992); three (*S. gunteri*, *S. micrurum* and *S. papillosum*) inhabit the Atlantic coast from south Carolina, USA, to Rio de Janeiro, Brazil including Gulf of Mexico and the Caribbean Sea; and four species (*S. longidorsale*, *S. latifrons*, *S. maculiferum* and *S. ovale*) are found along the Pacific coast

from Baja California, Mexico to Ecuador. One species, *S. guineensis*, inhabits the Atlantic coast of tropical Africa from Western Sahara to Angola (Murakami and Amaoka 1992).

Norman (1934) reviewed four genera, *Cyclopsetta*, *Syacium*, *Citharichthys* and *Etropus* and noted that they were closely related, in particular, *Citharichthys* and *Etropus*. He placed the four genera under the subfamily Paralichthinae, family Bothidae. Hensley and Ahlstrom (1984) defined *Cyclopsetta*, *Syacium*, *Citharichthys* and *Etropus* as a monophyletic group and placed them within the family Paralichthyidae. The monophyly was based on six synapomorphies: urinary papilla on the blind side, the base of ocular-side pelvic fin on mid-ventral line of the body; that of the blind-side on the blind side and slightly in advance of the ocular side fin, 17 caudal fin rays, these caudal rays were not supported by pleural, neural or hemal spines and the fifth hypural was fused to an epural. Moreover, Ahlstrom et al. (1984), divided the four genera into two pairs, *Citharichthys*-*Etropus* and *Cyclopsetta*-*Syacium* based on three larval characters indicated respectively: 2-3 vs. 5-11 elongated dorsal fin rays on the crest of head, 0-2 vs. 3-6 elongated rays of the left pelvic fin, and small vs. large preopercular spines.

Berendzen and Dimmick (2002) conducted a phylogenetic study of the order Pleuronectiformes based on mitochondrial DNA from 43 species representing 11 of the 12 families of flatfishes resolved by Cooper and Chapleau (1998). Included in the analysis were *Citharichthys xanthostigma*, *Etropus microstomus* and *Syacium papillosum*. Their results confirmed that *Citharichthys*, *Etropus* and *Syacium* were monophyletic as proposed by Ahlstrom et al. (1984); and that the *Citharichthys*-*Etropus* clade was monophyletic, also proposed by Ahlstrom et al. (1984) and suggested by Norman (1934). They did not, however, have material for the genus *Cyclopsetta*. The purpose of this study is to test the

monophyly of the *Cyclopsetta-Syacium* clade, the monophyly and intrarelationships of each genus.

Materials and Methods: The phylogenetic analysis was based on 29 morphological, meristic and osteological characters (Appendix 2.1) of 14 terminal taxa. Autapomorphies were excluded from the character matrix. All morphological characters were observed on the ocular side except for character 13 (origin of first dorsal ray relative to blind side nostrils) which was observed on the blind side. Larval characters were taken from Ahlstrom et al. (1984). For *Syacium*, information about the following characters were taken from Murakami and Amaoka (1992): one or two dark lines extend from the anterior margin of the upper eye to the snout (4), width of interorbital space in mature males relative to females (7), presence of one or two extended and filamentous pectoral fin rays in mature males (15), presence of dark bars on pectoral fin (16), presence of ocelli on dorsal and anal fins (17), number of caudal vertebrae (23), number of pectoral fin rays (24) and number of lateral line scales (25).

States of characters 23 and 25 of *Etropus crossotus* were taken from Leslie and Stewart (1986). Otherwise, information about the characters was obtained from whole preserved specimens, radiographs and cleared and stained material. Cleared and stained specimens were prepared according to Taylor and Van Dyke (1985). Terminology of bones follows Cooper and Chapleau (1998). Institutional abbreviations follow Leviton et al. (1985). SL is standard length in mm (Hubbs and Lagler 1958).

The ingroup consisted of 12 species: the four species of *Cyclopsetta* and the eight species of *Syacium*: *Cyclopsetta chittendeni* Bean, *C. fimbriata* (Goode and Bean), *C. panamensis* (Steindachner), *C. querna* (Jordan and Bollman), *Syacium guineensis*

(Bleeker), *S. gunteri* Ginsburg, *S. latifrons* (Jordan and Gilbert), *S. longidorsale* Murakami and Amaoka, *S. maculiferum* (Garman), *S. micrurum* Ranzani, *S. ovale* (Günther), *S. papillosum* (Linnaeus).

