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René Duplain
AUTEUR DE LA THÈSE / AUTHOR OF THESIS

M.Sc. (Biology)
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FACULTÉ, ÉCOLE, DÉPARTEMENT / FACULTY, SCHOOL, DEPARTMENT

Taxonomic Revision and Phylogenetic Analysis of the Flatfish Genus *Trinectes)Pleuronectiformes : Achiridae)*

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

EXAMINATEURS (EXAMINATRICES) DE LA THÈSE / THESIS EXAMINERS

Christiane Charest

Julian Starr

Jeff Skevington

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

Taxonomic revision and phylogenetic analysis of the flatfish genus *Trinectes* (Pleuronectiformes: Achiridae)

René R. Duplain

Thesis submitted to the Faculty of Graduate and Postdoctoral Studies

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ABSTRACT

The taxonomic status of the 16 nominal species of the genus *Trinectes* (Pleuronectiformes: Achiridae) Rafinesque 1832 was revised based on a morphological study of 647 type and non-type specimens. Nine species were recognized as valid. *Trinectes inscriptus*, *T. maculatus*, *T. microphthalmus*, and *T. paulistanus* are found in the Atlantic Ocean, from the Northern United States to Southern Brazil, whereas *T. fimbriatus*, *T. fluviatilis*, *T. fonsecensis*, *T. opercularis*, and *T. xanthurus* are found in the Pacific Ocean, from Mexico to Peru. An identification key to species is provided. The phylogenetic relationships of the species recognized were hypothesized based on a cladistic analysis of 22 morphological, meristic, and osteological characters. The analysis resulted in one most parsimonious tree with a length of 39 steps (CI = 0.69; RI = 0.79). The tree showed that *Trinectes* is monophyletic on the basis of two synapomorphies: an unpierced interbranchial septum, and seven to nine pterygiophores anterior to the neural spine of the third precaudal vertebra. *Trinectes inscriptus* is the most plesiomorphic species of the genus, and all other species form a monophyletic group subdivided into two clades. The first contains (from most plesiomorphic to recent): *T. paulistanus*, *T. fonsecensis*, and the *T. fluviatilis*-*T. xanthurus* clade. The second clade includes (from most plesiomorphic to recent): *T. maculatus*, *T. opercularis*, and the *T. fimbriatus*-*T. microphthalmus* clade. The resulting cladogram depicts a sequence of speciation events and provides an opportunity to propose a biogeographical hypothesis on the evolution of *Trinectes*.

RÉSUMÉ

Le statut taxinomique des 16 espèces nominales appartenant au genre *Trinectes* Rafinesque 1832 a été examiné grâce à une étude morphologique de plus de 647 spécimens types et non-types. Neuf espèces ont été établies comme étant valides. *Trinectes inscriptus*, *T. maculatus*, *T. microphthalmus*, et *T. paulistanus* sont réparties dans l'Océan Atlantique, du nord des États-Unis jusqu'au sud du Brésil, tandis que *T. fimbriatus*, *T. fluviatilis*, *T. fonsecensis*, *T. opercularis*, et *T. xanthurus* sont distribuées dans l'Océan Pacifique, du golfe de Californie au Pérou. Une clé d'identification des espèces de *Trinectes* est présentée. Les relations phylogénétiques des espèces reconnues du genre ont été déterminées grâce à une analyse cladistique de 22 caractères morphologiques, méristiques, et ostéologiques. L'analyse a permis de découvrir un seul arbre entièrement résolu et parcimonieux avec 39 transformations de caractères (IC = 0.69; IR = 0.79). La monophylie de *Trinectes* est fondée sur deux synapomorphies : un septum interbranchial entier, et sept à neuf ptérygiophores de la nageoire dorsale antérieurs à l'épine neurale de la deuxième vertèbre pré-caudale. Les résultats indiquent que *T. inscriptus* est la plus plésiomorphique espèce du genre, les autres espèces formant un groupe monophylétique subdivisé en deux clades. Le premier clade (en ordre d'ancienneté) contient *T. paulistanus, T. fonsecensis*, ainsi que le clade *T. fluviatilis-T. xanthurus*. Le deuxième clade contient *T. maculatus, T. opercularis* et le clade *T. fimbriatus-T. microphthalmus*. Le cladogramme démontre une séquence de spéciation qui se prête à l'élaboration d'une hypothèse biogéographique sur l'évolution de *Trinectes*.

GENERAL INTRODUCTION

Order Pleuronectiformes (Flatfishes)

The order Pleuronectiformes, collectively known as flatfishes, was first named by Carl Linnaeus in *Systema Naturae* (Linnaeus 1758). Flatfishes, which include such popular commercial fishes as plaice (four species: *Pleuronectes quadrituberculatus*, *Hippoglossoides platessoides*, *Pleuronectes platessa*, and *Acanthopsetta nadeshnyi*), sole (family Soleidae), turbot (family Scophthalmidae), flounder (five species: *Paralichthys dentatus*, *Paralichthys lethostigma*, *Pseudopleuronectes americanus*, *Platichthys flesus*, and *Paralichthys olivaceus*), and halibut (family Pleuronectidae), are characterized by their adult asymmetry, in which both eyes are on the same side of the head. This is the result of eye migration, a process that leads to the "most remarkable asymmetrical development seen in any vertebrate" (Okada *et al.* 2001:59). Swimming (nectos) on their side (pleuro), flatfishes have an "eyed-side" (side with both eyes) which faces upwards and a "blind-side" (side without eyes), which typically faces the substrate. Linnaeus (1758) described 18 pleuronectid species under the genus *Pleuronectes* (Linneaus 1758). After Linnaeus, flatfishes have been studied by a multitude of taxonomists, naturalists, and curious minds alike. However, it was not until the late 19th century that the Pleuronectiformes were more thoroughly studied. This heightened interest was prompted by the increase in awareness of the impact of commercial fisheries on local fish populations (Munroe 2005).

Flatfishes have been featured in the human diet for millennia, and still represent a large proportion of the world's current groundfish catch (Gibson 2005). Globally, they remain an economically important group, representing 2.7 % of the global fisheries income in 2003 (Food and Agriculture Organization 2004). In Canada, flatfishes have also played an important role in commercial fisheries, making up 25 % of the total catch weight, excluding hake (families Gadidae and Merlucciidae), in the temperate Pacific Ocean (Wilderbuer *et al.* 2005). In 2003, Canadian fisheries of flatfishes generated 37% of the revenues for bottom-dwelling fishes, translating to 23 % of the revenues of all Canadian fisheries.

Despite their economic importance, the systematics of the Pleuronectiformes remains largely unresolved (Desoutter *et al.* 2001). Cuvier (1816) was the first to find morphological differences in the species described by Linnaeus and subdivided the large genus *Pleuronectes* into multiple genera. The first comprehensive revision of Pleuronectiformes was conducted by Jordan & Goss (1889), who proposed that the order consisted of a single family, seven subfamilies, and multiple subgenera. Regan (1910) followed with a morphological classification of Pleuronectiformes, which was then known as Heterostomata. Norman (1934) did a taxonomic review and provided a key to flatfish species (excluding families Soleidae, Achiridae and Cynoglossidae).

For many years, the combined works of Regan (1929), Hubbs (1945), and Norman (1934; 1966) formed the basis of recognized patterns of flatfish evolution, commonly referred to as the 'Regan-Norman model' (Hensley 1997). Ahlstrom *et al.* (1984) proposed three suborders within the order: the Psettoidei, the Pleuronectoidei, and the Soleoidei. However, Chapleau & Keast (1988) later determined that the suborder Soleoidei should be included in the Pleuronectoidei to render it a natural monophyletic group. *Tephrinectes*, a genus whose position was recently worked on by Hoshino & Amaoka (1998) and later by Hoshino (2001), was found to be basal within the Pleuronectoidei (following that of the Citharidae), and proposed that this taxon was the sister group to the other pleuronectoids (Munroe 2005). The order currently has 14 recognized families, with *Tephrinectes* representing a distinct lineage (Hoshino 2001; Munroe 2005).

Although pleuronectiforms were believed to be a natural group for many years (Regan 1910; Norman 1934; Hubbs 1945), Chapleau (1993) was the first to conduct a cladistic analysis of the order and to establish their monophyletic status. According to Chapleau (1993), their monophyly was based on the following three synapomorphies: (1) a dorsal fin continuous with the head; (2) an asymmetrical development of the cranium in which one eye migrates to the opposite side of the head, resulting in adult asymmetry; and (3) presence of a *recessus orbitalis*, a muscle which allows flatfishes to protrude their eyes (Chapleau 1993). Previously, sidedness (eye positioning) had been used as an important character in the classification of Pleuronectiformes (Berendzen & Dimmick 2002). As a result of his cladistic analysis, Chapleau (1993) suggested that classifying flatfishes based on their sidedness is "phylogenetically misleading" as it has been derived multiple times within the group. Other morphological (Hoshino 2001) and molecular (Berendzen & Dimmick 2002) studies have supported the monophyly of Pleuronectiformes as well as the conclusion that sidedness is not phylogenetically relevant. Flatfishes are currently considered part of the Percomorpha (*sensu* Johnson & Patterson 1993), though the sister group to the Pleuronectiformes remains unknown (Berendzen & Dimmick 2002).

A recent study by Friedman (2008) showed, through fossilized evidence, that the fossil genus *Amphistium* Friedman 2008 and the new fossil genus *Heteronectes* Friedman 2008 might be the most basal pleuronectiforms known (from the Eocene epoch, approximately 34–55 million years ago). These now extinct fishes show many primitive characteristics of modern flatfishes (Friedman 2008). Most notable was the incomplete eye migration, suggesting that the evolution of the pleuronectiforms' curious asymmetry was gradual in nature (Friedman 2008). Prior to this discovery, intermediate forms between pleuronectiforms and their symmetrical relatives were unknown (Chanet 1997; Chanet 1999). This lack of transitional species had long been a source of interest and controversy in evolutionary biology (e.g. Darwin 1872; Wallace 1889; Goldschmidt 1933; Goldschmidt 1940; von Wahlert 1965).

As larvae, flatfishes are bilaterally symmetrical and exhibit a pelagic lifestyle. After several months (depending on the species), they undergo a metamorphosis in which many drastic changes occur. Some of these changes include: their bodies become laterally compressed or flattened; one eye migrates to the opposite side of the head; several osteological features become modified; and they undertake a benthic lifestyle (Munroe 2005). Adult flatfishes, defined as post-metamorphic individuals, are asymmetric organisms due to several characters besides the position of their eyes. Examples of this asymmetry include the loss or reduction of several blind-side structures such as their pelvic and pectoral fins, their more prominent eyed-side pigmentation, and their asymmetrical mouths (Munroe 2005). Many flatfish not only have a more distinctly pigmented eyed-side than blind-side, which is often devoid of pigment, but also have the ability to change their eyed-side pigmentation (colour and pattern) to match that of their environment (Gibson 2005).

Adults range in size from a few centimeters to over two meters. Occurring predominantly in marine or brackish water, flatfishes inhabit all the world's oceans with a few species occurring in freshwater (Nelson 1994). Many flatfishes have wide distributions, and they often occur in depths ranging from the intertidal zone to the continental slope (Gibson 2005).

Of the 1339 nominal species of flatfishes that have been named, approximately 716 species are considered valid (Munroe 2005). The valid species within the order are divided among 123 genera (Munroe 2005). This high number of species and genera places flatfishes as the third most diverse order of primarily marine euteleostean fishes in the world (Munroe 2005).

Family Achiridae (American Sole)

Family Achiridae currently includes the following six recognized genera: *Hypoclinemus* Chabanaud 1928, *Catathyridium* Chabanaud 1928, *Achirus* Lacepède 1802, *Trinectes* Rafinesque 1832, *Gymnachirus* Kaup 1858, and *Apionichthys* Kaup 1858. These genera contain approximately 31 species, making this a small, but diverse family of dextral flatfish (Munroe 2005). Generally small-bodied fishes, Achirids are restricted to both American continents (amphi-american) (Ramos 2003b), which explains their common name, the "American Soles." They primarily occur in coastal waters, but often inhabit estuaries and freshwater. Although achirids have no significant commercial value, some species regularly feature in artisanal and subsistence fisheries in Central and South America and others contribute to by-catch in shrimp fisheries (Munroe 2005).

Paul Chabanaud worked extensively on the Achiridae, then known as the sub-family Achirinae (e.g. Chabanaud 1928; 1930; 1935a; 1935b; 1939). In an initial study, Chabanaud (1928) reviewed the Achirinae in which he included nine genera (with two new genera, *Hypoclinemus* and *Nodogymnus*), two new subgenera of the genus *Baeostoma* (also known as *Baiostoma* Bean 1882) (*Anathyridium* and *Catathyrdium*), and 17 species (with four new species; *Achirus austrinus*, *A. microphthalmus*, *Baeostoma (Catathyridium) grandirivi*, and *Hypoclinemus paraguayensis*). Chabanaud (1928:7) defined Achirinae in a key of the achirid genera as having the following characteristics (translated from French): right (eyed-side) pelvic fin continuous with the anal fin; presence of a number of "achirid lines" (=transverse bands) of varying number and thickness on their eyed-side body; no external membrane connecting their operculo-mandibular region to the urohyal or cleithrum; confluent opercular slits at the pelvic region; and the presence of teeth and scales. Norman (1934) later distinguished achirids in an identification key as having a continuous right pelvic fin with the anal fin, as well as a dorsal and anal fin separate from the caudal fin.

The family Soleidae, which contained subfamilies Achirinae and Soleinae, was placed in the suborder Soleodei in 1984 (Ahlstrom *et al.* 1984). Three years later, Chapleau & Keast (1987) conducted a cladistic analysis that revealed that the subfamilies, but not the family, were monophyletic. Both subfamilies were therefore raised to the family level; Achirinae became Achiridae, and Soleinae became Soleidae (*sensu novo*). Additionally, Chapleau & Keast (1987) suggested that the suborder Soleodei should be eliminated and the now three families (Achiridae, Soleidae, and Cynoglossidae) within the suborder be incorporated into the Pleuronectoidei, which would then become monophyletic. Chapleau & Keast (1987) defined the monophyletic status of family Achiridae on the basis of five autapomorphies (see Chapter 2 for more details). Recent morphological (Ramos 1998) and molecular (Azevedo *et al.* 2008) studies of the family have supported the monophyletic status of Achiridae proposed by Chapleau & Keast (1987).

In 1998, Ramos conducted the first extensive phylogenetic study of Achiridae. He found that freshwater species of both the genera *Hypoclinemus* and *Catathyridium* were the most plesiomorphic of the family (Ramos 1998). This led the author to suggest that this family may have had a freshwater origin. Azevedo *et al.* (2008) conducted a molecular phylogenetic analysis of Pleuronectiformes, including four achirid genera represented by five species. They tested to see how molecular evidence, based on sequences of 12S and 16S mitochondrial genes, compared to the morphological results obtained by Ramos (1998). Although Azevedo *et al.*

(2008) admitted they did not have enough representatives to accurately resolve the origin of achirids, they hypothesized that the most parsimonious explanation would favour a saltwater origin. They explained that since the sister families of Achiridae (i.e. Soleidae and Cynoglissidae) are exclusively marine groups, the achirid genera *Hypoclinemus* and *Catathyridium* likely "derived directly and independently" from saltwater ancestors (Azevedo *et al.* 2008:290). The origin of family Achiridae (i.e. freshwater or saltwater) remains unresolved and will be explored in Chapter 2.

This thesis will focus primarily on the achirid genus *Trinectes*, which contains 16 nominal (putative) species. The purpose of this thesis is to revise all nominal species within *Trinectes* (Chapter 1) and to determine phylogenetic relationships within the genus (Chapter 2). Results of this study will clarify the taxonomic status and systematics of *Trinectes* and lead to a better understanding of the biogeographical history and speciation pattern within this group and related taxa.

CHAPTER 1

A taxonomic revision of the flatfish genus *Trinectes*

(Pleuronectiformes: Achiridae)

ABSTRACT

The flatfish genus *Trinectes* (Pleuronectiformes: Achiridae) and the taxonomic status of its nominal species are revised based on a morphological study of 647 type and non-type specimens. Of the 16 nominal species examined, only nine are found valid and are re-described. The following species with synonyms in parentheses are recognized as valid: *T. fimbriatus*, *T. fluviatilis*, *T. fonsecensis* (*Solea panamensis*), *T. inscriptus* (*Monochir reticulatus*), *T. maculatus* (*Achirus fasciatus*, *Pleuronectes mollis*, *T. scabra*), *T. microphthalmus*, *T. opercularis*, *T. paulistanus* (*A. affinis*, *A. austrinus*), and *T. xanthurus*. An up-to-date identification key to *Trinectes* species is given.

RÉSUMÉ

Le genre de poisson plat *Trinectes* (Pleuronectiformes: Achiridae) et le statut taxinomique de ses 16 espèces nominales sont éxaminés grâce à une étude morphologique de 647 spécimens types et non-types. Neuf espèces sont valides et sont re-décrites. Les espèces valides et leurs synonymes, montrés entre parenthèses, sont: *T. fimbriatus*, *T. fluviatilis*, *T. fonsecensis* (*Solea panamensis*), *T. inscriptus* (*Monochir reticulatus*), *T. maculatus* (*Achirus fasciatus*, *Pleuronectes mollis*, *T. scabra*), *T. microphthalmus*, *T. opercularis*, *T. paulistanus* (*A. affinis*, *A. austrinus*), et *T. xanthurus*. Une nouvelle clé d'identification des espèces de *Trinectes* est élaborée.

INTRODUCTION

Trinectes Rafinesque (1832) is an amphi-american genus, ranging from Maine (USA) to Southern Brazil in the Atlantic, and from the North of the Gulf of California to Southern Peru in the Pacific. Members of this genus are predominantly shore fishes, occurring on the continental shelf and are often found on muddy or sandy bottoms in estuarine environments. They inhabit warm-temperate to tropical marine water, and commonly penetrate rivers. One species, *T. fluviatilis*, occurs almost exclusively in freshwater (Meek & Hildebrand 1928; Walker & Bollinger 2001).

Trinectes has never been revised. However, several taxonomists have studied the genus and a variety of its nominal species (Jordan & Goss 1889; Jordan 1923; Meek & Hildebrand 1928; Chabanaud 1928, 1930, 1935a, 1939; Myers 1929; Hubbs (1932); Walker & Bollinger 2001). The taxonomic history of nominal species of *Trinectes*, complete with associated authors and current status, is found in Appendix A.