Given that *Citharichthys*, *Etropus*, *Cyclopsetta* and *Syacium* were monophyletic according to Hensley and Ahlstrom (1984) and that *Citharichthys*, *Etropus* and *Syacium* were monophyletic according to Berendzen and Dimmick (2002), *Citharichthys* and *Etropus* were chosen as the outgroup. *Citharichthys* was represented by *C. gilberti* and *C. stigmaeus*, and *Etropus* was represented by *E. crossotus*.

The analysis was performed using the Branch and bound and heuristic options (with 100 replicates) of PAUP version 4.0 beta 10 (Swofford 2003); all characters were unordered; accelerated character optimization (ACCTRAN) and Bootstrap (Felsenstein 1985) with 1000 replicates were used. The character matrix is shown in Table 2.1.

Materials examined

Citharichthys gilberti; NMC 68-1930, Pacific Ocean, Ecuador; 3 (1 c&s); Oct., 1968; 100-120mm SL.; *C. stigmaeus*; NMC 74-216, Pacific Ocean, California; 33° 25' N, 118° 30' W; 35 m; 23 June 1973, 28 (2 c&s); 62-85 mm SL. *Cyclopsetta*: materials examined are listed in Appendix 1.1. *Etropus crossotus*; USNM 286059, Atlantic Ocean, Florida; 28° 13' 30" N, 80° 21' W; 21.6 m; 16 (1 c&s); 13.3-86 mm SL. *Syacium guineensis*; USNM 270657; Atlantic Ocean, Guinea; 9° 24' N, 15° 26' W; 50 m; 5 (1 c&s); 13 May 1985; 171.7-205 mm SL. *S. gunteri*; USNM 266488; Caribbean Sea, Venezuela; 11° 25' N, 63° 49' W; 48.6 m; 24 Sept. 1965; 9 (1 c&s) 21 May 1984; 99-118 mm SL. *S. micrurum*; USNM 266482; Caribbean Sea, Venezuela; 12° 27' N, 70° 6' W; 72 m; 13 (2 c&s); 21 May 1948; 119.6-181.7 mm SL. *S. papillosum*; USNM 286676; Gulf of Mexico, Florida; 26°

24' N, 83° 22' W; 54 m; 3 Oct. 1965; 7 (2 c&s); 99-159.3 mm SL. *S. longidorsale*; USNM 317827; Pacific Ocean, Ecuador; 3° 1' N, 77° 50' W; 35-38 m; 16 Sept. 1966; 15 (2 c&s); 85-120.5 mm SL. *S. ovale*; USNM 317828; Pacific Ocean, Ecuador; 3° 1' N, 77° 50' W; 35-38 m; 16 Sept. 1966; 12 (2 c&s); 98.5-168.2 mm SL. *S. maculiferum*; Pacific Ocean, Costa Rica, 3 (2 c&s); 98-112mm SL. *S. latifrons*; CAS 36624; Pacific Ocean, Baja California, Mexico; 2 (1 c&s); 27 Apr. 1976; 110.8-118 mm SL.

Results: Branch and bound and heuristic searches resulted in one most parsimonious tree with 49 steps, consistency index (CI) =0.76, retention index (RI) = 0.85, and 22 of 29 characters with CI=1, Fig. 2.1

The clade *Cyclopsetta-Syacium* is monophyletic (bootstrap value 85%), based on six synapomorphies: scaled snout (3), spinulate gill rakers (22), five haemal parapophyses (26), 5-11 prolonged dorsal fin rays at the crest of head in larvae (27), large preopercular spines in larvae (28) and 3-6 prolonged rays of the left pelvic fin in larvae (29).

Cyclopsetta is monophyletic (bootstrap value 100%), with eleven synapomorphies: convex interorbital except in *C. querna* where the character reverts to concave (8); eyes not exceeding posterior end of maxillary (10); no notch in front of upper eye (12); dorsal fin commencing between blind side nostrils or anterior to this location (13); presence of three dark lappets along the opercular opening (14); presence of ocelli on the dorsal and anal fins (17); cycloid scales except in *C. panamensis* where the scales revert to ctenoid (18); a triangle-like lachrymal (19); subopercular process tear drop shaped (20); metapterygoid overlapped with the quadrate (21), and 72-103 lateral line scales (25).

Cyclopsetta is divided into two new subgenera: *Cyclopsetta* and *Azevia*. *Cyclopsetta* (subg. nov.) (bootstrap value 58%) has two synapomorphies, presence of a flap of skin on

the ventral side of lower jaw (11), and dorsal fin commencing on top of or advanced relative to anterior blind side nostril (13). *Cyclopsetta* (subg. nov.) gave rise to *C. fimbriata* with anterior nostril at the same level as posterior (5) and *C. chittendeni* with anterior nostril slightly dorsal to posterior, Fig. 2.1.

The second subgenus, *Azevia* (subgen. nov.) (bootstrap 51%), has two synapomorphies: caudal vertebrae in the range 28-31 (23), pectoral fin rays in the range 14-18 (24). *Azevia* (subg. nov.) gave rise to *C. panamensis* and *C. querna*. *Cyclopsetta panamensis* has three apomorphies: anterior nostril at the level of the posterior (5); flap of skin on the posterior angle of the lower jaw (11); and ctenoid scales (18), a reversal. *C. querna* has three apomorphies: scaled interorbital (6), a reversal, concave interorbital (8), a reversal, and upper eye slightly advanced relative to lower eye (9).

The monophyly of *Syacium* is supported by five synapomorphies (bootstrap value 70%): rows of teeth on the upper jaw revert from one to two (1), papillae present along entire lips (2), dark bars on pectoral fin (16), short stout and posteriorly spinulate gill rakers (22) and all rays of the left pelvic fin being elongated in larvae (29).

The cladogram suggests that the ancestor to *Syacium* branched into *S. longidorsale*, with a naked interorbital space, and the ancestor to the remaining species with the interorbital space reverting to scaled (6). This ancestor in turn gave rise to *S. ovale*, with eyes at the same level, and the ancestor to the remaining six species with two synapomorphies: lower eye in advance of the upper (9), a reversal, and flap of skin on the ocular side lower jaw either only on posterior angle or beyond (11). Next, this ancestor branched into *S. gunteri* with no elongation of the pectoral fin rays and the ancestor to the remaining five species with elongated and filamentous rays of the pectoral fin (15). Subsequently, this ancestor gave rise to *S. maculiferum*, and the ancestor to the next four species with a flap of skin on

lower jaw restricted to posterior angle (11) except for *S. latifrons* where this character is reversed to none. The remaining four species are grouped in a trichotomy of *S. guineensis*, *S. micrurum* and two sister species *S. latifrons* and *S. papillosum*. These sister species have two synapomorphies: one or two dark lines from upper eye to tip of snout in mature males (4) and a wide interorbital space in mature males (7).

Discussion: *Cyclopsetta* and *Syacium* were monophyletic when either *Citharichthys* or *Etropus* was included in the ingroup. This result confirmed the pairing of *Cyclopsetta* and *Syacium* as close genera based on larval characters by Ahlstrom et al. (1984). In addition, the phylogenetic analysis confirmed the monophyly of *Cyclopsetta* based on the shape of gill rakers (Chapter 1). *Syacium* was monophyletic; this result further supported the taxonomic study by Murakami and Amaoka (1992) who did not specifically mention that *Syacium* was monophyletic.

The cladogram suggests that the ancestor of *Cyclopsetta* was distributed on the Atlantic and Pacific sides of North and South America before the formation of the landbridge which connected the two continents. When the landbridge formed in the late Pliocene, 5.2 million years ago (Briggs 1974), it separated the populations on the Atlantic side from those on the Pacific side. Speciation followed giving rise to two species on each side of the landbridge; *C. chittendeni* and *C. fimbriata* on the Atlantic side and *C. querna* and *C. panamensis* on the Pacific side.

With respect to *Syacium*, although weakly supported, the cladogram suggests that speciation may have occurred on the Atlantic and Pacific coasts of the Americas before the formation of the landbridge. After the landbridge appeared, four species survived on the Pacific side and three on the Atlantic. In addition, the larvae of the ancestor may have been

transported with ocean currents to the West African coast of the Sahara where it gave rise to *S. guineensis*.

Repeating the analysis using DNA characters is needed to further test the speciation patterns observed in this study and to resolve the trichotomy within *Syacium*.

Classification: The results of this study indicate that *Cyclopsetta* is monophyletic and is divided into two subgenera *Cyclopsetta* and *Azevia*. *Syacium* comprised eight species (Murakami and Amaoka 1992) and is also monophyletic.

Taxonomic list of *Cyclopsetta* and *Syacium*: an asterisk indicates that the ordering for the species is not clear; *S. latifrons* and *S. papillosum* are sister species.

Genus *Cyclopsetta*

Cyclopsetta (subg. nov.)

C. chittendeni

C. fimbriata

Azevia (subg. nov.)