Trinectes was first named and described by Rafinesque (1832) in a Zoological Letter to Cuvier, a colleague at the Musée National d'Histoire Naturelle (MNHN) of Paris. Rafinesque's (1832) letter, dated March 1831, contained the description of *Trinectes scabra* Rafinesque 1832, translated in English in The Atlantic Journal and Friend of Knowledge in 1832. It reads: "I send you, as you request, the figure, description, and a specimen of my *Trinectes scabra*, a new genus of fish near to *Achirus* found in the River Schuylkill; it has only three fins, dorsal, anal and caudal." Though this description is rather short and vague, it is the only known documentation associated with the original description of *Trinectes scabra*. Chabanaud (1930), who worked at the MNHN, found no trace of the original letter containing the original description and figure, or of the type specimen of *T. scabra.* He determined that both items should be considered "*irrémédiablement perdus*" or "irremediably lost" (Chabanaud 1930:260).

Jordan & Goss (1889) determined that *Trinectes* should be synonymized with *Achirus*. Included in their study were the following fourteen species they deemed valid: *A. achirus* (Linnaeus 1758), *A. inscriptus* (Gosse 1851), *A. klunzingeri* (Steindachner 1880), *A. mentalis* (Günther 1862), *A. lineatus* (Linnaeus 1758), *A. mazatlanus* (Steindachner 1869), *A. fonsecensis* (Günther 1862), *A. punctifer* (Castelnau 1855), *A. scutum* (Günther 1862), *A. garmani* Jordan & Goss 1889, *A. fimbratus* (Günther 1862), *A. fasciatus* (Lacepède 1802), *A. panamensis* (Steindachner 1876), and *A. jenynsi* (Günther 1862). Following Lacépède's synonymization of *Pleuronectes achirus* to *P. fasciatus* (Lacépède 1802), Jordan & Goss (1889) assigned *A. fasciatus* as the type species for *Achirus*.

In a later study on the family Achiridae, Jordan (1923) suggested that Lacépède (1802) had been incorrect in his synonymy and proposed that the type designation should stand as *A. achirus* and not *A. fasciatus*. Jordan (1923) no longer recognized *Trinectes* as a synonym of *Achirus* and assigned it as a subgenus within *Achirus*. He grouped members of *Achirus* into the following subgenera: *Achirus*, *Grammichthys*, and *Trinectes*. Jordan (1923:5) defined the subgenus *Achirus* on the basis of the following characteristics: "Pectoral fin present on both sides, that of the left side rudimentary, of a single ray, that of the right side with about 3; scales small; fin rays relatively numerous." He grouped two species in the subgenus *Achirus*: *A. achirus,* and *A. inscriptus.* Jordan (1923:5) defined the subgenus *Grammichthys* on the basis of the following characteristics: "Pectoral of right side only present of one to 6 rays." He grouped the following nine species in the subgenus *Grammichthys*: *A. klunzingeri, A. mentalis, A. lineatus, A. comifer, A. mazatlanus, A. fonsecensis, A. punctifer, A. paulistanus,* and *A. scutum.*

However, Chabanaud (1928) lumped several nominal species of *Trinectes* in his assessment of *Achirus* (Chabanaud 1928). He deemed the following six species as valid under *Achirus*: *A. fasciatus, A. austrinus (n. sp.), A. fonsecensis, A. inscriptus, A. microphthlamus (n. sp.),* and *A. fimbriatus* (Chabanaud 1928).

Chabanaud (1928:7) used two characters to distinguish *Achirus* from the other achirid genera in a dichotomous key of Achirinae (=Achiridae): (1) "*Septum interbranchial entier*" or "unpierced interbranchial septum", and (2) "*Membrane operculaire non soudée à l'urohyal*" or "opercular membrane not connected to urohyal." Chabanaud (1928) was the first to introduce the unpierced interbranchial septum as a defining character within Achiridae. The character refers to the absence of a foramen in the interbranchial septum which, when present, would connect both gill chambers as is common in most achirids (Chabanaud 1928) and in the Pleuronectiformes. Chabanaud's (1928) second character, the connection of the opercular membrane to the urohyal, was used to distinghish *Baiostoma* from other achirids. This character was investigated in this study and found to be too variable to have any taxonomic value.

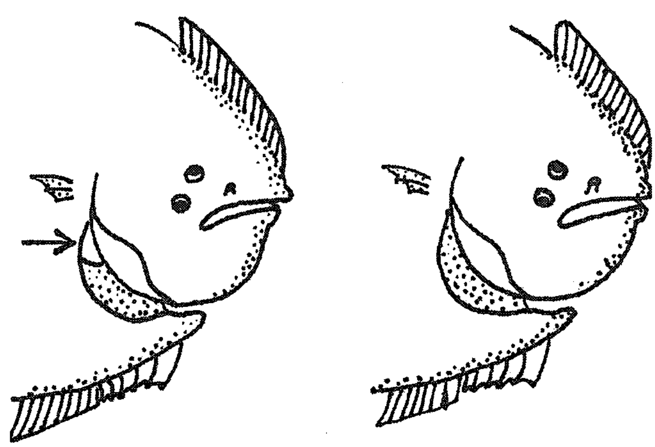


Figure 1.1: Two states of the interbranchial septum, found under the gill operculum, in achirids: (A) pierced with a foramen, (B) unpierced.

Myers' (1929) criticized several of Chabanaud's (1928) nomenclatorial decisions regarding *Achirus*. One of Myers' (1929) recommended changes was that Chabanaud's (1928) *Baiostoma* be known as *Achirus*, and his *Achirus* be known as *Trinectes*. The latter was prompted by Myers' (1929) synonymization of *T. scabra* with *A. fasciatus*, which he based on two pieces of evidence: (1) though excessively short, the description provided by Rafinesque (1832) fit the description of *A. fasciatus*, and (2) that *A. fasciatus* was the only species within the group (*Achirus*) that was known to occur where the lone representative of *T. scabra* was collected (River Schuylkill, around Pennsylvania and New Jersey). Myers (1929) determined that *Trinectes* and *Achirus* should be recognized as valid genera, and that the former should include the following species: *T. fasciatus*, *T. austrinus*, *T. fonsecensis*, *T. inscriptus*, *T. microphthalmus*, and *T. fimbriatus*. Additionally, the unpierced interbranchial septum became a diagnostic character of *Trinectes*, and has been recognized as such since that time (e.g. Chabanaud 1930; Hubbs 1932; Norman 1934).

Chabanaud (1930) subsequently supported Myers' (1929) conclusions regarding *Trinectes* and agreed that the species of the genus *Achirus* defined in his 1928 study (and all its species) should bear the name *Trinectes*. Chabanaud (1930) also claimed that he found the types of *Pleuronectes lineatus* Linneus 1766 to be identical to those of *A. fasciatus* Lacépède 1802, *Solea achirus* Günther 1862, and *Pleuronectes maculatus* Bloch & Schneider 1801. He concluded that these species should all be synonymized with one another under *P. lineatus*. Therefore, although Chabanaud (1930) now recognized the majority of Myers' (1929) *Trinectes* as valid species, he had the following exception: that *T. fasciatus* be a synonym of *T. lineatus*.

Hubbs (1932) re-evaluated the status of several species within *Achirus* and *Trinectes*, as well as the status of *Trinectes*. He determined that: (1) Chabanaud's (1930) *Baiostoma* should be syononymized with *Achirus* and Chabanaud's (1930) *Achirus* (including *A. fasciatus*) should be syononymized with *Trinectes*, as suggested by Myers (1929); (2) *Achirus* and *Trinectes* should be considered valid genera, as was suggested by Chabanaud (1928) in separating his *Baiostoma* and *Achirus*; (3) that *T. scabra* should be synonymized with *A. fasciatus* and *Trinectes* should be a valid name for the species, as was suggested by Chabanaud (1930); (4) that *A. fasciatus* be synonymized with *Pleuronectes maculatus*, as was also suggested by Chabanaud (1930), and (5) that *A. fasciatus* not be synonymized with *P. lineatus*, contrary to Chabanaud's (1930) suggestion. Therefore, Hubbs (1932) established that *Trinectes* be considered a valid genus, separate of *Achirus*, and that its type species be *T. maculatus*, as *P. maculatus* Bloch & Schneider 1801 had been described prior to *A. fasciatus* Lacépède 1802.

Chabanaud (1935a) took an in-depth look at the type species *Trinectes maculatus* to re-assess this species and several other members of the genus. Chabanaud (1935a) created several subdivisions within the genus, dividing *T. maculatus* into two subspecies, *T. m. maculatus* and *T. m. fonsecensis*, and three natios (=subdivision within a subspecies), *T. m. m. maculatus*, *T. m. m. browni*, and *T. m. m. paulistanus*. Chabanaud (1930) based his subdivisions largely on geographical locations and on the following structures: the shape and position of the eyed-side and blind-side nostrils and the size and shape of the eyed-side and blind-side scales. We examined these characters and found them to be too variable to have any taxonomic value.

Chabanaud (1939) abandoned his former subdivisions (Chabanaud 1935a) and finally recognized the following seven nominal species as distinct species of *Trinectes*: *T. maculatus*, *T. paulistanus*, *T. fonsecensis*, *T. fluviatilis*, *T. inscriptus*, *T. microphthalmus*, and *T. fimbriatus*.

Recently, Walker & Bollinger (2001) described the new species *T. xanthurus* and included comments on the other four congeneric Eastern Pacific species. They also provided an identification key for this subgroup, based on morphological characters (Walker & Bollinger 2001). They generally relied on the following characters, all of which have been examined in this study: nostrils (presence/absence of ring of cirri), eyed-side pigmentation, and meristics (e.g. pectoral fins, anal fin, and caudal vertebrae) (Walker & Bollinger 2001).

Trinectes therefore contains the following 16 nominal species: *Achirus affinis* Steindachner 1915; *Achirus austrinus* Chabanaud 1928; *Achirus fasciatus* Lacepède 1802; *Solea fimbriata* Günther 1862; *Achirus fluviatilis* Meek & Hildebrand 1928; *Solea fonsecensis* Günther 1862; *Monochirus inscriptus* Gosse 1851; *Pleuronectes maculatus* Bloch & Schneider 1801; *Achirus microphthalmus* Chabanaud 1928; *Pleuronectes mollis* Mitchill 1814; *Achirus opercularis* Nichols & Murphy 1944; *Solea panamensis* Steindachner 1876; *Achirus paulistanus* Miranda Ribeiro 1915; *Monochir reticulatus* Poey 1860; *Trinectes scabra* Rafinesque 1832; and *Trinectes xanthurus* Walker & Bollinger 2001.

The objective of this study is to conduct the first revision of *Trinectes* and all of its nominal species to determine valid taxa. All available type specimens were examined and an exhaustive analysis of non-type specimens was also included. The genus and each of its recgonized species have been re-described. An up-to-date morphological identification key of *Trinectes* is also provided. The results of this study will provide a stronger taxonomic foundation required to conduct the first intraspecific phylogenetic analysis within this group (Chapter 2).

MATERIALS AND METHODS

Specimen acquisition

A total of 647 specimens were examined; 34 specimens from the species *Trinectes fimbriatus*, 31 from *T. fluviatilis*, 71 from *T. fonsecensis* (including one specimen from *Solea panamensis*), 109 from *T. inscriptus*, 105 from *T. maculatus* (including specimens from *T. fasciatus*), 100 from *T. microphthalmus*, 15 from *T. opercularis*, 126 from *T. paulistanus* (including seven specimens from *Achirus austrinus*), and 56 from *T. xanthurus*. Specimens were examined at, or obtained on loan from, the following institutions (abbreviations follow Leviton *et al.* 1985): AMNH, ANSP, CAS, FMNH, LACM, MNRJ, SIO, UMMZ, BMNH, MNHN, NMW, UFPB, USNM, ZMB. Whenever possible, specimens were selected to account for as much of the known geographic distribution of their representative species. Eight of the nine species recognized had over 25 specimens analyzed in this study, with the exception of *T. opercularis* (15 specimens).

Measurements

Morphological, meristic, and several qualitative measurements that were found to be taxonomically relevant in distinguishing *Trinectes* species, are described in Appendix B. Additionally, a detailed glossary of the ichthyological, taxonomic, and phylogenetic terms and structures used within this thesis is provided in Appendix C. Meristic measurements were taken from digital and film radiographs (i.e. X-rays). Radiographs were primarily taken by the author at the Smithsonian Institution (USMN) or at the Canadian Museum of Nature (CMNFI, formerly NMC). Morphological measurements were taken with an electronic caliper, sensitive to the nearest hundredth (0.01) of a mm, but rounded to the nearest tenth (0.1) of a millimeter for analyses. Measurements are expressed as percentages of standard length (% SL) or head length (% HL). Unless otherwise indicated, specimen lengths and proportional measurements in the text correspond to SL. Descriptions of pigmentation were made on preserved specimens only. Measurements and counts followed the methods of Hubbs & Lagler (1958), except for the following characters: body thickness, preorbital head length, eyed-side mouth length, and blind-side mouth lengths, nostril to snout distance, ventral eye diameter, and width of orbits. Measurements were primarily taken on the eyed-side (ES). The following measurements were taken from the blind-side (BS): standard length (SL), body depth (BD), caudal fin base depth (CFBD), BS pelvic fin length (PelBS), BS pectoral fin length (PecBS), longest dorsal fin ray (LDR), and longest anal fin ray (LAR).

Mapping

Occurrence maps were completed with the use of ArcGIS (ArcMap 9.2) (ESRI 2006). All occurrence data used in the production of these maps were based on specimens identified in this study. Latitude and longitude coordinates (lat-longs) were obtained for each lot that had, at the very least, a specified location in its collection information (e.g. city, river, basin, etc). When provided, the lat-longs were taken directly from the collection tag and entered into Google Earth 5.0 to then be converted into decimal degrees and entered into ArcGIS. When the lat-longs were not provided, the specified location was manually entered into Google Earth 5.0 and then converted into decimal degrees. In both cases, the lat-longs were rounded to the nearest tenth of a degree for consistency and to minimize the accuracy.

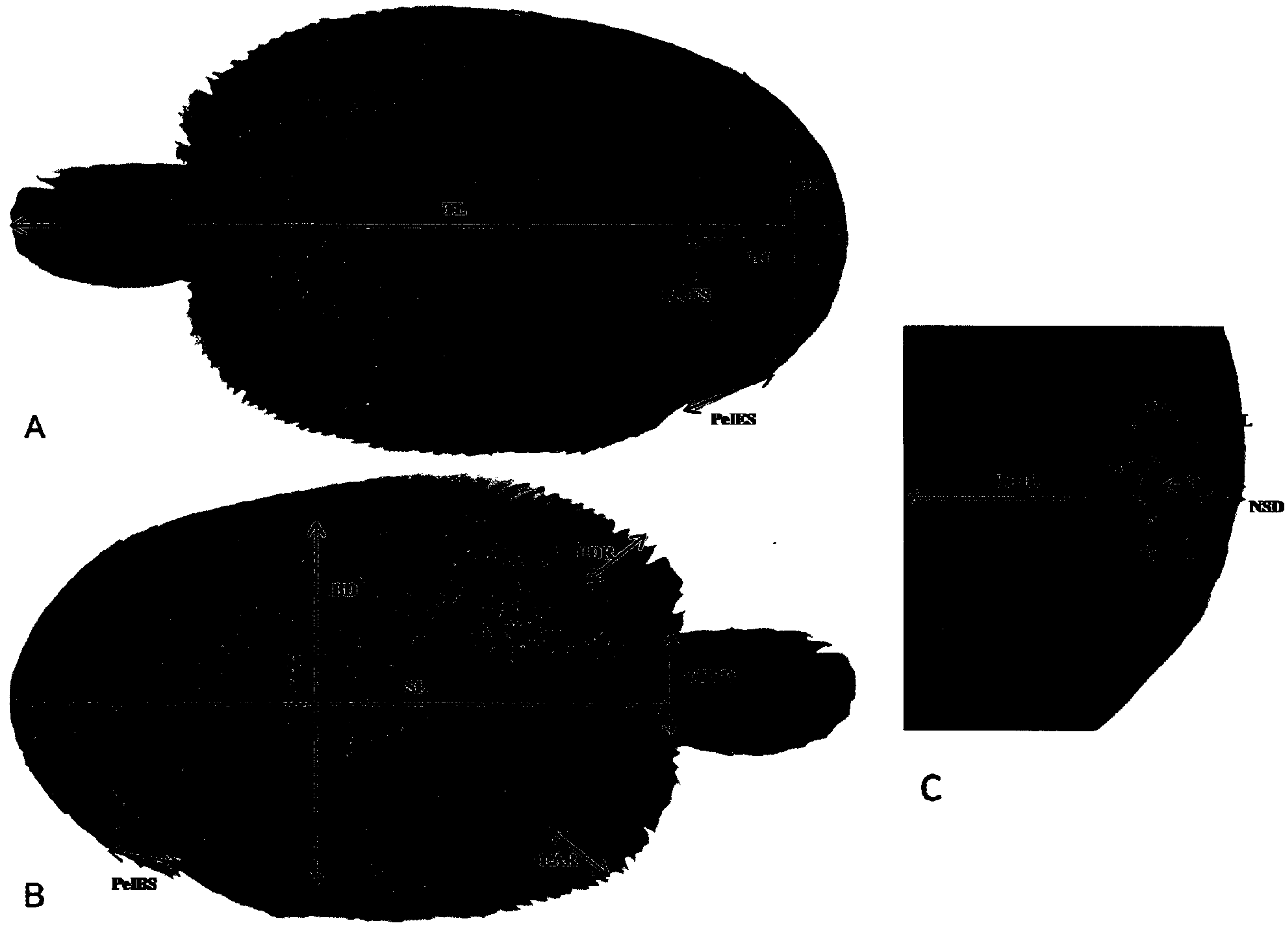


Figure 1.2: Examination of several morphological characters used in this study displayed on the eyed-side (A), blind-side (B), and closeup head region (C) of the holotype specimen of *Trinectes paulistanus* (MNRJ 1963, 117.2 mm). Descriptions of structures and description of abbreviations are in Appendix B.