C. panamensis

C. querna

Genus *Syacium*

S. longidorsale

S. ovale

S. gunteri

S. maculiferum

*S. latifrons**

*S. papillosum**

*S. micrurum**

*S. guineensis**

Acknowledgments: We thank the following people for loan of specimens and permission to clear and stain some of them: Susan L. Jewett (USNM), Sylvie Laframboise Canadian Museum of Nature (CMN), David Catania (CAS). William Bussing (UCR) donated 3 specimens of *Syacium maculiferum* to the Canadian Museum of Nature; Jennifer Scott (CMN) helped with the figures. This work was supported by an operating grant to François Chapleau by the National Sciences and Engineering Research Council of Canada.

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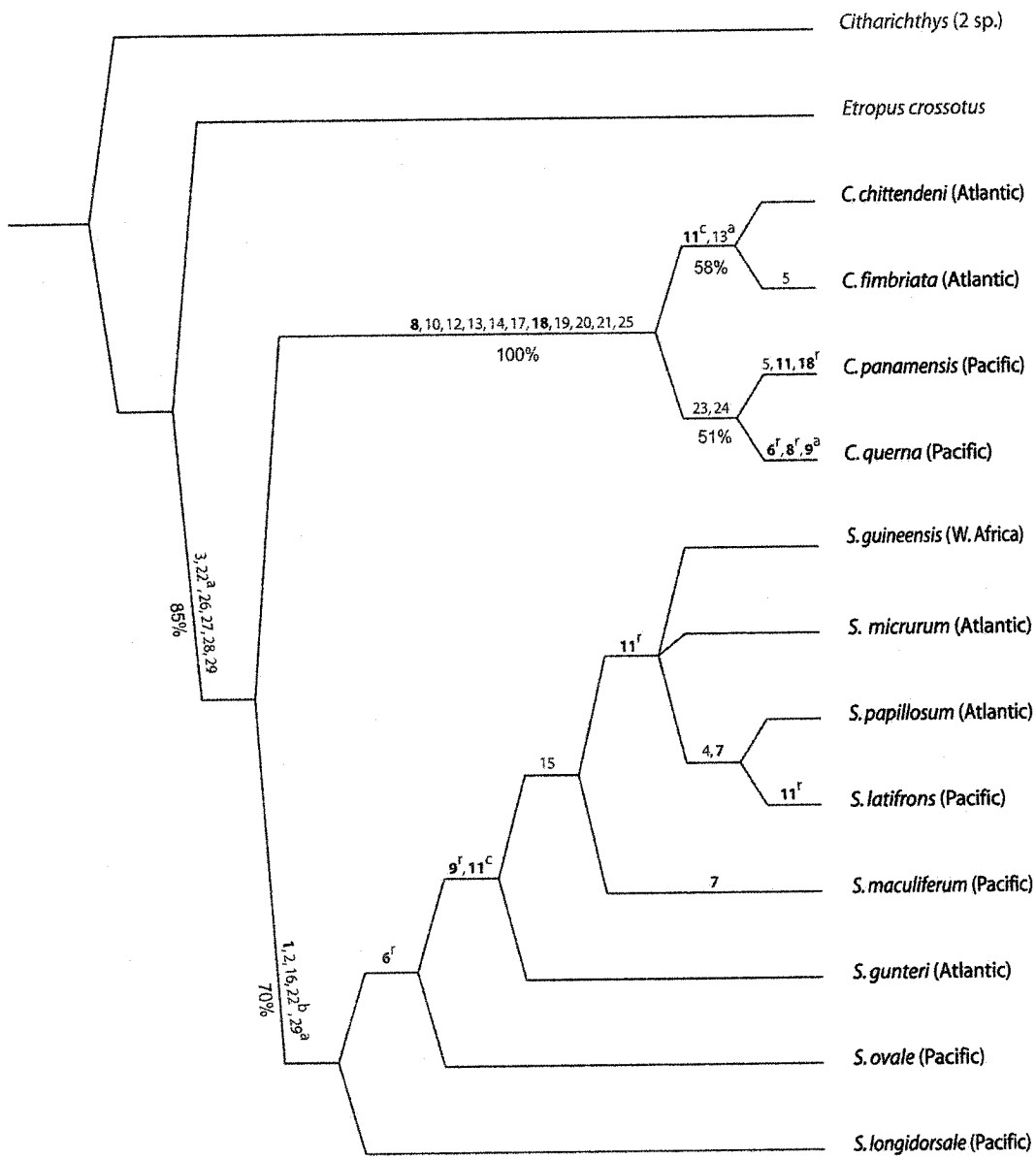


Fig. 2.1 : Cladogram from an analysis of 29 characters for 12 ingroup species of *Cyclopsetta* and *Syacium* and three outgroup species of *Citharichthys* and *Etropus*. Character change is 0→1 except: a: 1→2, b: 2→3, c: 0→2, bold: homoplasy, r: reversal 1→0 except reversal in character 11: 2→1. Bootstrap values are shown as percentages.