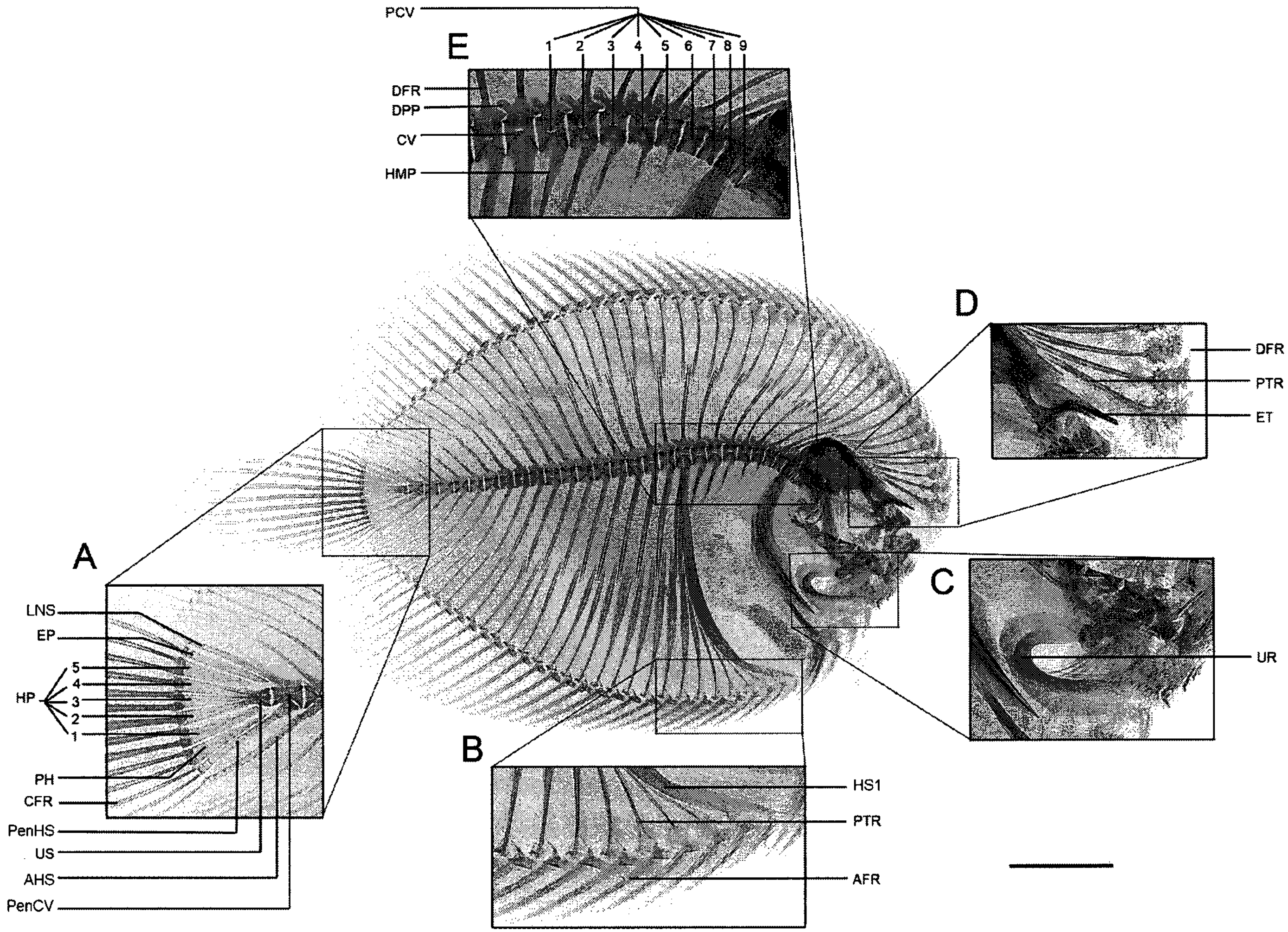


Figure 1.3: Inverted X-ray of *Trinectes opercularis* (USNM 361517, 55.7 mm), depicting numerous bone assemblages and meristic structures used within this study. (A) Hypural plates, (B) pterygiophores, (C) urohyal, (D) supracranium, (E) precaudal vertebrae. Descriptions of structures and explanation of abbreviations are in Appendix C (glossary).

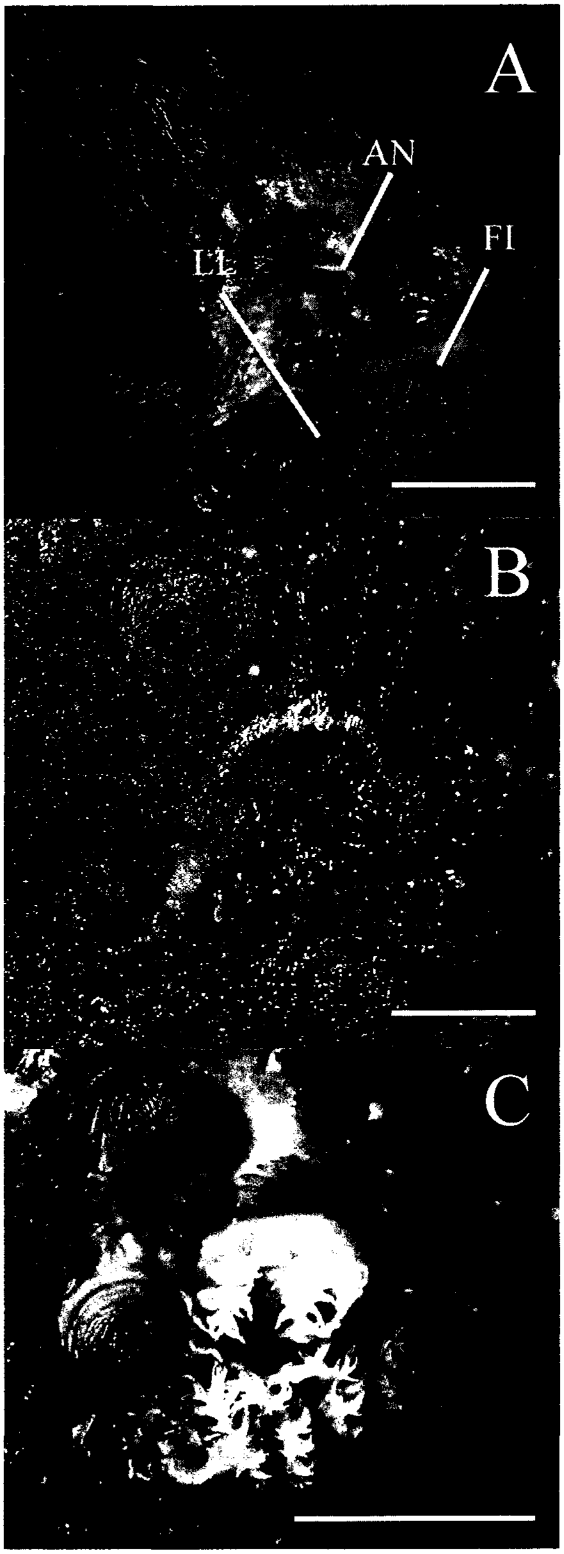


Figure 1.4: Close-up of two characters; fimbriae (FI) on lower eyed-side lip (LL), and anterior eyed-side nostril (AN), in three specimens of *Trinectes*. Branching of fimbriae occurs in three states in species within the genus: (A) unbranched, (B) lightly-branched, or (C) heavily-branched. Anterior eyed-side nostril occurs in two states in species within this genus: (A&B) with smooth aperture, or (C) with ring of cirri around aperture. Representative specimens shown are: (A) *T. xanthurus*, LACM 33805–27, 77.3 mm; (B) *T. paulistanus*, USNM 286990, 86.5 mm; and (C) *T. microphthalmus*, LIUFES 130184, 37.4 mm. Scale bars correspond to 2 mm.

Genus ***Trinectes*** Rafinesque 1832

Synonyms. — None

Common name. — None

Type species. — *Trinectes maculatus* (Bloch & Schneider 1801)

Diagnosis. — Dextral fishes with an interbranchial septum not pierced by a foramen (Fig. 1); seven or more pterygiophores anterior to the neural spine of the third precaudal vertebra (Fig. 3).

Description. — Body round to oval. Anteriormost point of eyed-side mouth in line with ventral eye, posteriormost point curving under ventral eye. Posterior nostril wide slit immediately anterior to ventral eye, under posterior upper lip, over upper jaw. Blind-side mouth very short, curving sharply ventrally. Blind-side anterior nostril surrounded by rosebud of tentacles. Dorsal eye slightly in advance of lower eye. Scales ctenoid on both sides. Eyed-side scales larger dorso-anteriorly on cephalic region, and ventro-anteriorly between mouth and gill opening. Patch of cirri between anterior nostril and ventral eye. Fimbriae present on upper lip, extending from anteriormost point of lip to anterior nostril, variable in length. Fimbriae present on lower lip, extending throughout entire length of lip; length and branching variable between species. Upper lip overhanging lower lip. Short, pointed, villiform teeth on blind-side jaws. Anus located along ventral mid-line, between pelvic fins, anterior to first anal fin ray. Anterior end of dorsal fin extending to tip of snout. Lengthiest median fin rays branched. Caudal fin with 16 rays, free of dorsal and anal fins. Lateral line on both sides nearly straight, visibly curving dorsally on head and splitting in branches. Transverse bands present in varying number (5–11) on eyed-side body with an additional 2–5 bands on head, extending from base of dorsal fin (occasionally to tip of fin rays) to the base of the anal fin (occasionally to tip of rays) on body and from base of dorsal fin to lateral line on head. Transverse bands also occasionally pigmented. Eyed-side pectoral fin rudimentary or absent. Blind-side pectoral fin usually absent.

Etymology. — Greek *tri*, "three" and *nektes* (Latinized *nectes*), "swimmer", making reference to the presence of only three fins in most members of this genus: dorsal, anal, and caudal.

Comparison. — *Trinectes* is the only genus in Achiridae with an interbranchial septum not pierced by a foramen. All other achirids have the presence of a conspicuous foramen connecting the eyed-side and blind-side interbranchial chambers, although the form and position of this foramen can vary between genera. In addition, *Trinectes* has seven or more pterygiophores anterior to the neural spine of the third precaudal vertebra, whereas its related genera all have six or fewer.

KEY TO SPECIES OF *TRINECTES*

1 Lower lip with highly-branched fimbriae (Fig. 1.4); margin of eyed-side anterior nostril with ring of cirri (Fig. 1.4); deep body (average 66.0–68.3 % SL); eyes very small (average 7.1–9.8 % HL); 33–36 anal fin rays 2

- Lower lip with unbranched or lightly-branched fimbriae (Fig. 1.4); margin of eyed-side anterior nostril bare of cirri (Fig. 1.4); narrow body (average 53.0–59.9 %); eyes small to large (average 10.7–19.0 % HL); 39–45 anal fin rays 4

2 Eyed-side body covered with conspicuous white spots (Fig. 1.5) .... *T. fimbriatus* *p. 33*

- Eyed-side body without white spots 3

3 Eight pterygiophores anterior to the neural spine of the third precaudal vertebra (Fig. 1.3) .... *T. opercularis* *p. 86*

- Seven pterygiophores anterior to the neural spine of the third precaudal vertebra (Fig. 1.3) .... *T. microphthalmus* *p. 78*

4 Lower lip with unbranched fimbriae (Fig. 1.4); 21 caudal vertebrae; narrow caudal fin base (average 13.3–13.4 %); large eyes (average 16.0–19.0 % HL) 5

- Lower lip with lightly-branched fimbriae (Fig. 1.4); 19–20 caudal vertebrae; deep caudal fin base (average 15.8–16.4 %); small eyes (average 10.7-14.4 % HL) 6

5 Dorsal and anal fins with same or lighter pigmentation than body (Fig. 1.7) .... *T. fluviatilis* *p. 40*

\- Dorsal and anal fins with darker pigmentation than body (Fig. 1.24) .... *T. xanthurus* *p. 102*

6 Eyed-side body and vertical fins covered with a conspicuous network of dark lines on a lighter background (Fig. 1.13); presence of rudimentary blind-side pectoral fin ray (Fig. 1.12B); eyed-side pectoral fin developed, with 2–4 rays and membranous connections (Fig. 1.13)........ *T. inscriptus* *p. 57*

\- Eyed-side body and vertical fins without network of dark lines on a lighter background; absence of blind-side pectoral fin ray; eyed-side pectoral fin with 0–2 rays without membranous connections 7

7 Eyed- and blind-side pelvic fins with 4 rays; median fins with dark striations (Fig. 1.16) .... *T. maculatus* *p. 67*

\- Eyed- and blind-side pelvic fins with 5 rays; median fins without dark striations 8

8 Caudal fin with conspicuous dark spots (Fig. 1.10); nine or more thick, pigmented transverse bands on eyed-side body (Fig. 1.10); eyed-side body with dark brown pigmentation (Fig. 1.9) .... *T. fonsecensis* *p. 48*

\- Caudal fin without spots; eight or fewer thin, unpigmented transverse bands on eyed-side body; eyed-side body with light beige pigmentation (Fig. 1.22) .... *T. paulistanus* *p. 93*

Table 1.1: Frequency distribution of dorsal and anal fin rays in recognized *Trinectes* species. Counts for holotypes and paratypes are underlined or indicated by an asterisk (*), respectively. Counts for holotype of *T. xanthurus* obtained from Walker & Bollinger (2001).

Dorsal fin rays

	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	n	Mean	SD
T. fimbriatus			1		5	3	3	6	1											19	50.5	1.6
T. microphthalmus	1	2	3	19	26	23	16	4	2	1										97	49.5	1.5
T. opercularis						1	5	6	2											14	51.6	0.8
T. inscriptus							1	4	17	20	7	5	3	3					1	62	54.2	2.0
T. maculatus								7	10	8	9	6	4	4	2	1				51	54.8	2.1
T. paulistanus									4	2	13	19	22	3	4	7	1	1		76	56.7	1.9
T. fonsecensis											3	4	6	12	8	4	4	1		42	58.2	1.7
T. fluviatilis										1*	3*	6*	6*	4*	4*					24	56.9	1.4
T. xanthurus										2	6	13	13	9	5	2	1			51	57.0	1.5

Anal fin rays

	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	48	n	Mean	SD
T. fimbriatus		1	3	4	8	1	1	1									19	35.6	1.4
T. microphthalmus	6	16	24	28	19	2			2								97	34.6	1.4
T. opercularis		3	1	6	3	1											14	34.9	1.2
T. inscriptus					1	1	3	10	22	13	7	4			1		62	40.4	1.6
T. maculatus						2	1	8	7	16	9	4	3				50	40.8	1.6
T. paulistanus							2	2	11	27	28	5		1			76	41.3	1.1
T. fonsecensis									1	9	11	10	7	2	1		41	42.6	1.3
T. fluviatilis										2*	4*	10	5*	3*			24	43.1	1.1
T. xanthurus										4	8	17	13	8	1		51	43.3	1.2

Table 1.2: Frequency distribution of caudal and precaudal vertebrae in recognized *Trinectes* species. Included are the number of specimens (n), mean, and standard deviation (SD). Counts for holotypes and paratypes are underlined or indicated by an asterisk (*), respectively. Caudal vertebrae count includes urostylar centrum.

Caudal vertebrae								
	18	**19**	**20**	**21**	**22**	**n**	**Mean**	**SD**
T. fimbriatus		17	1			18	19.1	0.2
T. microphthalmus	7	83	6			96	19.0	0.4
T. opercularis		14				14	19.0	0.0
T. inscriptus	1	40	1			42	19.0	0.2
T. maculatus	6	27	17			50	19.2	0.6
T. paulistanus		7	45			52	19.9	0.3
T. fonsecensis		7	26	7		40	20.0	0.6
T. fluviatilis			4*	19*		23	20.8	0.4
T. xanthurus			12	38	1	51	20.8	0.5

Precaudal vertebrae								
	8	**9**	**10**			**n**	**Mean**	**SD**
T. fimbriatus	1	17				18	8.9	0.2
T. microphthalmus	3	93				96	9.0	0.2
T. opercularis		14				14	9.0	0.0
T. inscriptus	2	38	2			42	9.0	0.3
T. maculatus	3	43	3			49	9.0	0.4
T. paulistanus	10	39	4			53	8.9	0.5
T. fonsecensis	6	31	3			40	8.9	0.5
T. fluviatilis		24*				24	9.0	0.0
T. xanthurus	6	45				51	8.9	0.3

Table 1.3: Frequency distribution of eyed-side (ES) and blind-side (BS) pectoral fin rays in recognized *Trinectes* species. Included are the number of specimens (n), mean, and standard deviation (SD). Counts for holotypes and paratypes are underlined or indicated by an asterisk (*), respectively.

Pectoral fin rays (ES)									
	0	**1**	**2**	**3**	**4**	**5**	**n**	**Mean**	**SD**
T. fimbriatus	34						34	-	-
T. microphthalmus	98						98	-	-
T. opercularis	15						15	-	-
T. inscriptus		3	14	77	13	1	108	3.0	0.6
T. maculatus	97	7					104	0.1	0.3
T. paulistanus	51	65	7			1	124	0.7	0.7
T. fonsecensis	12	28	24	4	1	1	70	1.4	1.0
T. fluviatilis	25*	5*					30	0.2	0.4
T. xanthurus	56*						56	-	-

Pectoral fin rays (BS)							
	0	**1**	**2**	**3**	**N**	**Mean**	**SD**
T. fimbriatus	34				34	-	-
T. microphthalmus	98				98	-	-
T. opercularis	15				15	-	-
T. inscriptus	5	53	36	13	107	1.5	0.8
T. maculatus	104				104	-	-
T. paulistanus	125				125	-	-
T. fonsecensis	69	1			70	-	0.1
T. fluviatilis	30*				30	-	-
T. xanthurus	56*				56	-	-

Table 1.4: Frequency distribution of eyed-side (ES) and blind-side (BS) pelvic fin rays in recognized *Trinectes* species. Included are the number of specimens (n), mean, and standard deviation (SD). Counts for holotypes and paratypes are underlined or indicated by an asterisk (*), respectively.

	Pelvic fin rays (ES)					
	4	**5**	**6**	**n**	**Mean**	**SD**
T. fimbriatus		34		34	5.0	-
T. microphthalmus		97		97	5.0	-
T. opercularis		14	1	15	5.1	0.3
T. inscriptus	4	103	1	108	5.0	0.2
T. maculatus	102	2		104	4.0	0.1
T. paulistanus	12	112	2	126	4.9	0.3
T. fonsecensis	1	67	1	69	5.0	0.2
T. fluviatilis	1	29*		30	5.0	0.2
T. xanthurus		56		56	5.0	-

	Pelvic fin rays (BS)						
	3	**4**	**5**	**6**	**n**	**Mean**	**SD**
T. fimbriatus			34		34	5.0	-
T. microphthalmus			97		97	5.0	-
T. opercularis			15		15	5.0	-
T. inscriptus		7	101		108	4.9	0.2
T. maculatus	1	100	2		103	4.0	0.2
T. paulistanus		16	107	2	125	4.9	0.4
T. fonsecensis		1	69		70	5.0	0.1
T. fluviatilis		1	29*		30	5.0	0.2
T. xanthurus		2	54		56	5.0	0.2

Trinectes fimbriatus (Günther 1862)

Figures 1.5–1.6, Tables 1.1–1.5

Synonym(s). — *Solea fimbriata* Günther 1862

Common name(s). — Fringed sole, Whitespotted sole, Sole ronde, Suela pintada, Suela redonda

Materials examined. — ***Trinectes fimbriatus***, 34 specimens (33.06–71.07 mm)

Solea fimbriata

Holotype: BMNH 1848.3.18.184, 1(60.80 mm), Gulf of Fonseca, Honduras.

Other material: UMMZ 194671, 8(49.15–59.02 mm), 9°53'--" N, Puntarenas, Gulf of Nicoya, off Puntarenas, Pacific drainage, Costa Rica; LACM 30714–13, 3(38.98–56.30 mm), Gulf of Nicoya, Isla Chira, Costa Rica; LACM 33806–38, 10(49.00–69.98 mm), Puntarenas, Boca de Barranca, Costa Rica; SIO 94–132, 3(58.29–67.10 mm), 9°47.8′ N, Puntarenas, G. de Nicoya, Costa Rica; LACM 9754–13, 1(56.32 mm), Gulf of Nicoya, between Isla San Lucas and Isla Negritas, Costa Rica; USNM 220647, 1(33.06 mm), La Venadona, Jiquilisco Bay, El Salvador; FMNH 61596, 1(71.07 mm), Chiapas, Mexico; CAS 213419, 2(63.21–67.86 mm), North of Island Gobernadora and South of Island Santa Catalina, Panama; CAS 213433, 1(58.70 mm), off Chitre, Panama; LACM 25890, 1(61.92 mm), Gulf of Panama, Chame Bay, Panama; SIO 57–134, 1(69.55 mm), Golf of Rio Anton, off estuary, Panama; USNM 85767, 1(51.40 mm), Chame Point, Panama.

Diagnosis. — A species of *Trinectes* characterized by a combination of the following characters: distinct white spots covering eyed-side body and vertical fins (Fig. 1.5); eyed-side lips with numerous, long, highly-branched fimbriae (Fig. 1.4C); ring of cirri present around margin of eyed-side anterior nostril (Fig. 1.4C); body very deep, 59.6% to 78.0% (mean = 68.3%); eyes very small, 5.5% to 10.2% (mean = 8.2%) in HL; pectoral fins absent; 46–52 dorsal fin rays; 34–36 anal fin rays; ethmoid process shorter than width of dorsal orbit (Fig. 2.4AB); angle of urohyal closed (Fig. 2.6A2); dorso-posterior process of neural arc pointed (Fig. 1.3); hemal spine of posteriormost precaudal hemapophysis with posterior wing (Fig. 1.3); haemal arch of anteriormost precaudal vertebrae thick (Fig. 1.3).

Description. — Morphometrics of type and non-type specimens are given in Table 1.5. Body small and round, reaching 71.1 mm (measured specimens). Head short, 28.3% to 36.0% (mean = 31.3%) and deep, 36.9% to 69.8% (mean = 46.3%). Body very deep, 59.6% to 78.0% (mean = 68.3%). Eyed-side gill opening at least one eye diameter's length ventral to ventral eye. Eyed-side anterior nostril a short tube with ring of cirri along margin. Blind-side posterior nostril a thick tube of medium length. A few short, fleshy tentacles on blind-side head and at the base of the opercular region. Short tentacles projecting from proximal half of rays on blind-side vertical fins. Scales found on base of median fin rays. Caudal fin of moderate length, alternating in shape from round to rectangular, with wide base, caudal fin base depth 13.7% to 18.7% (mean = 15.7%). Eyed-side and blind-side pelvic fins of moderate length, 17.9% to 25.8% (mean = 21.1%) and 15.9% to 22.5% (mean = 18.9%), respectively. Pectoral fins wholly absent. Body thin, 8.8% to 12.5% (mean = 10.6%).

Longest dorsal ray 17.0% to 24.6% (mean = 21.1%), longest anal ray 17.6% to 24.5% (mean = 21.7%). Dorsal and anal fins longest at mid-point of body.

Preorbital head length is relatively wide, 27.1% to 36.5% (mean = 31.8%) in HL. Postorbital head length is wide, 50.1% to 62.3% (mean = 56.0%) in HL. Snout of moderate length, 30.9% to 43.1% (mean = 35.4%) in HL. Posterior corner of mouth on eyed-side reaching proximal quarter to half of ventral eye. Eyed-side mouth long, 29.5% to 38.4% (mean = 34.2%) in HL, and slightly curved downward. Blind-side mouth short, 14.5% to 29.3% (mean = 21.6%) in HL, and sharply curved downward. Nostril to snout distance 19.8% to 35.0% (mean = 29.0%) in HL. Eyes small, ventral eye diameter 5.5% to 10.2% (mean = 8.2%) in HL. Distance between orbits approximately equivalent to half to one eye diameter, 6.3% to 12.7% (mean = 9.7%) in HL. Width of orbits narrow, 8.0% to 17.9% (mean = 12.0%). Eyed-side opercular region scaly, rarely with scaleless patch. Lower lip with many long, highly-branched fimbriae (Fig. 1.4C). Eyed-side body usually with numerous scattered patches of cirri. Frequency distributions of the following meristics are shown in Tables 1.1–1.4: 47–53 dorsal fin rays, 33–39 anal fin rays, 19 caudal vertebrae, 9 precaudal vertebrae, pectoral fins absent, 5 eyed-side pelvic fin rays, and 5 blind-side pelvic fin rays.

Colour of preserved specimens. — Head, body, and vertical fins covered with round, liver-shaped white spots on a darker, beige to brown background. Caudal fin either with coalesced white spots, forming streaks, or light beige without spots or streaks. Six to nine faint, unpigmented transverse bands on body. Blind-side usually devoid of pigmentation, occasionally with brown pigmentation covering posterior half.

Distribution. — *Trinectes fimbriatus* is a Pacific species distributed from Guatemala to Peru (Fig. 1.6). Members of this species inhabit flat sand or mud bottoms (Allen & Robertson 1994).

Remarks. — Original description by Günther (1862) with holotype taken from Honduras, Gulf of Fonseca. The original description does not make mention of the presence of tentacles on blind-side head nor the body cirri often covering the eyed-side body as was usually found in specimens examined in this study (also noted by Meek & Hildebrand 1928).

Comparisons. — *Trinectes fimbriatus* most closely resembles the Pacific species *T. opercularis* and the Atlantic species *T. microphthalmus.* It differs from these two species in having distinctive white spots covering its eyed-side body and median fins. With the exception of *T. opercularis* and *T. microphthalmus*, *T. fimbriatus* can be distinguished from other congeneric species in having the following: highly-branched fimbriae on the eyed-side lower lip, 34–36 anal fin rays, a very deep body, the presence of a ring cirri on the margin of anterior eyed-side nostril, and very small eyes, an ethmoid process shorter than the width of its dorsal orbit, a closed urohyal, a dorso-posterior process of neural arc that is pointed, the haemal spine of the posteriormost precaudal haemapophysis with a posterior wing, a haemal arch of anteriormost precaudal vertebrae thick.

Table 1.5: Twenty-two morphometric variables of body shape in *Trinectes fimbriatus* (n = 34). Proportional measurements of both standard length (% SL) and head length (% HL) are included. Measurements for the holotype are shown separately, and combined with non-type specimens under 'All specimens'. Included are the ranges, means (in parentheses), and standard deviations (SD). Measurements and abbreviations are described in Appendix B.

	Holotype of *Solea fimbriata* BMNH 1848.3.18.184	All specimens (n = 34)	SD
SL (mm)	60.8	33.1–71.1 (57.4)	8.0
TL (mm)	78.5	45.4–97.3 (76.2)	10.7
% SL			
HL	30.7	28.3–36.0 (31.3)	1.5
BD	70.9	59.6–78.0 (68.3)	3.7
HD	41.0	36.9–69.8 (46.3)	7.0
CFBD	16.4	13.7–18.7 (15.7)	1.2
PelES	24.8	17.9–25.8 (21.1)	1.7
PelBS	17.8	15.9–22.5 (18.9)	1.5
PecES	-	-	-
PecBS	-	-	-
Th	12.5	8.8–12.5 (10.6)	0.9
LDR	17.0	17.0–24.6 (21.1)	1.5
LAR	17.6	17.6–24.5 (21.7)	1.5
% HL			
PreHL	30.0	27.1–36.5 (31.8)	2.5
PosHL	58.4	50.1–62.3 (56.0)	2.9
SnL	32.7	30.9–43.1 (35.4)	2.7
MES	32.1	29.5–38.4 (34.2)	2.5
MBS	14.4	14.5–29.3 (21.6)	3.8
NSD	19.8	19.8–35.0 (29.0)	3.0
EdV	7.2	5.5–10.2 (8.2)	1.1
DBO	7.7	6.3–12.7 (9.7)	1.6
WO	12.8	8.0–17.9 (12.0)	2.8

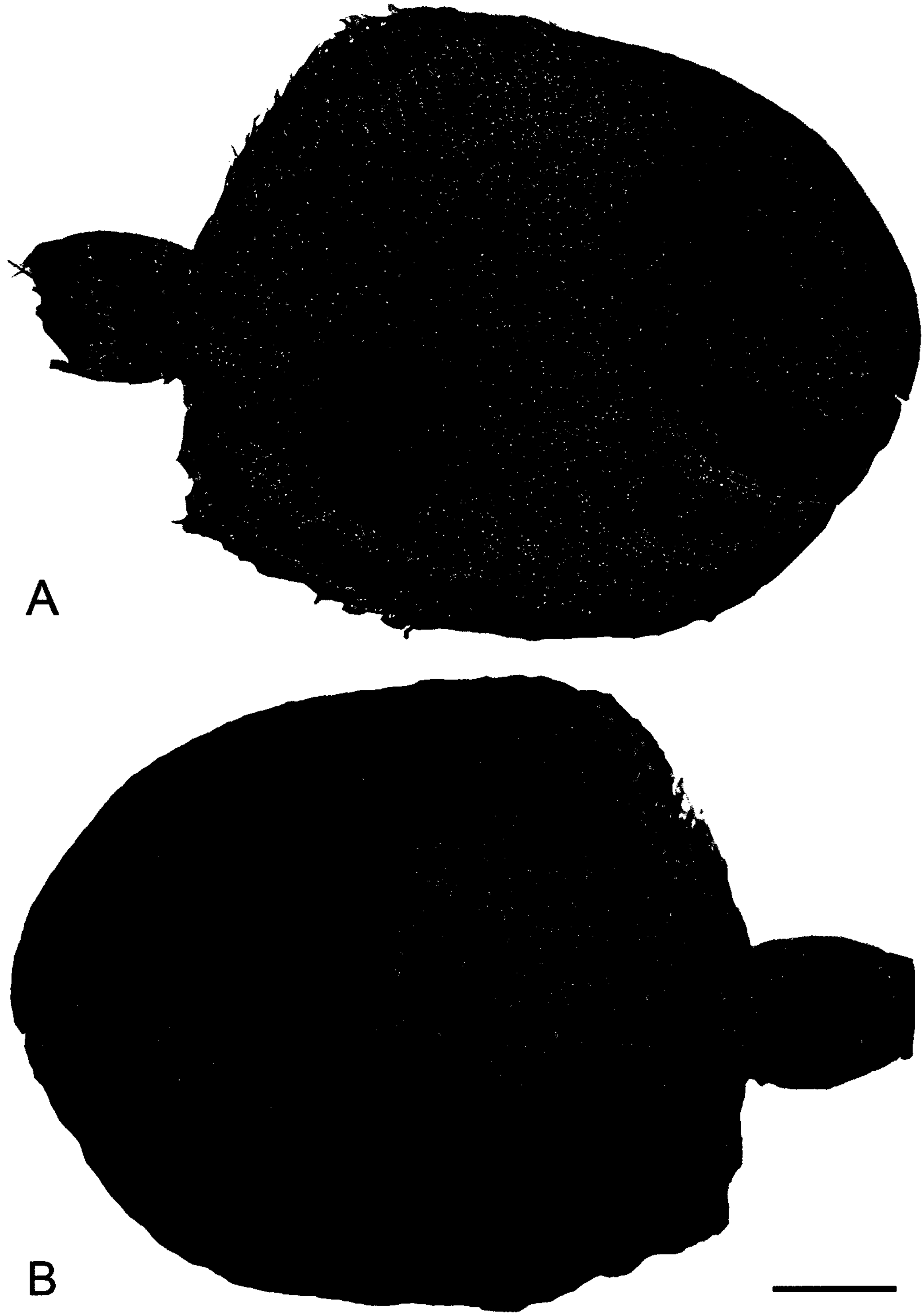


Figure 1.5: Eyed-side (A) and blind-side (B) of the holotype of *Trinectes fimbriatus*, BMNH 1848.3.18.184, 60.8 mm, Honduras (Gulf of Fonseca). Scale bar corresponds to 10 mm.

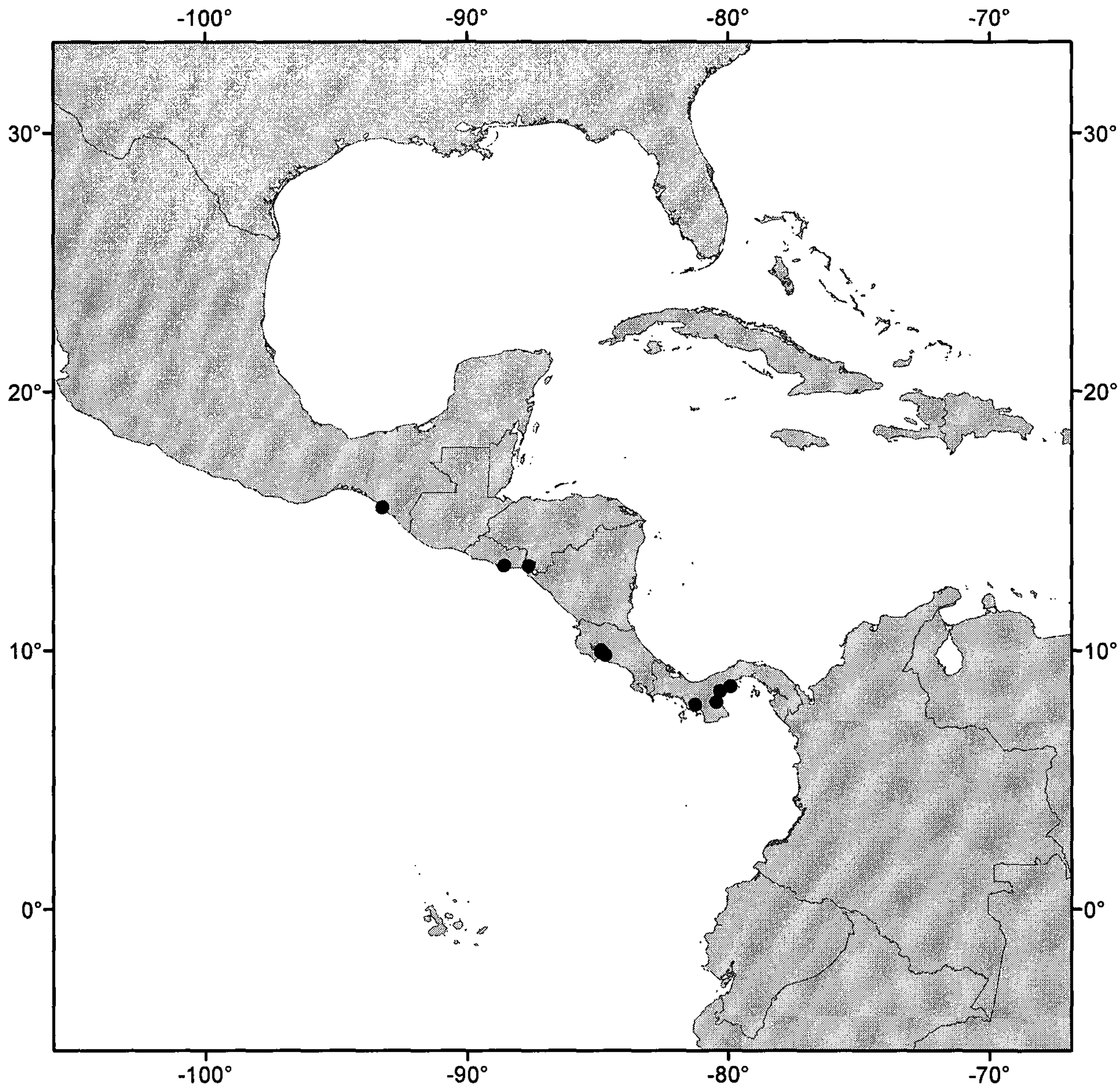


Figure 1.6: Occurrences of *Trinectes fimbriatus* specimens included in this study.

Trinectes fluviatilis (Meek & Hildebrand 1928)

Figures 1.7–1.8, Tables 1.1–1.4 & 1.6

Synonym(s). — *Achirus fluviatilis* Meek & Hildebrand 1928

Common name(s). — Freshwater sole, Sole fluviatile, Lenguado, Suela fluvial

Materials examined. — ***Trinectes fluviatilis***, 31 specimens (14.50–40.62 mm)

Achirus fluviatilis

Paratypes: USNM 081668, 9(25.32–35.42 mm), El Capitan, Panama.

Other material: USNM 361533, 2(35.40–38.45 mm), 01°36'20" N 077°02'30" W, Mouth of Rio Mira at Cubo Manglares South of Tumaco, Colombia; FMNH 18210, 1(40.23 mm), Rio Chame, Chame Point, Panama; SIO 02-129, 1(38.62 mm), 10°02.6' N, Puntarenas, Costa Rica; USNM 081621, 1(38.15 mm), Rio Calobre, Panama; USNM 144780, 4(14.50–24.93 mm), Canal Zone, Pedro Miguel Locks, Panama; USNM 144772, 1(36.58 mm), Canal Zone, Miraflores Locks, Panama; USNM 081669, 2(29.97–40.62 mm), Rio Culebra, Panama; USNM 293639, 2(23.51–26.18 mm), Rio Tuira Drain, between Calle Larga + Pinogarna above El Real, Panama; USNM 293643, 2(29.11–29.53 mm), Darien, Panama; USNM 293386, 5(28.00–34.57 mm), Rio Pirre CA 1/2 km above, Panama Darien; USNM 293390, 1(24.34 mm), 08°09'--" N 077°45'--" W, Darien, lower Rio Chucunaque just above confl. with Rio Tuira, Panama.