Table 2.1: Character states of *Cyclopsetta* and *Syacium* species; *Citharichthys* (*C. gilberti* and *C. stigmaeus*) and *Etropus crossotus* are outgroups. Question mark (?) is unknown or uninformative state. List of characters is in Appendix.

Taxon	Character		
	1-10	11-20	21-29
<i>Citharichthys</i>	0 (0,2) 00010110	0(0,1)(0,1)0000000	00 (0,1) 000000
<i>Etropus crossotus</i>	1 0 0 0 0 0 0 0 0 2	0 0 0 0 0 0 0 0 0 ??	? 1 0 0 0 0 0 0 0
<i>Cyclopsetta chittendeni</i>	1 0 1 0 0 ? 0 1 1 1	2 1 2 1 0 0 1 1 1 1	1 2 0 ? 1 1 1 1 1
<i>C. fimbriata</i>	1 0 1 0 1 1 0 1 1 1	2 1 2 1 0 0 1 0 1 1	1 2 0 0 1 1 1 1 1
<i>C. panamensis</i>	1 0 1 0 1 1 0 1 1 1	1 1 1 1 0 0 1 0 1 1	1 2 1 1 1 1 ? 1 1
<i>C. querna</i>	1 0 1 0 0 0 0 0 2 1	0 1 1 1 0 0 1 1 1 1	1 2 1 1 1 1 1 1 1
<i>Syacium guineensis</i>	0 1 1 0 0 0 0 0 0 0	1 0 0 0 1 1 0 0 0 0	0 3 0 0 0 1 1 1 2
<i>S. gunteri</i>	0 1 1 0 0 0 1 0 0 0	2 0 0 0 0 1 0 0 0 0	0 3 0 0 0 1 1 1 2
<i>S. latifrons</i>	0 1 1 1 0 0 1 0 0 0	0 0 0 0 1 1 0 0 0 0	0 3 0 0 0 1 ? 1 2
<i>S. longidorsale</i>	0 1 1 0 0 1 0 0 1 0	0 0 0 0 0 ? 0 0 0 0	0 3 0 0 0 1 ? 1 2
<i>S. maculiferum</i>	0 1 1 0 0 0 0 0 0 0	2 0 0 0 1 1 0 0 0 0	0 3 0 0 0 1 ? 1 2
<i>S. micrurum</i>	0 1 1 0 0 0 0 0 0 0	1 0 0 0 1 1 0 0 0 0	0 3 0 0 0 1 1 1 2
<i>S. ovale</i>	0 1 1 0 0 0 0 0 1 0	0 0 0 0 0 1 0 0 0 0	0 3 0 0 0 1 1 1 2
<i>S. papillosum</i>	0 1 1 1 0 0 1 0 0 0	1 0 0 0 1 1 0 0 0 0	0 3 0 0 0 1 1 1 2

Appendix 2.1

List of characters:

Character 1 (CI=0.5; RI=0.75); rows of teeth series on upper jaw: two rows (state 0), 1 row (state 1).

Character 2 (CI=1.00; RI=1.00); lip papillae: absent (state 0), present along entire lips (state 1), present only along front of lips (state 2).

Character 3 (CI=1.00; RI=1.00); scales on snout: absent (state 0), present (state 1).

Character 4 (CI=1.00; RI= 1.00); one or two dark lines from upper eye to tip of snout in mature males: absent (state 0); present (state 1).

Character 5 (CI=0.5; RI=0.00); position of anterior nostril relative to posterior: dorsal (state 0), same level (state 1).

Character 6 (CI=0.33; RI=0.33); scales in interorbital space: present (state 0), absent (state 1).

Character 7 (CI=0.5; RI=0.5); width of interorbital in mature males relative to females: similar width (state 0), much wider in males (state 1).

Character 8 (CI=0.33; RI=0.33); shape of interorbital bone: concave (state 0), convex (state 1).

Character 9 (CI=0.67 ; RI=0.80); upper eye position relative to lower eye: lower eye advanced with respect to upper eye (state 0), both eyes at same level (1), upper eye slightly advanced with respect to lower eye (state 2).

Character 10 (CI=1.00; RI=1.00); lower eye position relative to maxillary: posterior margin of lower eye extending beyond maxillary (state 0), lower eye not exceeding maxillary (state 1), all of lower eye exceeds maxillary (state 2).

Character 11 (CI=0.4; RI=0.5); flap of skin on ventral side of lower jaw: absent (state 0), present only on posterior angle (state 1), present beyond posterior angle (state 2).