Diagnosis. — A species of *Trinectes* characterized by the following combination of characters: eyes large, 15.8% to 24.2% (mean = 19.0%) in HL; fimbriae on lower lip short and unbranched

(Fig. 1.4A); caudal fin base narrow, 11.4% to 16.4% (mean = 13.4%); 21 caudal vertebrae; 9 pterygiophores anterior to the neural spine of the third precaudal vertebrae (Fig. 1.3); presence of a small coracoscapular complex on both eyed- and blind-side pectoral fins; short ethmoid process (Fig. 2.4CD).

Description. — Morphometrics of type and non-type specimens are given in Table 1.6. Body short and oval, reaching up to 40.6 mm (measured specimens). Head short, 29.9% to 36.7% (mean = 32.8%), and deep, head depth, 35.3% to 47.8% (mean = 41.5%). Body shallow, body depth 46.3% to 61.6% (mean = 53.0%). Eyed-side gill opening extending the length of one eye diameter ventrally to ventral eye. Eyed-side anterior nostril a wide slit, often with cirri around base. Blind-side posterior nostril wide slit, mostly covered by skin flap. Short fleshy tentacles covering blind-side head and under mouth. Scales on head and lower jaw twice the size of those on body, no cirri on body. Caudal fin oval-shaped, approximately same length of head. Caudal fin base very narrow, caudal fin base depth 11.4% to 16.4% (mean = 13.4%) (Fig. 1.7). Eyed-side and blind-side pelvic fins of moderate length, 10.3% to 21.5% (mean = 18.4%) and 10.4% to 21.9% (mean = 17.2%), respectively. Eyed-side pectoral fin, when present, rudimentary. Blind-side pectoral fin absent. Body thin, 7.1% to 15.4% (mean = 8.8%). Longest dorsal ray 14.3% to 25.4% (mean = 19.8%), longest anal ray 14.0% to 27.4% (mean = 19.6%). Dorsal and anal fins longest in posterior half of body.

Preorbital head is relatively wide, 22.1% to 34.0% (mean = 27.4%) in HL. Postorbital head short, 40.1% to 58.4% (mean = 47.4%) in HL. Snout of moderate size, 30.6% to 40.3% (mean = 35.5%) in HL. Posterior corner of mouth on eyed-side reaching anterior quarter of ventral eye. Eyed-side mouth long, 29.6% to 41.1% (mean = 34.7%) in HL, sharply curving downward. Blind-side mouth short, 20.9% to 31.2% (mean = 25.2%) in HL, sharply curving downward. Nostril to snout distance 20.7% to 36.5% (mean = 28.1%) in HL. Opercular slit extending to the ventral margin of the ventral eye. Opercular regions bare of tentacles or cirri. Many short tentacles projecting from anteriormost rays of blind-side dorsal fin. Eyes large, ventral eye diameter 15.8% to 24.2% (mean = 19.0%) in HL. Interorbital space scaly, distance between orbits approximately half of orbital width, 5.0% to 25.4% (mean = 9.8%) in HL. Width of orbits moderate, 18.8% to 31.8% (mean = 25.7%). Eyed-side opercular region scaly. Short, unbranched fimbriae on lower lip (Fig. 1.4A). Little to no cirri on eyed-side body. Frequency distributions of the following characters are shown in Tables 1.1–1.4: 54–59 dorsal fin rays, 41–45 anal fin rays, 20–21 caudal vertebrae, 9 precaudal vertebrae, 0-1 eyed-side pectoral fin, blind-side pectoral fin absent, 5 eyed-side pelvic fin rays, and 5 blind-side pelvic fin rays.

Colour of preserved specimens. — Body brown, with darker brown blotches, also with eight to twelve faint, unpigmented transverse bands from anterior edge of head to base of caudal fin. Median fins slightly lighter brown than body. Caudal fin often without pigment, occasionally with faded spots. Blind-side usually beige, without distinctive pattern.

Distribution. — *Trinectes fluviatilis* is a Pacific species distributed from Costa Rica to Peru (Fig. 1.8). It is a freshwater species; occasionally reported in brackish and marine waters.

Remarks. — Upon examination of a syntype of *Trinectes fluviatilis*, Chabanaud (1935b) was the first to recognize it as a member of *Trinectes*. Chabanaud (1935b) determined that *T. fluviatilis* most closely resembled *T. maculatus*, but differed in having smaller scales, larger eyes, and a different eyed-side pigmentation. He assigned *T. fluviatilis* as a subspecies of *T. maculatus* (=*T. m. fluviatilis*), but subsequently recognized *T. fluvatilis* as valid species in 1939. Of the three characters Chabanaud (1935b) used to differentiate *T. fluviatilis* from *T. maculatus*, our results support only the use of eye size. However, several other distinguishing features between these species were found in this study (see section below).

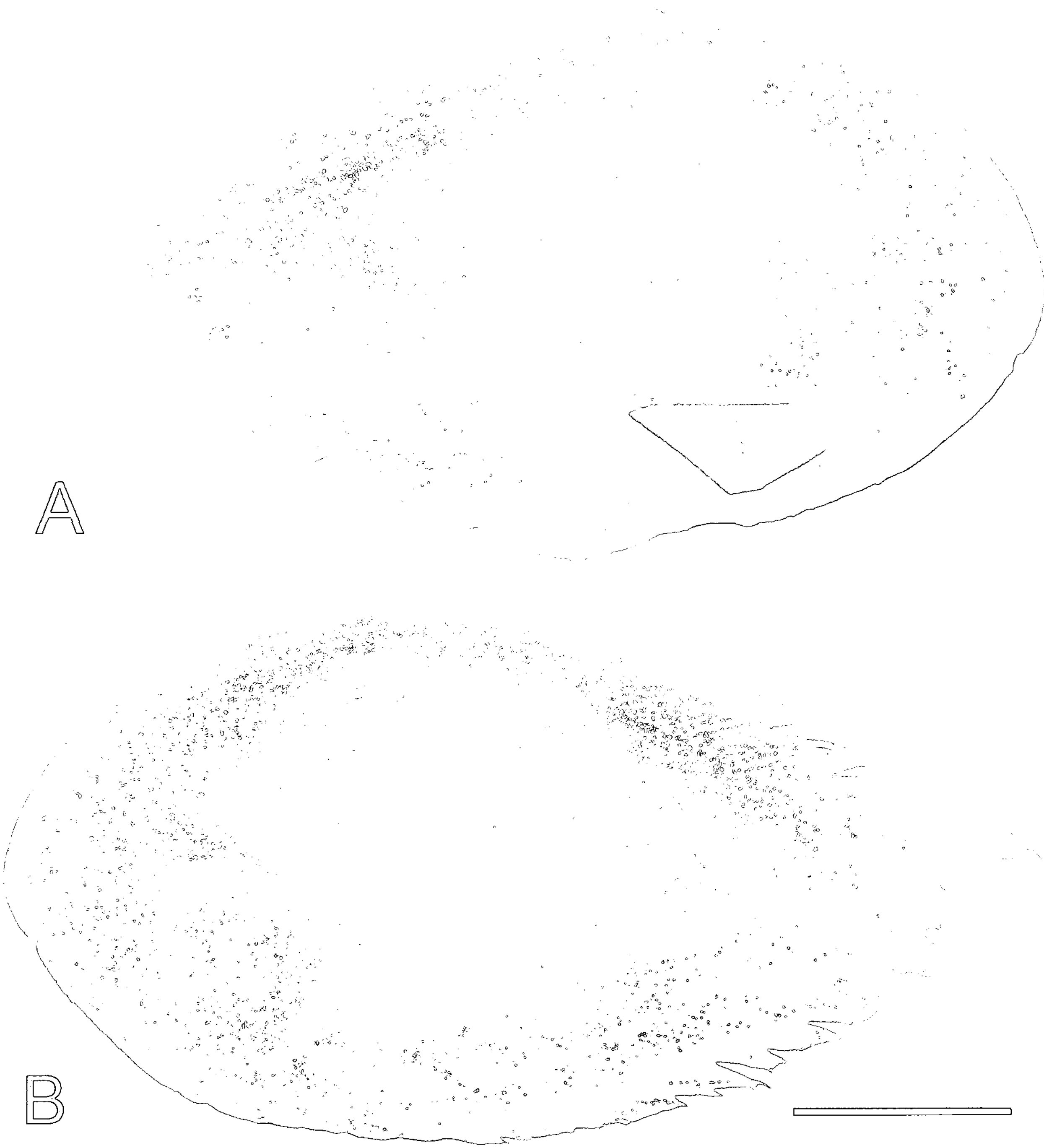
Trinectes fluviatilis is the smallest species (max. length: 50 mm) within the genus (Walker & Bollinger 2001). Museum collections often have specimens well beyond 50 mm (often over 100 mm) labelled as *T. fluviaitlis*. The vast majority of these specimens were determined to be mislabelled *T. fonsecensis* specimens. Characters useful in differentiating these two species are also shown in the section below. *Trinectes fluviatilis* is the only species in the genus to occur almost exclusively in freshwater.

Comparisons. — *Trinectes fluviatilis* can be distinguished from all *Trinectes* species (except *T. xanthurus*) in having the following combination of characters: 21 caudal vertebrae, large eyes, short, unbranched fimbriae on lower lip, and a narrow caudal fin base. *Trinectes fluviatilis* can be further distinguished from all congeners, with the exception of *T. xanthurus* and *T. fonsecensis*, in having 9 pterygiophores as opposed to 7 or 8 anterior to the neural spine of the third precaudal vertebra. *Trinectes fluviatilis* can be distinguished from *T. xanthurus* in having lightly pigmented as opposed to darkly pigmented eyed-side vertical fins, a round, beige caudal fin as opposed to a yellow, trapezoid-shaped caudal fin, and an ethmoid process that is shorter as opposed to longer than the width of its dorsal eye (Fig. 2.4CD). *Trinectes fluviatilis* is often confused with juvenile collections of *T. fonsecensis*. Specimens that do not overlap with *T. fluviatilis*' size range (i.e. under 60 mm) can generally be assumed to be *T. fonsecensis*.

However, irrespective of body length, characters that can be used to distinguish specimens of *T. fluviatilis* from *T. fonsecensis* are: eight or fewer transverse bands on the eyed-side body (excluding head), the unbranched fimbriae on the lower lip, the higher number of caudal vertebrae, the narrower caudal fin base depth, the unpigmented or lightly spotted caudal fin, lack of pigmentation around the transverse bands, and larger eyes. Note that as size may vary in proportion to body length with age, eye size should be used with caution when differentiating *T. fluviatilis* from juvenile (≥60 mm) *T. fonsecensis*.

Table 1.6: Twenty-two morphometric variables of body shape in *Trinectes fluviatilis* (n = 31). Proportional measurements of both standard length (% SL) and head length (% HL) are included. Measurements for the paratypes (n = 9) are shown separately, and combined with those of non-type specimens under 'All specimens'. Included are the ranges, means (in parentheses), and standard deviations (SD). Measurements and abbreviations are described in Appendix B.

	Paratypes of *Trinectes fluviatilis* BMNH 1846.10.28.24 (n = 9)	All specimens (n = 31)	SD
SL (mm)	25.3–35.4 (29.5)	14.5–40.6 (30.4)	6.4
TL (mm)	33.2–44.1 (38.8)	16.7–52.3 (40.1)	8.4
% SL			
HL	31.5–34.0 (32.8)	29.9–36.7 (32.8)	1.5
BD	50.4–56.2 (53.3)	46.3–61.6 (53.0)	2.9
HD	39.9–47.1 (43.0)	35.3–47.8 (41.5)	2.9
CFBD	12.4–14.1 (13.3)	11.4–16.4 (13.4)	1.3
PelES	17.7–21.2 (19.4)	10.3–21.5 (18.4)	2.4
PelBS	16.1–21.4 (18.0)	10.4–21.9 (17.2)	2.5
PecES	0–18.4 (2.9)	0–18.4 (2.0)	3.7
PecBS	0–12.6 (1.4)	0–12.6 (0.3)	2.0
Th	7.6–9.6 (8.4)	7.1–15.4 (8.8)	1.4
LDR	19.6–24.5 (21.4)	14.3–25.4 (19.8)	2.7
LAR	17.7–23.0 (20.2)	14.0–27.4 (19.6)	2.6
% HL			
PreHL	22.1–30.0 (26.6)	22.1–34.0 (27.4)	2.9
PosHL	40.1–50.0 (44.6)	40.1–58.4 (47.4)	3.7
SnL	33.4–40.3 (36.8)	30.6–40.3 (35.5)	2.6
MES	32.7–41.1 (37.0)	29.6–41.1 (34.7)	3.0
MBS	23.2–30.1 (26.2)	20.9–31.2 (25.2)	2.6
NSD	25.1–34.7 (28.1)	20.7–36.5 (28.1)	3.8
EdV	18.8–24.2 (21.2)	15.8–24.2 (19.0)	2.1
DBO	9.2–12.1 (10.3)	5.0–25.4 (9.8)	3.3
WO	22.4–31.8 (29.4)	18.8–31.8 (25.7)	3.6



A

B

Figure 1.7: Eyed-side (A) and blind-side (B) of a paratype of *Trinectes fluviatilis*, USNM 81668, 35.4 mm, Panama (El Capitan). The white object in the gill of the eyed-side specimen (A) is a fiberglass tag used to identify the specimen. The scale bar corresponds to 10 mm.

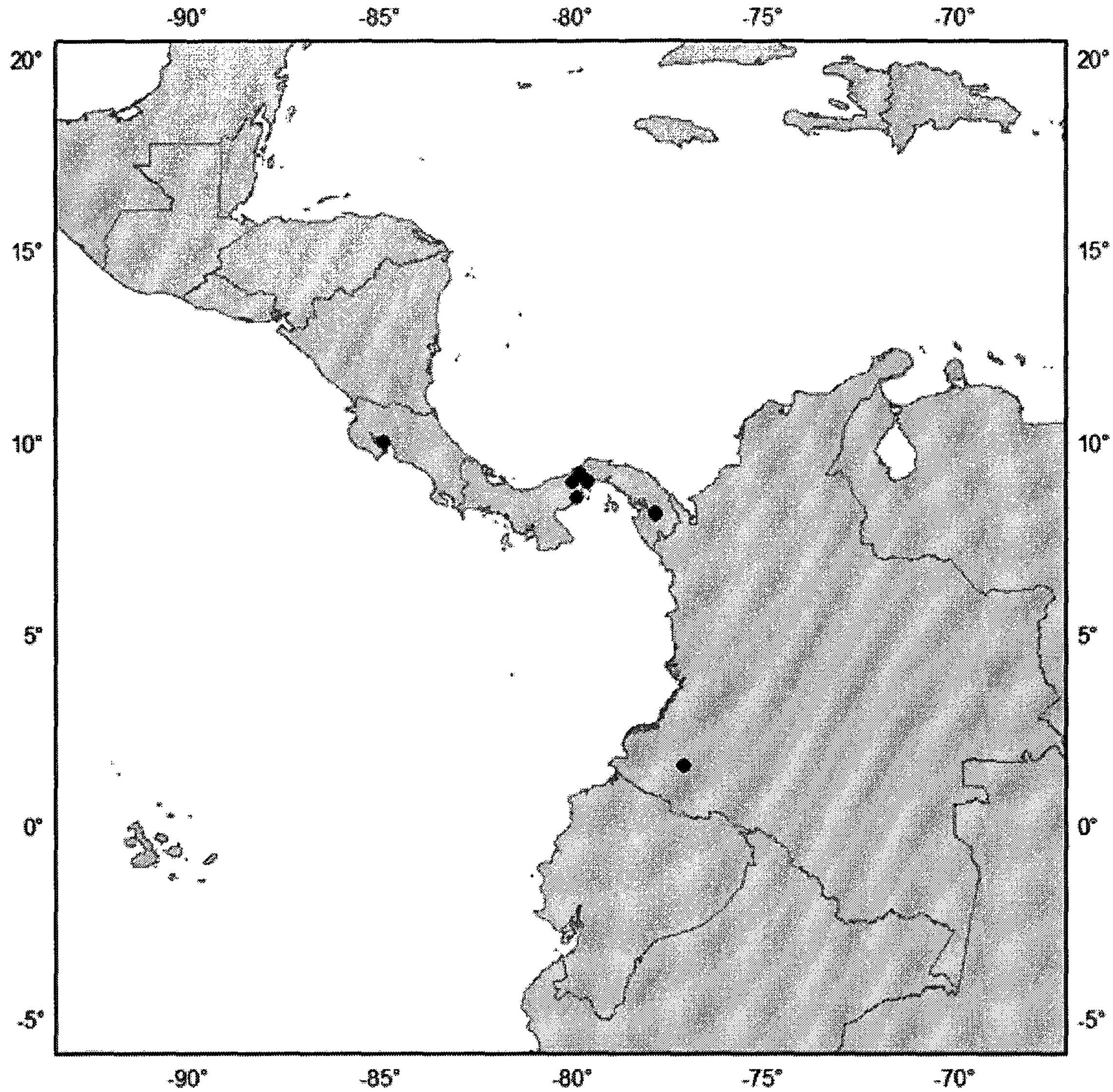


Figure 1.8: Occurrences of *Trinectes fluviatilis* specimens included in this study.

Trinectes fonsecensis (Günther 1862)

Figures 1.9–1.11, Tables 1.1–1.4 & 1.7

Synonym(s). — *Solea fonsecensis* Günther 1862, *Solea panamensis* Steindachner 1876

Common name(s). — Spottedfin sole, Fonseca sole, Sole tachetée, Guardaboya, Guardaboya tapadera, Lenguado Redondo, Sol rayado, Suela rayada

Materials examined. — ***Trinectes fonsecensis***, 71 specimens (22.34–172.43 mm)

Solea fonsecensis

Holotype: BMNH 1848.3.18.189, 1(82.60 mm), Gulf of Fonseca, Honduras.

Other material: USNM 361542, 7(73.79-130.97 mm), Buenaventura, Colombia, USNM 361528, 1(152.43 mm), 01°42'--" N 079°00'--" W, Colombia; USNM 361521, 1(152.75 mm), Buenaventura, Colombia; USNM 361524, 2(112.02–117.93 mm), Buenaventura, Colombia; USNM 361525, 1(89.31 mm), 06°58'--" N 077°41'--" W, Buenaventura, Colombia; USNM 361526, 2(103.71–121.39 mm), 06°58'--" N, Humboldt Bay, Colombia; USNM 361527, 1(128.51 mm), 06°58'--" N 077°41'--" W, Buenaventura, Colombia; LACM 33806–102, 2(93.55–131.44 mm), Puntarenas, Costa Rica; USNM 121905, 1(53.04 mm), El Salvador; SU 48834, 1(77.48 mm), Gulf of Fonseca, La Union, El Salvador; USNM 366791, 1(110.4 mm), 13°07'--" N 087°52'--" W; 13°10'--" N 087°48'--" W, El Salvador; AMNH 32923, 3(32.91–40.86 mm), Guatemala; SIO 62–70, 3(79.26–91.60 mm), 22°00.5' – 02' N, Mexico; SIO 63–517, 1(104.13 mm), 14°45'--" N, Golfo de Tehuantepec, Mexico; UMMZ 171931, 2(84.09–85.99 mm), Sonora, Rio Yaqui, ca. 5 miles West of Potrun, Yaqui delta, Mexico; UMMZ 192147, 15(38.81–56.07 mm), 21°50'--" N, Nayarit, Rio Grande de Santiago above HWY 15 crossing, Mexico; USNM 130871, 4(61.02–72.70 mm), Tepic, Mexico; ANSP 146807, 1(40.42 mm), Panama; SU 496, 1(97.86 mm), Panama; SU 6763, 1(153.23 mm), Panama; USNM 050332, 1(120.62 mm), Panama; USNM 065404, 1(144.68 mm), Panama Bay, Panama; USNM 076826, 1(172.43 mm), Panama city, Panama; USNM 081019, 2(134.85–139.31 mm), MKT Panama, Canal zone, Panama; USNM 081020, 2(128.76–136.59 mm), Panama MKT Pan., Panama; USNM 165540, 7(22.34–42.96 mm), Rio Chorrera, Panama; UMMZ 164553, 4(51.92–56.36 mm) No data.

Solea panamensis

Holotype: NMW 8023, 1(154.70 mm), Panama.

Other material: N/A

Diagnosis. — A species of *Trinectes* with the following combination of characteristics: caudal fin with dark spotting (Fig. 1.10); 20 caudal vertebrae; nine or more conspicuous darkly pigmented transverse bands on eyed-side body, excluding head (Fig. 1.10); nine pterygiophores anterior to the neural spine of the third precaudal vertebra (Fig. 1.3; Fig. 2.4); presence of coracoscapular complex on eyed-side and blind-side pectoral fins.

Description. — Morphometrics of type and non-type specimens are given in Table 1.7. Body long and oval, reaching 172.4 mm (measured specimens). Head short, 23.9% to 33.5% (mean = 29.9%), deep, 30.9% to 45.4% (mean = 38.5%) and rounded. Body shallow, body depth 50.5% to 65.5% (mean = 56.0%). Eyed-side gill opening extending ventrally to ventral eye. Large eyed-side anterior nostril with ragged-edged margin absent of cirri; presence of cirri around base of nostril. Blind-side posterior nostril thick tube of medium length. Long fleshy tentacles covering blind-side head and opercular regions (Fig. 1.9B). Many short tentacles projecting from anteriormost rays of blind-side dorsal fin. Large and distinctly circular caudal fin with wide base, caudal fin base depth 10.8% to 20.3% (mean = 16.2%). Eyed-side and blind-side pelvic fins short, 11.3% to 17.8% (mean = 13.7%) and 11.0% to 16.2% (mean = 13.4%), respectively. Eyed-side pectoral fin, when present, rudimentary, rarely with more than three short rays. Blind-side pectoral fin absent. Body thin, 8.0% to 14.4% (mean = 9.7%). Longest dorsal ray 10.9% to 18.9% (mean = 15.1%), longest anal ray 11.8% to 21.2% (mean = 15.8%). Dorsal and anal fins longest in posterior third of body.

Preorbital head length moderate, 23.3% to 33.4% (mean = 28.9%) in HL. Postorbital head length is wide, 46.2% to 60.7% (mean = 54.1%) in HL. Snout of moderate length, 29.0% to 72.6% (mean = 34.5%). Posterior corner of mouth on eyed-side reaching half of ventral eye. Eyed-side mouth long, 27.7% to 69.1% (mean = 33.8%) in HL, with slight curve. Blind-side mouth short, 17.1% to 61.2% (mean = 22.8%), curving downward. Nostril to snout distance, 17.1% to 63.0% (mean = 25.0%) in HL. Eyes medium-sized, ventral eye diameter 9.1% to 20.2% (mean = 12.5%) in HL. Interorbital space scaly, distance between orbits approximately half in length to the ventral eye diameter, 5.2% to 10.9% (mean = 7.7%) in HL. Width of orbits of moderate length, 11.3% to 26.6% (mean = 16.7%). Eyed-side opercular region very scaly. Lower lip with many short, lightly-branched fimbriae (Fig. 1.4B). Scattered patches of cirri common on eyed-side body (Fig. 1.10). Frequency distributions of the following meristics are shown in Table 1.1–1.4: 55–62 dorsal fin rays, 40–46 anal fin rays, 19–21 caudal vertebrae, 9 precaudal vertebrae, 1–5 eyed-side pectoral fin rays, no blind-side pectoral fin rays, 5 eyed-side pelvic fin rays, and 5 blind-side pelvic fin rays.

Colour of preserved specimens. — Body light to dark brown, with 9 to 11 darkly pigmented transverse bands extending from the tip of the dorsal fin rays to the tip of the anal fin rays, between the base of the caudal fin to the vertical of the gill opening (i.e. excluding caudal fin and head). Head with an additional 2 to 4 pigmented bands extending from tip of the dorsal fin rays to the lateral line; bands shorten anteriorly. Dark spotting common on eyed-side body, notably along lateral line. Caudal fin also with several distinct spotting. Blind-side pigmentation typically yellowish-beige or light-brown with occasional dark blotches, lighter than that of eyed-side body.

Distribution. — *Trinectes fonsecensis* is a Pacific species distributed from the Gulf of California to Ecuador (Fig. 1.11). Grove & Lavenberg (1997) reportedly took two specimens from the Galápagos, but these were not analyzed in this study. *Trinectes fonsecensis* is a euryhaline species and is often known to occur in brackish water, such as river mouths and coastal estuaries (Castro-Aguirre 1978). These fish often inhabit flat sand bottoms (Allen & Robertson 1994). Fry and juveniles of this species are known to penetrate freshwater (Bussing 1998).

Remarks. — The original description is by Günther (1862) with holotype collected on the coast of Honduras, Gulf of Fonseca. *Solea panamensis* was originally described by Steindachner 1876. Our analysis of the holotype specimen is in agreement with our description of *Trinectes fonsecensis* (see Table 1.7), including the presence of the following diagnostic features: 11 darkly pigmented transverse bands, dark spots on a round caudal fin, and long, fleshy tentacles covering the blind-side head and operculum.

Comparisons. — *Trinectes fonsecensis* can be distinguished from all *Trinectes* species in having 9 or more pigmented transverse bands on the eyed-side body, as well as a large, round, distinctly spotted caudal fin. It can be further distinguished from all congeneric species, except *T. paulistanus*, in having 20 caudal vertebrae. It most closely resembles the Atlantic species *T. maculatus* and *T. paulistanus* in body shape, size, and general appearance. *Trinectes fonsecensis* can be further distinguished from *T. maculatus* in having: 5 pelvic fin rays on both sides as opposed to 4, and 1 to 3 eyed-side pectoral fin rays as opposed to none. *Trinectes fonsecensis* can be further distinguished from *T. paulistanus* in having brown pigmentation often with darker spotting as opposed to beige pigmentation without spotting. Young (i.e. $\geq$ 50 mm) specimens of *T. fonsecensis* are often mistaken for *T. fluviatilis*, but can be further distinguished in having a greater caudal fin base depth.

Table 1.7: Twenty-two morphometric variables of body shape in *Trinectes fonsecensis* (n = 71). Proportional measurements of both standard length (% SL) and head length (% HL) are included. Measurements for the holotype of both *Solea panamensis* and *S. fonsecensis* are shown separately, and combined with non-type specimens under 'All specimens'. Included are the ranges, means (in parentheses), and standard deviations (SD). Measurements and abbreviations are described in Appendix B.

	Holotype of *Solea panamensis* NMW 8023	Holotype of *Solea fonsecensis* BMNH 1848.3.18.189	All specimens (n = 71)	SD
SL (mm)	154.7	82.6	22.3–172.4 (86.3)	39.5
TL (mm)	197.4	106.4	29.5–210.0 (111.0)	48.2
% SL				
HL	23.8	29.1	23.8–33.5 (29.9)	1.8
BD	58.7	54.7	50.5–65.5 (56.0)	3.2
HD	33.6	37.0	30.9–45.4 (38.5)	3.0
CFBD	17.6	17.3	10.8–20.3 (16.2)	2.0
PelES	11.3	13.7	11.3–17.8 (13.7)	1.4
PelBS	11.1	12.7	11.0–16.2 (13.4)	1.2
PecES	-	2.9	0–7.7 (3.2)	2.3
PecBS	-	-	0–1.9 (0)	0.2
Th	8.2	9.4	8.0–14.4 (9.7)	1.1
LDR	11.8	15.9	10.9–18.9 (15.1)	2.4
LAR	11.8	12.4	11.8–21.2 (15.8)	2.1
% HL				
PreHL	27.6	23.3	23.3–33.4 (28.9)	2.1
PosHL	55.0	57.9	46.2–60.7 (54.1)	2.9
SnL	35.0	54.2	29.0–72.6 (34.5)	6.1
MES	33.3	31.2	27.7–69.1 (33.8)	5.1
MBS	25.8	20.8	17.1–61.2 (22.8)	5.4
NSD	17.1	17.5	17.1–63.0 (25.0)	5.6
EdV	11.6	10.8	9.1–20.2 (12.5)	2.4
DBO	7.6	5.4	5.2–10.9 (7.7)	1.3
WO	20.0	18.3	11.3–26.6 (16.7)	3.4

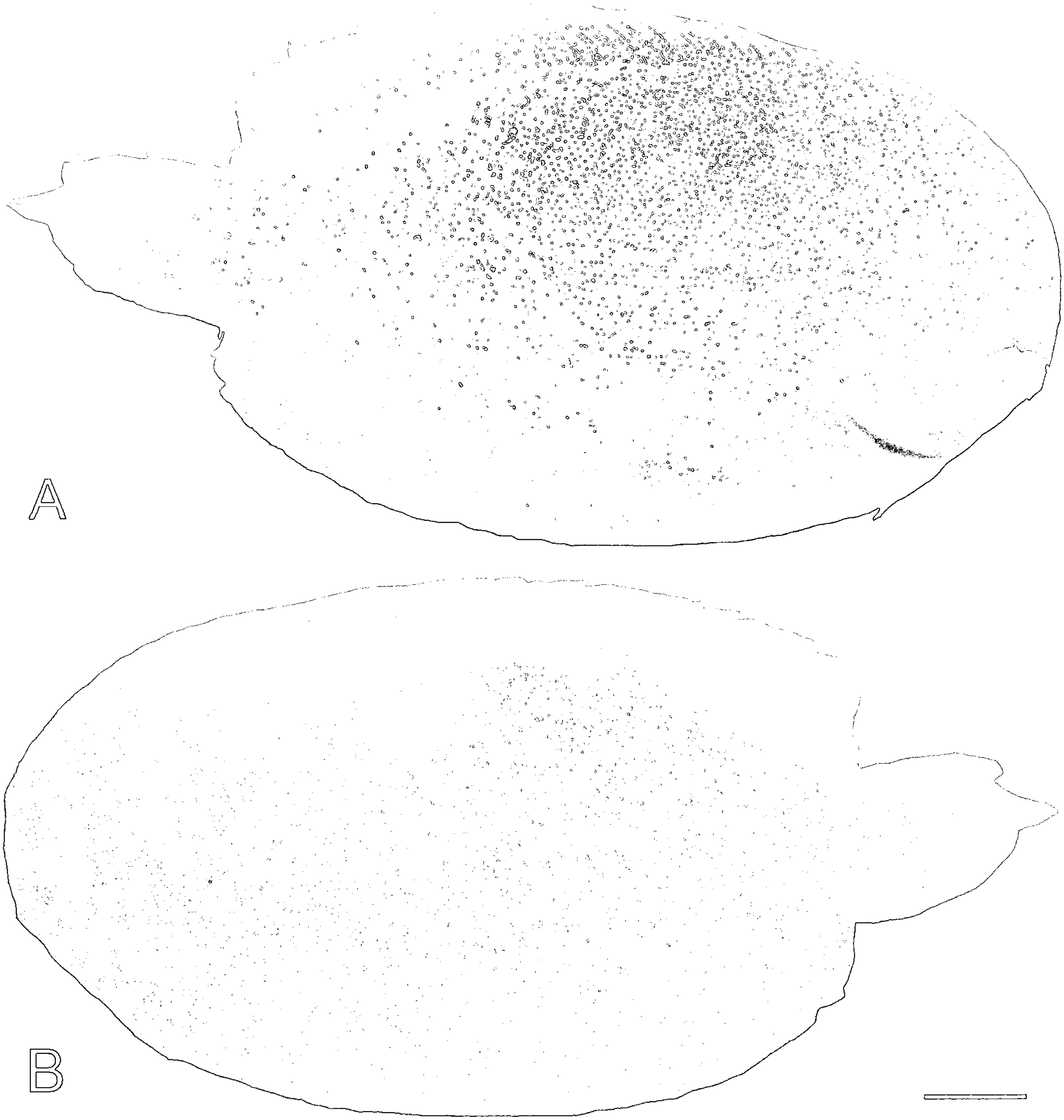


Figure 1.9: Eyed-side (A) and blind-side (B) of the holotype of *Trinectes fonsecensis*, BMNH 1848.3.18.189, 82.6 mm, Honduras (Gulf of Fonseca). The scale bar corresponds to 10 mm.

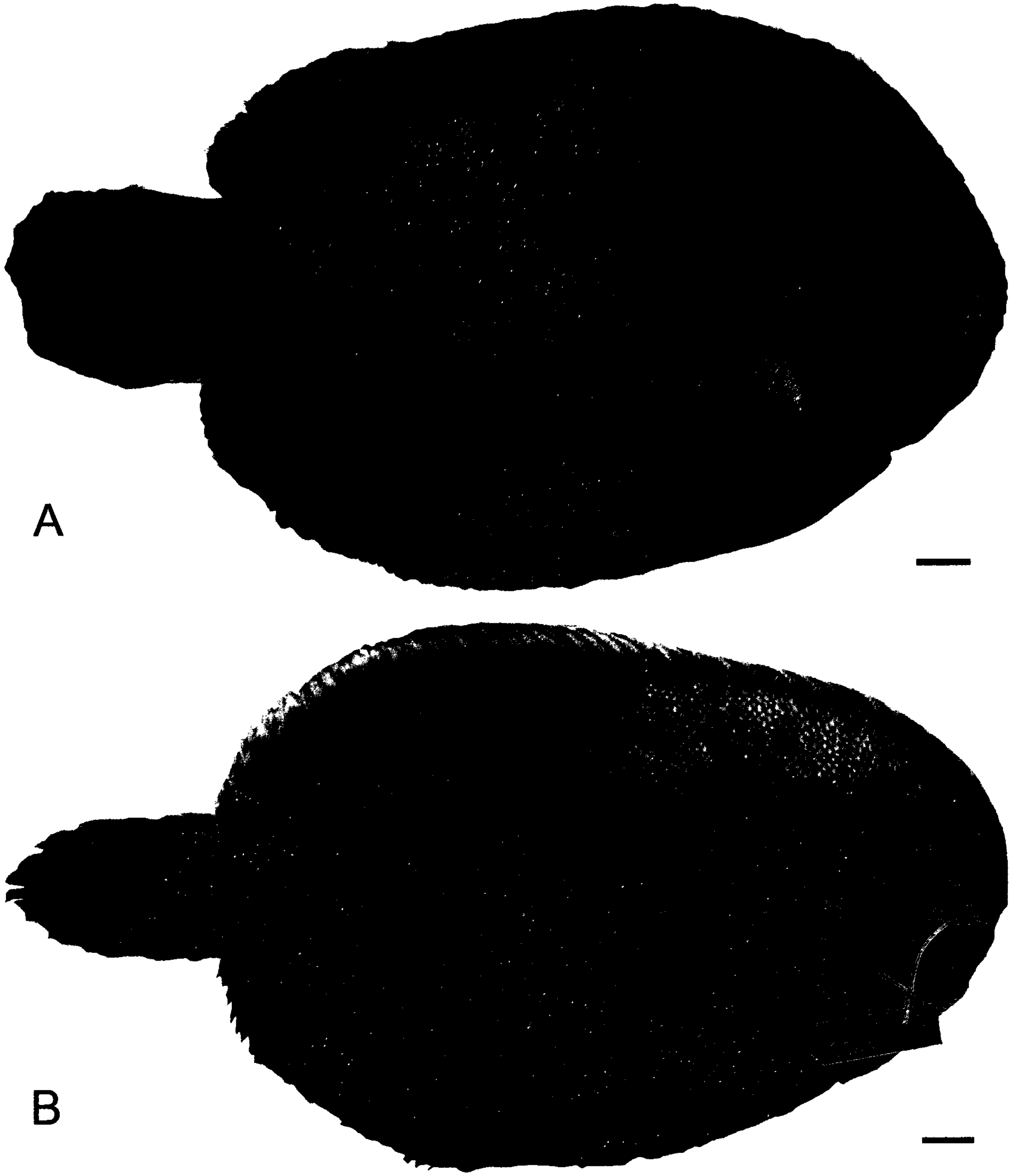


Figure 1.10: Variation in the eyed-side pigmentation in *Trinectes fonsecensis*. (A) USNM 361526, 121.4 mm; (B) holotype of *Solea panamensis*, NMW 8023, 154.7 mm. Note the pigmented transverse bands throughout the body and the circular spots on the caudal fin.