Character 12 (CI=1.00; RI=1.00); notch in front of upper eye: present (state 0), absent (state 1).

Character 13 (CI= 1.00; RI=1.00); position of first dorsal ray with respect to blind side nostrils: behind posterior nostril (state 0), between nostrils (state 1), above or advanced relative to anterior nostril (state 2).

Character 14 (CI=1.00; RI=1.00); lappets along opercular margin: not present but replaced by a continuous ribbon-like flap on skin (state 0), 3 distinct lappets (state 1).

Character 15 (CI=1.00; RI=1.00); first one or two pectoral fin rays extended and filamentous: absent (state 0), present (state 1).

Character 16 (CI=1.00; RI=1.00); dark bars on pectoral fin rays: absent (state 0), present (state 1).

Character 17 (CI=1.00; RI=1.00); ocelli on dorsal and anal fins: absent (state 0); present (state 1).

Character 18 (CI=0.50; RI=0.00); type of scales: ctenoid (state 0), cycloid (state 1).

Character 19 (CI=1.00; RI=1.00); shape of lachrymal: elongated (state 0, Fig2.2b and c), triangle-like (state 1, Fig2.2a).

Character 20 (CI=1.00; RI=1.00); shape of suboperculum process: straight (state 0, Fig2.3b and c), inverted tear drop (state 1, Fig2.3a).

Character 21 (CI=1.00; RI=1.00); quadrate overlap with metapterygoid: absent (state 0, Fig. 2.4b and c), present (state 1, Fig. 2.4a).

Character 22 (CI=1.00; RI=1.00); shape of gill rakers on first gill arch (Fig. 1.2 Chapter 1): long and slender (state 0, Fig. 1.2d), short and stout (state 1, Fig. 1.2c), short broad and spinulate posteriorly (state 2, Fig. 1.2a), short stout and serrated posteriorly (state 3, Fig. 1.2b).

Character 23 (CI=1.00; RI=1.00); caudal vertebrae: 24-27 (state 0), 28-31 (state 1).

Character 24 (CI=1.00; RI=1.00); Pectoral fin rays: 10-13 (state 0), 14-18 (state 1).

Character 25 (CI=1.00; RI=1.00); number of lateral line scales: 40-69 (state 0), 72-103 (state 1).

Character 26 (CI=1.00; RI=1.00); number of abdominal vertebrae with haemal parapophyses: six (state 0), five (state 1).

Character 27 (CI=1.00; RI=1.00); number of dorsal fin rays on crest of head in larvae: 0-3 (state 0), 5-11 (state 1).

Character 28 (CI=1.00; RI=1.00); preopercular spines in larvae: small (state 0), large (state 1).

Character 29 (CI=1.00; RI=1.00); elongated fin rays of left pelvic fin in larvae: 0-2 (state 0), three (state 1), all six (state 2).

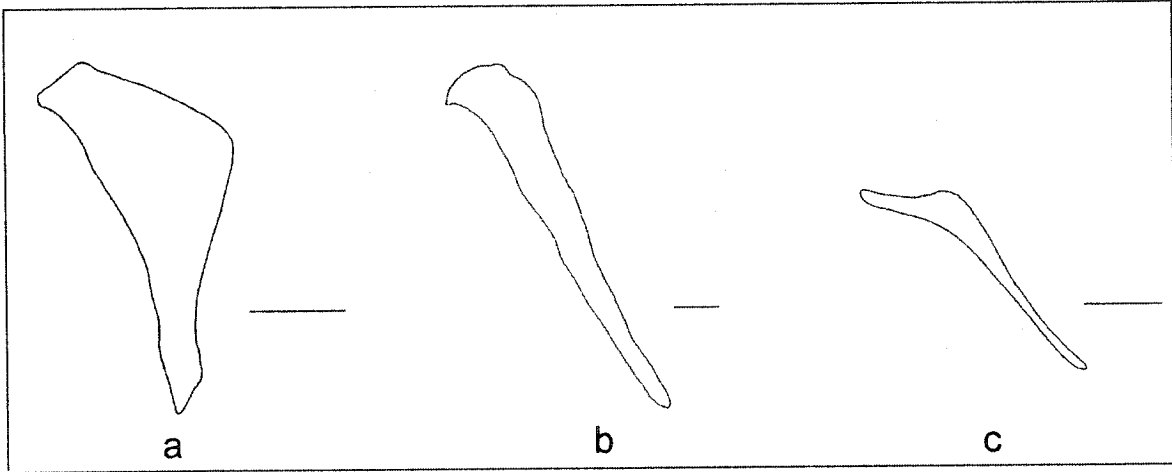


Fig. 2.2: Lachrymal on ocular side; a: *Cyclopsetta chittendeni*, AMNH 81153 (118 mm SL); b: *Syacium micrurum*, USNM 266482 (190.5 mm SL); c: *Citharichthys stigmaeus*, NMC 74-216 (80 mm SL). Scale bars are 1 mm.

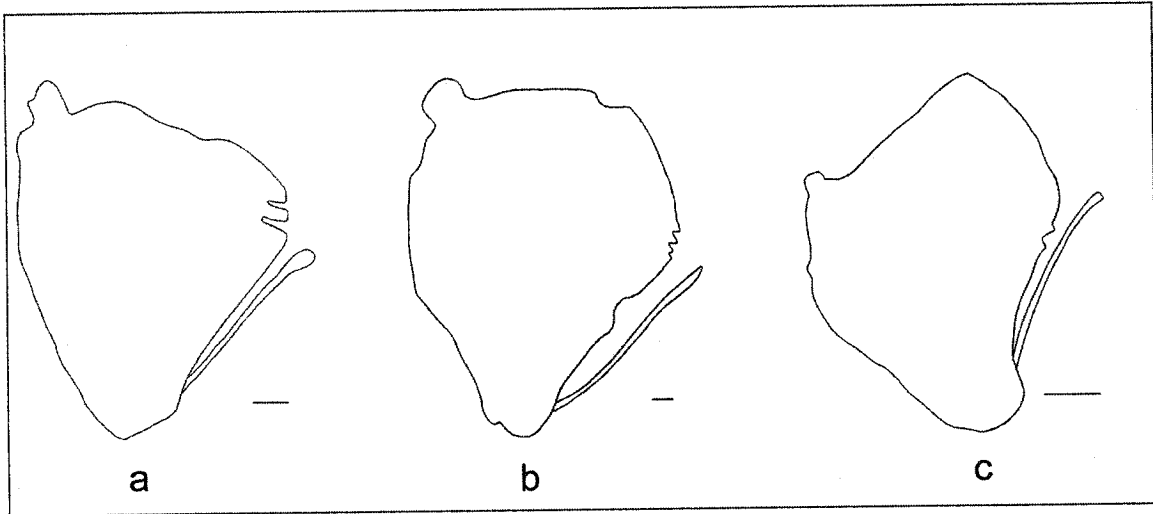


Fig. 2.3: Suboperculum on ocular side; a: *Cyclopsetta panamensis*, USNM 220796 (110 mm SL); b: *Syacium micrurum*, USNM 266482 (mm 190.5 SL); c: *Citharichthys stigmaeus*, NMC 74-216 (80 mm SL). Scale bars are 1 mm.