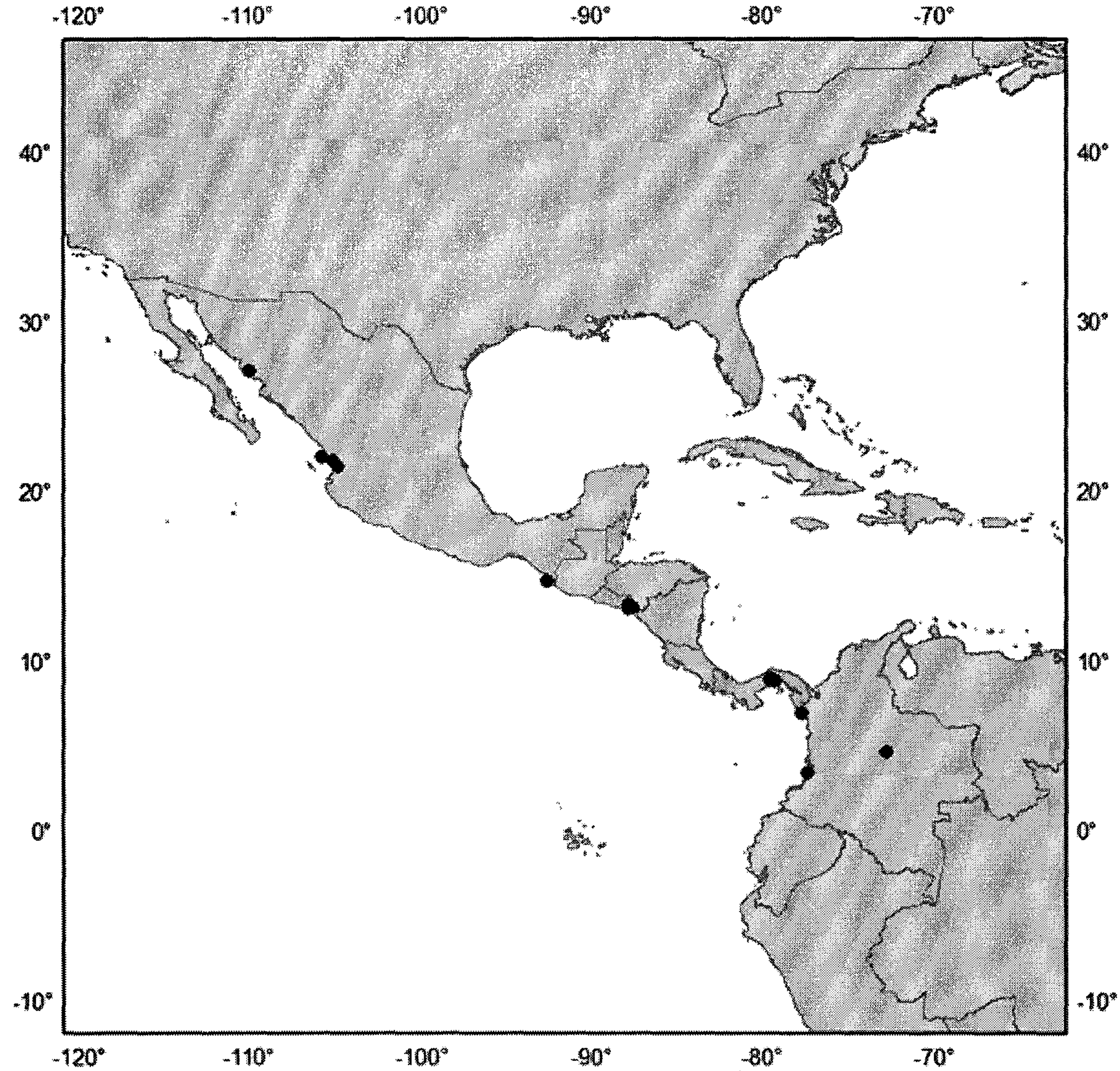


Figure 1.11: Occurrences of *Trinectes fonsecensis* specimens included in this study.

Trinectes inscriptus (Gosse 1851)

Figures 1.12–1.14, Tables 1.1–1.4 & 1.8

Synonym(s). — *Monochirus inscriptus* Gosse 1851, *Monochir reticulatus* Poey 1860

Common name(s). — Scrawled sole, Sokkeloantura, Sole réticulée, Acedía reticulada, Arreves pintado, Miracielo, Suela reticulada, Tapaculo

Materials examined. — ***Trinectes inscriptus***, 108 specimens (17.76–83.02 mm)

Monochirus inscriptus

Holotype: BMNH 1846.10.28.24, 1(49.40 mm), Caribbean Sea, Jamaica

Other material: ANSP 126006, 1(51.35 mm), North of entrance to Hope Town harbor, Elbow Cay, Great Abaco, Bahamas; FMNH 104721, 1(54.09 mm), Turneffe, NW, 5 miles South of Rendezvous Points, Belize; MNRJ 30829 8(31.58□61.99 mm), Rio de Janeiro, Angra dos Reis, Brazil; MZUSP 51065, 4(49.81–67.46 mm), Macae, Rio de Janeiro, Brazil; FMNH 66378, 1(61.72 mm), Caribbean Sea, NA, Oregon; FMNH 65427, 1(72.41 mm), 18°12'00" N, Caribbean Sea, NA, Oregon; FMNH 65426, 2(66.88–69.27 mm), 18°30'00" N, Caribbean Sea, NA, Oregon; FMNH 65430, 26(57.17–83.02 mm), Caribbean Sea, NA, Oregon; USNM 332471, 1(48.15 mm), 23°01'08" N 082°43'06" W, Caribbean Sea, Mosquito River, West of Havana, Cuba; USNM 332464, 2(34.10–48.04 mm), 23°01'08" N 082°43'06" W, Mosquito River, West of Havana City, North Coast, Cuba; USNM 331922, 1(55.2 mm), Caribbean Sea, Pasa Boca Del Seron, Cuba; USNM 357181, 3(35.57–46.05 mm), 23°01'30" N 082°42'--" W, Rio Guajaibon, West of Havana, North coast, Cuba; CAS 11994, 15(38.47–53.63 mm), 085°16'30" W, West indies, prov. Matanzas, Rio Yumuri Drainage, Rio Yumuri outlet to ocean at Matanzas; below fresh water, Cuba; USNM 205013, 1(47.84 mm), R. W. I. at extreme mouth of Merou River, Dominica; USNM 205011, 3(63.09–69.75 mm), 19°48'--" N 70°26'--" W, Hispaniola, Caribbean Sea, Dominican Republic; USNM 163272, 1(50.24 mm), Caribbean, Montego River, Jamaica; ANSP 144512, 1(42.76 mm), West Indies, Curacao, Inner Piscadera Bay, Netherland Antilles; SU 18587, 15(17.76–58.92 mm), Rio Portogandi, Mosquito Point, San Juan, Panama; USNM 125476, 2(70.23–71.55 mm), Caribbean Sea, Puerto Rico; USNM 050193, 1(52.77 mm), Aguadilla, Porto Rico, Puerto Rico; ANSP 142987, 1(53.88 mm), Rincon beach, Puerto Rico; UMMZ 175874, 1(55.99 mm), San Juan, Dos Hernandos Bridge, Puerto Rico; USNM 205012, 1(80.22 mm), 18°13'--" N 64°21'--" W, Puerto Rico; ANSP 70666, 1(45.92 mm), Mangrove Island, South of Virginia Keys, South of Miami, Florida, USA; USNM 03500, 1(45.34 mm), Gulf of Mexico, Key West, Florida, USA; USNM 179299, 1(37.79 mm), Caribbean Sea, Los Roques Islands, Espenky, Venezuela; USNM 286851, 3(55.44–57.68 mm), 11°13'--" N 060°52'--" W, Caribbean Sea, Venezuela; AMNH 215235, 4(32.01–33.28 mm), No data; USNM 44120, 1(55.04 mm), No data.

Monochir reticulatus

Type: N/A

Other material: N/A

Diagnosis. — A species of *Trinectes* characterized by the following combination of characteristics: eyed-side head, body, and vertical fins covered in an intricate network of dark lines on a lighter background (Fig. 1.13); eyed-side pectoral fin well developed, with 2–4 rays and membranous connections (Fig. 1.12A; Fig. 1.13); 1–3 blind-side pectoral fin rays; patches of body covering eyed-side body (Fig. 1.12A; Fig. 1.13); presence of coracoscapular complex on eyed- and blind-side pectoral fins.

Description. — Morphometrics of type and non-type specimens are given in Table 1.8. Body small and oval, reaching 83.0 mm (measured specimens). Head short, 26.8% to 36.4% (mean = 31.2%), and deep, head depth 32.3% to 55.6% (mean = 42.2%). Body shallow, body depth 49.4% to 70.4% (mean = 59.9%). Eyed-side gill opening extending to ventral eye. Eyed-side anterior nostril large tube, positioned anterior and slightly dorsal to ventral eye. Blind-side posterior nostril thick tube of medium length. Short fleshy tentacles covering blind-side head. Several short tentacles projecting from anteriormost rays of blind-side dorsal fin. Caudal fin large and rounded with wide base, caudal fin base depth 12.2% to 19.9% (mean = 15.8%). Eyed-side and blind-side pelvic fins short, 9.7% to 23.6% (mean = 14.7%) and 10.6% to 19.8% (mean = 13.5%), respectively. Eyed-side pectoral fin always present, composed of 1 to 3 rays. Rudimentary blind-side pectoral fin present, usually a single ray. Body thin, 7.3% to 12.5% (mean = 9.9%). Longest dorsal ray 14.0% to 29.7% (mean = 18.9%), longest anal ray 14.7% to 31.0% (mean = 19.7%). Dorsal and anal fins longer posteriorly, giving this species a rectangular-shaped posterior region.

Preorbital head relatively long, 21.7% to 34.8% (mean = 29.6%) in HL. Postorbital head relatively long 30.3% to 60.2% (mean = 51.7%) in HL. Snout of moderate length, 26.1% to 42.9% (mean = 33.7%). Eyed-side mouth long, 25.8% to 43.2% (mean = 33.4%) in HL, and curving downward. Posterior corner of eyed-side mouth reaching proximal quarter to half of ventral eye. Blind-side mouth short, 18.5% to 37.7% (mean = 25.8%) in HL, and sharply curving downward. Nostril to snout distance 19.3% to 42.7% (mean = 28.0%) in HL. Eyes average-sized, ventral eye diameter 11.3% to 20.5% (mean = 14.4%) in HL. Interorbital space approximately half to one eye diameter, 4.4% to 12.8% (mean = 7.7%) in HL. Width of orbits moderate, 13.5% to 25.4% (mean = 18.6%) in HL. Eyed-side opercular region scaly, often covered with cirri. Lower lip with many short lightly-branched fimbriae (Fig. 1.4B). Eyed-side body covered in patches of cirri, often aggregating along bands and lateral line (Fig. 1.12A; Fig. 1.13). Blind-side opercular region with naked patch; blind-side head with few, short, fleshy tentacles. Frequency distributions of the following meristics are shown in Tables 1.1–1.4: 51–63 dorsal fin rays, 36–46 anal fin rays, 18–20 caudal vertebrae, 9 precaudal vertebrae, 1–5 eyed-side pectoral fin rays, 0–3 blind-side pectoral fin rays, 5 eyed-side pelvic fin rays, and 5 blind-side pelvic fin rays.

Colour of preserved specimens. — Body and vertical fins with olive to dark-brown pigmentation, overlain with darker, distinct intricate network of lines. Body with 5 to 7 indistinct, unpigmented transverse bands. Caudal fin usually unpigmented, occasionally with lighter body pigmentation at base. Blind-side generally unpigmented.

Distribution. — *Trinectes inscriptus* is an Atlantic species distributed from Key West (Florida, USA) to as far South as Venezuela (Fig. 1.14). This species occurs throughout much of the Caribbean Sea, including (but not exclusive to) these countries: Jamaica, Cuba, Barbados, Hispaniola, Puerto Rico, Saint Vincent, and Trinidad and Tobago. It is a coastal species, occurring in marine and estuarine waters (McEachran & Fechhelm 2005). Also known to inhabit small, mangrove-lined tidal creeks in only a few feet of water (Böhlke & Chaplin 1993).

Remarks. — The original description is by Gosse (1851) with holotype taken from Jamaica. He based his description on a single specimen, collected with an insect net among weeds in shallow water, with the following notable characteristics (original description includes more than the following): "body with netted pattern of confluent lines", "right pectoral [eyed-side] composed of two minute filaments, left [blind-side] composed of a single one almost obsolete", "anal and dorsal united to the caudal", "form nearly oval, slightly tapering", "caudal rounded", "mouth and chin fringed with short bristles", and "mouth much decurved" (Gosse 1851:52). Though fairly short, Gosse (1851) included the following two characters that remain diagnostic to this species: presence of eyed-side pectoral fins, with two rays; and the presence of one blind-side pectoral fin ray. Of note is the mention of "anal and dorsal united to the caudal fin", which should be regarded as an error by Gosse as all achirids have a free caudal fin from the dorsal and anal.

Monochir reticulatus was originally described by Poey (1860). No types of this species are known (Eschmeyer 2009). Poey (1860) claimed that this species differed from Gosse's (1851) *M. inscriptus* (=*T. inscriptus*) in having: a free caudal fin as opposed to united to the dorsal and anal fin, a brown pigmentation with rounded reticulations as opposed to bluish grey with oblong reticulations, and the presence of transverse bands as opposed to an absence of bands. Of these characters, the first can be dismissed as an error by Gosse (1851), and the second and third can be accounted for due to the intraspecific variation of these characters within *T. inscriptus* (transverse bands are always present, but occasionally nearly invisible).

Monochir reticulatus was first synonymized to *inscriptus* by Jordan & Goss (1889:312), who looked at specimens from Key West and Haiti and determined that the specimens "belong undoubtedly to the species called *reticulatus* by Poey, and this is apparently not different from the *inscriptus* of Gosse, as the agreement with the latter is even closer than with the former description."

My designation of Poey's (1860) *Monochir reticulatus* is to synonymize it with Gosse's (1851) *inscriptus*, as was suggested by Jordan & Goss (1889) and followed by almost all authors (e.g. Meek & Hildebrand 1928, Chabanaud 1928, Norman 1934). I based this designation on the following evidence presented in Poey (1860) in describing *M. reticulatus*: presence of eyed- and blind-side pectoral fin (4 and 2 rays, respectively), highly ciliated body, longest vertical fin rays found at posterior quarter of body (first three-quarters short), and brown in pigmentation covered with numerous, round, darker brown reticulations.

Comparisons. — *Trinectes inscriptus* can be distinguished from all congeners in having: an intricate network of dark lines on lighter background covering eyed-side head, body, and vertical fins; 1 blind-side pectoral fin ray, as opposed to none, and 2–4 long eyed-side pectoral fin rays 2–4 with membranous connections, as opposed to 0–3 short unconnected rays.

Table 1.8: Twenty-two morphometric variables of body shape in *Trinectes inscriptus* (n = 109). Proportional measurements of both standard length (% SL) and head length (% HL) are included. Measurements for the holotype are shown separately, and combined with non-type specimens under 'All specimens'. Included are the ranges, means (in parentheses), and standard deviation (SD). Measurements and abbreviations are described in Appendix B.

	Holotype of *Solea inscripta* BMNH 1846.10.28.24	All specimens (n = 109)	SD
SL (mm)	49.4	17.8–83.0 (54.7)	15.0
TL (mm)	64.9	23.3–109.8 (71.9)	19.6
% SL			
HL	30.6	26.8–36.4 (31.2)	1.5
BD	56.3	49.4–70.4 (59.9)	4.4
HD	39.5	32.3–55.6 (42.2)	4.0
CFBD	14.4	12.2–19.9 (15.8)	1.4
PelES	13.6	9.7–23.6 (14.7)	1.8
PelBS	11.3	10.6–19.8 (13.5)	1.5
PecES	7.9	0–11.5 (7.9)	1.9
PecBS	3.8	0–6.4 (3.5)	1.4
Th	7.3	7.3–12.5 (9.9)	1.1
LDR	17.2	14.0–29.7 (18.9)	2.4
LAR	18.6	14.7–31.0 (19.7)	2.3
% HL			
PreHL	32.5	21.7–34.8 (29.6)	2.7
PosHL	52.3	30.3–60.2 (51.7)	4.0
SnL	33.1	26.1–42.9 (33.7)	3.2
MES	27.8	25.8–43.2 (33.4)	3.3
MBS	18.5	18.5–37.7 (25.8)	3.1
NSD	21.2	19.3–42.7 (28.0)	3.5
EdV	12.6	11.3–20.5 (14.4)	1.6
DBO	8.6	4.4–12.8 (7.7)	1.5
WO	17.2	13.5–25.4 (18.6)	2.7

Figure 1.12: Eyed-side (A) and blind-side (B) of the holotype of *Trinectes inscriptus*, BMNH 1846.10.28.24, 49.4 mm, Jamaica (Caribbean Sea). The scale bar corresponds to 10 mm.

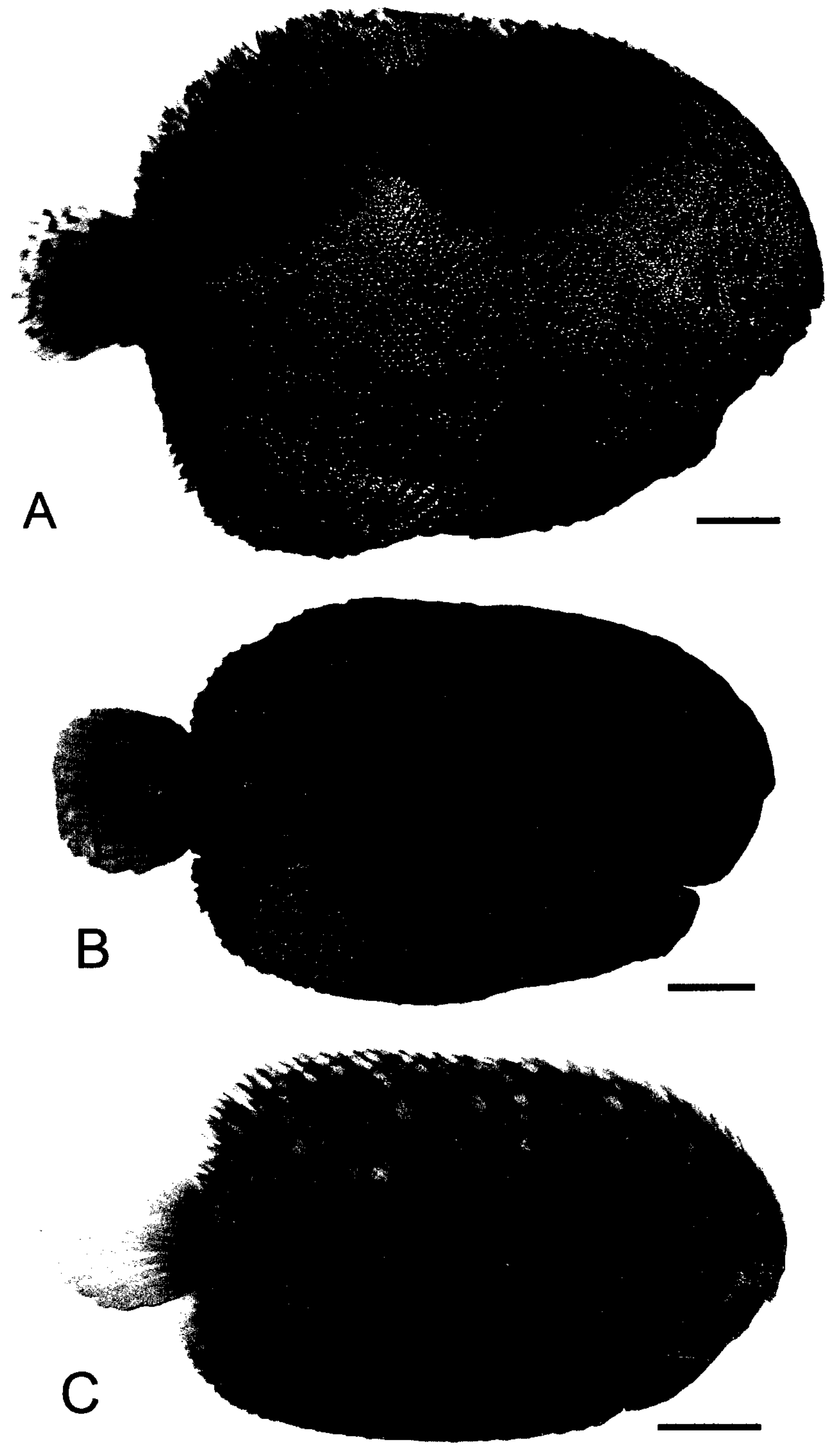


Figure 1.13: Variation of the eyed-side pigmentation within *Trinectes inscriptus*. (A) FMNH 65430, 78.3 mm; (B) USNM 331922, 55.2 mm; (C) FMNH 104721, 54.1 mm. Scale bars correspond 10 mm.