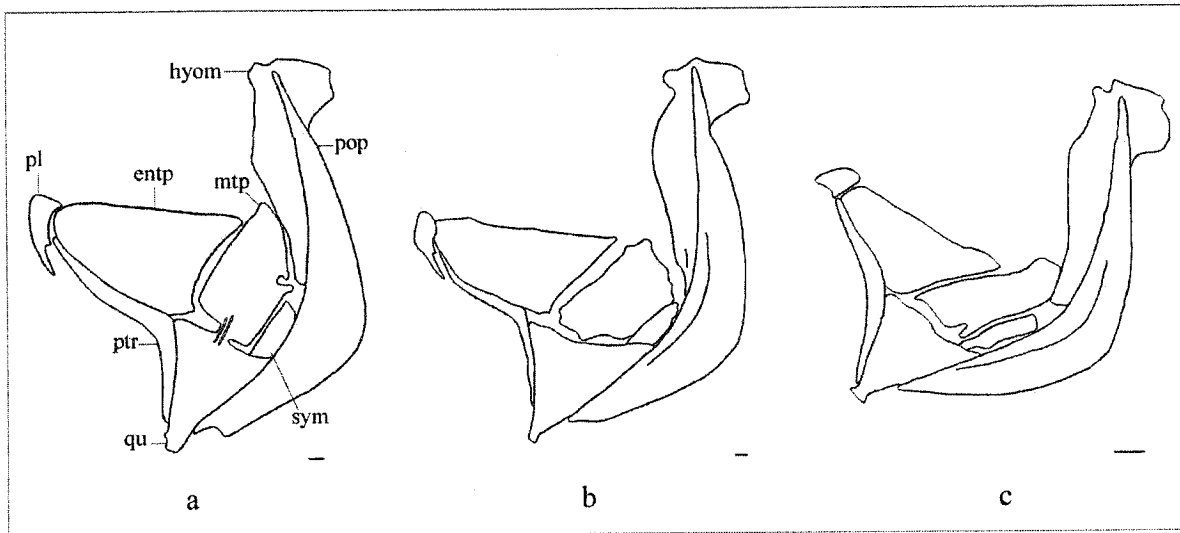


Fig. 2.4: Suspensorium on ocular side; a: *Cyclopsetta chittendeni*, AMNH 81153 (118 mm SL); b: *Syacium micrurum*, USNM 266482 (190.5 mm SL); c: *Citharichthys stigmaeus*, NMC 74-216 (80 mm SL). Acronyms: entp: entopterygoid; hyom: hyomandibular; mtp: metapterygoid; pl: palatine; pop: preopercle; ptr: pterygoid; qu: quadrate; sym: symplectic. Scale bars are 1 mm.

General Conclusion

In Chapter 1, the taxonomic review of the flatfish genus *Cyclopsetta* confirmed the previous review by Norman (1934), based on 13 specimens only, that *C. chittendeni*, *C. fimbriata*, *C. panamensis* and *C. querna* are valid species in this genus. Moreover, this study agreed with the subsequent transfer of *C. maculifera* to *Syacium maculiferum* by Murakami and Amaoka (1992); accepted two synonymies, that of *Cyclopsetta decussata* with *C. chittendeni* by Swingle (1971) and that of *Dorsopsetta norma* with *Cyclopsetta querna* by van der Heiden and Mussot-Pérez (1993).

No new taxonomic changes resulted from this review; nonetheless, this review was needed since the previous studies were based on very small sample sizes. The thorough examination of 180 specimens of *Cyclopsetta*, including type material for all four recognised species, now puts the taxonomy of this genus on much firmer ground.

Additionally, a new key using novel characters (number of caudal vertebrae, number of ocular side pectoral fin rays, position of ocular side nostrils relative to each other, length of flap of skin bordering ocular side lower jaw, position of first dorsal fin ray relative to blind side nostrils, presence of dark band on ocular side pectoral fin, presence of papilla on one or both eyes) improves our ability to correctly identify these fishes.

Moreover, this thesis proposes an explanation, related to the timing of oceanographic currents and spawning, for the distribution of two of the species. In fall and winter, the Gulf Stream circulates near the centre of the Gulf of Mexico, away from the continental shelf (Briggs 1974), and therefore, would not carry the newly-hatched larvae of *C. chittendeni* towards Atlantic Florida. In spring and summer, however, the Gulf Stream circulates near the continental shelf (Briggs 1974) and would probably carry the newly-

hatched larvae of *C. fimbriata* to the Atlantic Ocean and hence, explains the presence of this species along the eastern shores of the United States.

In Chapter 2, the phylogenetic analysis of two genera *Cyclopsetta* and *Syacium* confirmed the monophyly of each genus and clarified interspecific relationships within *Cyclopsetta*. More data are needed, however, to clarify the interspecific relationships within *Syacium* with sufficient confidence. This study has contributed to elucidating the relationships within the Pleuronectiformes at the species level and would serve as a basis for further such phylogenetic studies.

In conclusion, four valid species of *Cyclopsetta* were recognised and two synonymies accepted: *C. chittendeni*, *C. fimbriata*, *C. panamensis* and *C. querna*; *C. decussata* was a junior synonym of *C. chittendeni* and *Dorsopsetta norma* a junior synonym of *C. querna*. The cladistic analysis of *Cyclopsetta* and *Syacium* showed that each of *Cyclopsetta* and *Syacium* was strongly supported as monophyletic. *Cyclopsetta* was further divided into two subgenera, *Cyclopsetta* comprising *C. chittendeni* and *C. fimbriata* and *Azevia* comprising *C. panamensis* and *C. querna*.

Syacium longidorsale was the first species to branch off the ancestor followed subsequently by *S. ovale*, *S. gunteri* and *S. maculiferum*. *S. latifrons* and *S. papillosum* were sister species grouped with *S. guineensis* and *S. micrurum* in an unresolved trichotomy.

Finally, this is the first cladistic study contributing to our knowledge of relationships within the Paralichthyidae, an ill-defined flatfish group which includes important commercial species. Moreover, *Cyclopsetta*, *Syacium*, *Citharichthys*, and *Etropus*, have been proposed as a monophyletic group within Paralichthyidae (Hensley and Ahlstrom 1984), however the relationships between *Cyclopsetta* and *Syacium* and the other two genera have not been

established. To undertake this, taxonomic reviews of *Citharichthys* and *Etropus* have to be done first.