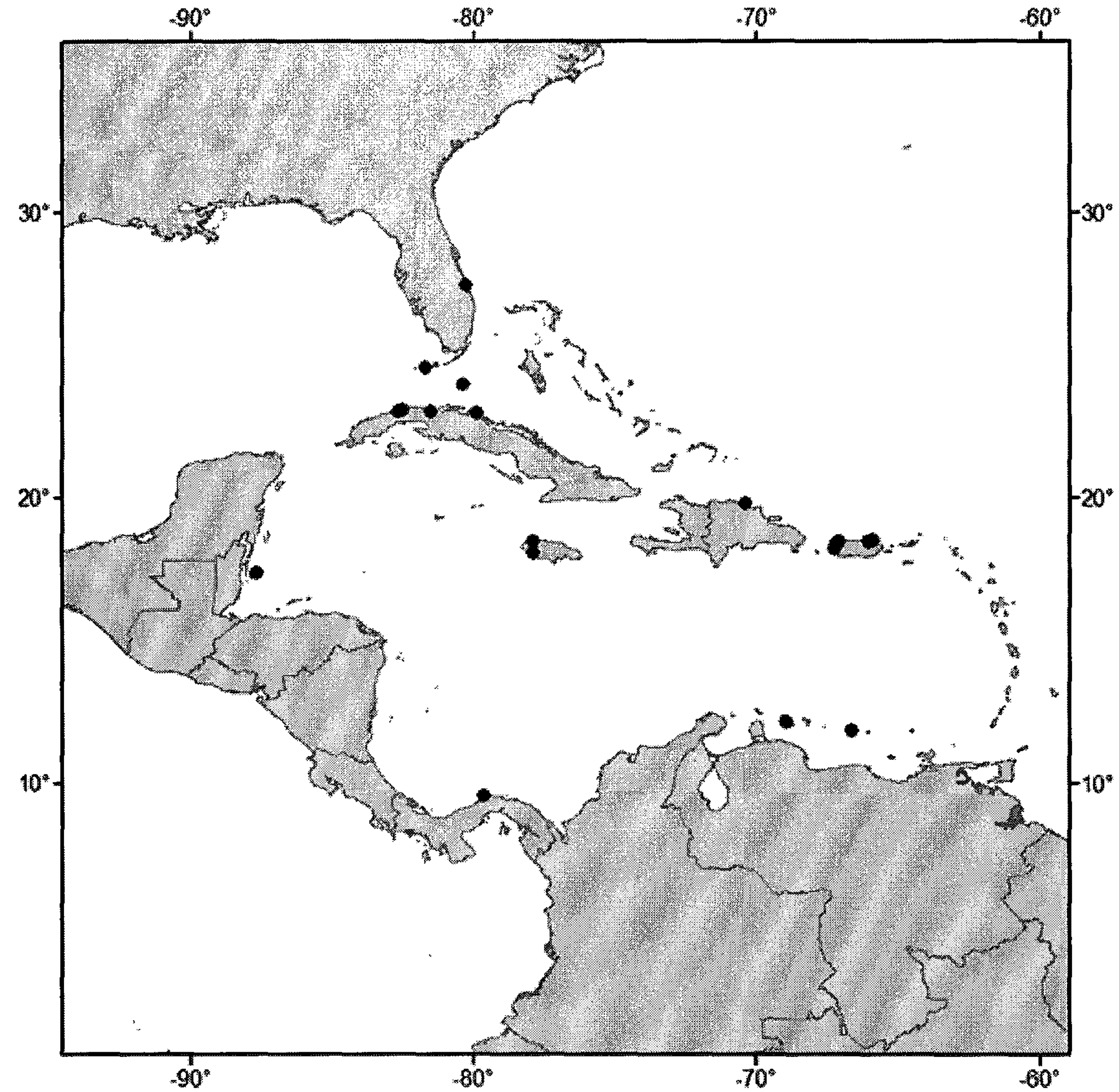


Figure 1.14: Occurrences of *Trinectes inscriptus* specimens included in this study.

Trinectes maculatus (Bloch & Schneider 1801)

Figures 1.15–1.17, Tables 1.1–1.4 & 1.9

Synonym(s). — *Pleuronectes maculatus* Bloch & Schneider 1801, *Achirus fasciatus* Lacépède 1802, *Pleuronectes mollis* Mitchill 1814, *Trinectes scabra* Rafinesque 1832

Common name(s). — Hogchoker, Plettet ferskvandstunge, Freshwater flounder, Freshwater sole, Järviantura, Järvikampela, Sole bavoche, Amerikanische Seezunge, Gefleckte Flunder, Sandflunder, Zwergflunder, Achira, Aramaçá, Linguado-lixa, Solha, Solha-mamona, Tapa, Suela tortilla

Materials examined. — ***Trinectes maculatus***, 105 specimens (49.32–132.00 mm)

Pleuronectes maculatus

Holotype: ZMB 7408, 1(130.60 mm), location unknown.

Other material: USNM 036905, 2(82.24–109.64 mm), Caribbean, Jamaica; USNM 163611, 4(53.96–70.52 mm), 83°54'--" W, Vera Cruz, 20 km Jesus Carranza, Mexico; USNM 290996, 1(103.03 mm), 06°16'--" N 055°36'--" W, Suriname; AMNH 30139, 2(68.54–70.15 mm), North Carolina, USA; AMNH 67257, 4(59.22–132.00 mm), New Jersey, USA; AMNH 67729, 4(82.18–96.90 mm), Maryland, USA, AMNH 74370, 4(76.83–101.23 mm), South Carolina, USA; ANSP 86613, 5(56.58–71.59 mm), New Castle Co., Delaware River, Delaware, USA; ANSP 140013, 28(52.57–111.20 mm), Dennis Cove, New Jersey, USA; FMNH 16158, 3(96.04–100.04 mm), Beaufort, North Carolina, USA; FMNH 40232, 4(49.34–111.04 mm), 57°47' W, within 50 miles of Corpus Christi, Texas, USA; FMNH 46364, 3(101.14–108.60 mm), Gulf of

Mexico, 29°35'00" N, 57°47' W; FMNH 50988, 12(59.03–81.29 mm), -38.483900, Gulf of Mexico, probably off Chandeleur Islands, Louisiana, USA; FMNH 64240, 1(77.67 mm), 27°14'42" N, -38.483900, Gulf of Mexico; SU 40552, 4(73.70–75.30 mm), Galveston, Texas, USA; SU 49869, 4(84.56–92.92 mm), Rappahannock river, Tafts whf; to Smith Pt. Light, Potomac, Virginia, USA; UMMZ 158833, 1(97.41 mm), Barnstable, Pines Beach, Cotuit, Massachusetts, USA; UMMZ 199073, 3(71.23–73.82 mm), 054°54'00" W, Galveston, Galveston Bay, near piers at Galveston, Texas, USA; UMMZ 244731, 11(71.78–84.52 mm), St. Simon's Sound from back river to St. Simon's Light, Georgia, USA; USNM 197444, 2(81.09–91.75 mm), Arkansas Bay, Gulf of Mexico, Texas, USA; USNM 156667, 1(84.18 mm), 27°32'30" N 097°09'00" W, Gulf of Mexico, South-East of Corpus Christi, Texas, USA.

Achirus fasciatus

Type: N/A

Other material: SU 1769, 1(78.25 mm), Beaufort, North Carolina, USA, AMNH 2494, 3(56.28–61.60 mm), Florida, USA

Pleuronectes mollis

Type: N/A

Other material: N/A

Trinectes scabra

Type: N/A

Other material: N/A

Diagnosis. — A species of *Trinectes* characterized by the following combination of characteristics: eyed-side and blind-side pelvic fins with 4 rays; pectoral fins usually absent (Fig.

1.15A); median fins covered with dark lines or striations (Fig. 1.16); 6–8 pigmented transverse bands on eyed-side body.

Description. — Morphometrics of type and non-type specimens are given in Table 1.9. Body oblong and oval, reaching body length of 132.0 mm (measured specimens). Head short, 24.9% to 33.3% (mean = 28.8%), deep, 27.3% to 50.1% (mean = 36.4%), and rounded. Body depth 47.9% to 64.3% (mean = 56.8%). Snout forming blunt hook. Eyed-side gill opening almost extending to the ventral margin of the ventral eye. Eyed-side anterior nostril moderately-sized, often with cirri around base. Blind-side posterior nostril wide tube. Long fleshy tentacles covering blind-side head and opercular regions. Many short tentacles projecting from anteriormost rays of blind-side dorsal fin. Eyed-side opercular region very scaly. Caudal fin long and oval with wide base, caudal fin base depth 12.4% to 20.0% (mean = 16.5%). Eyed-side and blind-side pelvic fins short, 8.6% to 17.8% (mean = 14.5%) and 7.7% to 16.9% (mean = 14.0%). Pectoral fins wholly absent. Body thin 6.5% to 12.9% (mean = 14.0%). Longest dorsal ray 12.0% to 21.9% (mean = 17.7%), longest anal ray 14.4% to 21.0% (mean = 18.1%). Dorsal and anal fins longest in posterior third of body.

Preorbital head moderately long, 20.2% to 36.7% (mean = 28.3%) in HL. Postorbital head long, 48.1% to 64.4% (mean = 56.4%) in HL. Snout moderately long, 25.1% to 38.3% (31.2%) in HL. Eyed-side mouth moderately long, 22.3% to 39.4% (mean = 31.4%) in HL, and curved downward. Posterior corner of mouth on eyed-side nearly reaching half of ventral eye. Lower eyed-side lip with numerous short, lightly-branched fimbriae (Fig. 1.4B). Blind-side mouth short, 16.9% to 30.7% (mean = 22.2%) in HL. Nostril to snout distance 16.1% to 30.2% (mean = 23.5%) in HL. Eyes medium-sized, ventral eye diameter 7.8% to 16.1% (mean =

11.5%) in HL. Interorbital space scaly, distance between orbits nearly one orbit in diameter, 4.3% to 11.0% (mean = 7.2%) in HL. Width of orbits moderate, 9.6% to 19.8% (mean = 14.7%) in HL. Scattered patches of cirri common on eyed-side body. Frequency distributions of the following meristics are shown in Tables 1.1–1.4: 52–60 dorsal fin rays, 37–44 anal fin rays, 18–20 caudal vertebrae, 8–10 precaudal vertebrae, pectoral fins absent, 4 eyed-side pelvic fin rays, and 4 blind-side pelvic fin rays.

Colour of preserved specimens. — There is a lot of variation in the eyed-side body colour; from beige to dark brown background, usually with darker spots or blotches throughout body. Occasionally with alternating dark and light thick lines. Presence of 8 or fewer darkly pigmented transverse bands extending from tip of dorsal fin rays to tip of anal fin rays, from base of caudal to vertical of gill opening. Head with an additional 2–4 bands similar to those of body, extending from tip of dorsal fin rays to lateral line; bands shorten anteriorly. Median fins covered with many dark striated lines. Vertical fins therefore have striations extending from transverse bands and additional striations (usually two) that look very similar (but that do not extend along the body) in between these bands. Blind-side of adults typically varies with distribution; where specimens from northern range (Maine, USA, to North Carolina, USA) usually have distinct dark brown spots, and specimens from the southern range (South Carolina, USA, to Mexico) usually have an unspotted blind-side (Fig. 1.16).

Distribution. — *Trinectes maculatus* is an Atlantic species distributed from Maine (USA) to Mexico (Fig. 1.17). However, there are few records north of Cape Cod (Smith 1986). It is a coastal species, often found in brackish waters, such as in bays and estuaries (Smith 1986).

Members of this species are often found hundreds of kilometres from the sea in freshwater. They commonly inhabit non-vegetated, muddy or sandy bottoms (Reid 1954; Castanga 1955; Martin & Drewry 1978; Smith 1986).

Remarks. — Original description by Bloch & Shneider (1801) with assigned type locality "Habitat ad Tranquebariam" or "Tranquebar" (Eastern India), which was later found to be an error (Chabanaud 1930; Hubbs 1932). Norman (1928) identified no such species in the Indian fauna, and no record of this species has ever been reported from that area.

The synonymizations of *Trinectes scabra* and *Achirus fasciatus* to *Pleuronectes maculatus* were proposed by Chabanaud (1930) and supported by Hubbs (1932) (see Introduction). These synonymizations established *T. maculatus* at the type species of the genus (Hubbs 1932).

Chabanaud (1935a) divided *T. maculatus* into several subgroups (subspecies and natios), basing his subdivisions on several characters, including nostril size, nostril position, scale size, and scale shape, all of which we found to be taxonomically uninformative due to intraspecific variation. However, Chabanaud (1935a) also used locality and blind-side pigmentation in creating his subspecies (*T. m. maculatus* and *T. m. fonsecensis*) and natios (*T. m. m. maculatus*, *T. m. m. browni*, and *T. m. m. paulistanus*). Specifically, *T. m. m. maculatus* is found in the northern range of the species (Maine, U.S.A. to North Carolina, U.S.A.) and has the presence of dark spots on the blind-side, whereas and *T. m. m. browni* is found in the southern range of the species (South Carolina, U.S.A. to Mexico) and has no dark spots on the blind-side. Chabanaud (1939) eventually abandoned these subdivisions and recognized *T. maculatus* as an individual species.

However, the correlation between locality and blind-side pigmentation was further explored by Hubbs & Allen (1943). They concluded that *Trinectes maculatus* should be considered as a single valid species with two subspecies: *T. m. maculatus* as the northern subspecies, and *T. m. fasciatus* as the southern subspecies (Hubbs & Allen 1943). They used *fasciatus* as their subspecies after examining topotypes of *Achirus fasciatus* (=*T. maculatus*) at the Charleston Museum (Charleston, South Carolina) (Hubbs & Allen 1943). They determined that despite a few specimens showing faded spots, the blind-side of the majority of these fish was generally unpigmented (Hubbs & Allen 1943).

After extensive review of these subspecies, we found presence of both spotted and unspotted specimens from the northern and southern range (see Fig. 1.16 for variation in BS pigmentation). The northern range had considerably more variation in blind-side pigmentation than the southern range. Many lots (jars) of specimens supposedly collected in the same location were found to have both spotted and unspotted fish that were otherwise nearly identical (i.e. in pigmentation, diagnostic charactersistics, etc). Therefore, the blind-side pigmentaiton was found to be too variable and unreliable to distinguish these as two separate valid species. No additional morphometric evidence was found to support this relationship. We therefore determine that without further evidence to support the intraspecific variability within this group, the best course of action is to simply recognize *T. maculatus* as a single valid species, without subspecies, for which there is much variation in blind-side pigmentation.

Pleuronectes mollis was first described by Mitchill in 1814 in his study on the Fishes of New York. There are no types known (Eschmeyer 2009). Storer (1846) placed this species in *Achirus*, and Jordan (1923) supported this designation and synonymized *mollis* to *fasciatus*.

Following the synonymization of *P. maculatus* to *A. fasciatus*, *P. mollis* therefore became a synonym of *P. maculatus* (=*Trinectes maculatus*).

Our appraisal of Mitchill's original description supports this synonymization on the basis of the following characters: dark striations along the anal, dorsal and caudal fins, pectoral fins absent, and dark spots on the otherwise white to pale brown blind-side (Mitchill 1814). Furthermore, Mitchill's common name for this species is the "New York Sole", as it was discovered in New York, where *Trinectes maculatus* specimens with blind-side spotted are known to be found.

Comparisons. — *Trinectes maculatus* can be distinguished from all other congeners in having: 4 as opposed to 5 eyed-side and blind-side pelvic fin rays, and dark striations along the median fins. It most closely resembles the Atlantic species *T. paulistanus* and the Pacific species *T. fonsecensis* in body shape, size, and general appearance. *Trinectes maculatus* can be further distinguished from *T. paulistanus* in having a darkly pigmented eyed-side body as opposed to light beige pigmentation, and pigmented bands on eyed-side body and vertical fins as opposed to unpigmented bands. *Trinectes maculatus* can be further distinguished from *T. fonsecensis* in having: 6–8 as opposed to 9–11 transverse bands on body, and no eyed-side pectoral fin, whereas *T. fonsecensis* generally has at least one rudimentary ray.

Table 1.9: Twenty-two morphometric variables of body shape in *Trinectes maculatus* (n = 105). Proportional measurements of both standard length (% SL) and head length (% HL) are included. Measurements for the holotype are shown separately, and combined with non-type specimens under 'All specimens'. Included are the ranges, means (in parentheses), and standard deviations (SD). Measurements and abbreviations are described in Appendix B.

	Holotype of *Pleuronectes maculatus* ZMB 7408	All specimens (n = 105)	SD
SL (mm)	130.6	49.3–132.0 (77.0)	15.5
TL (mm)	161.3	64.0–172.0 (100.3)	19.3
% SL			
HL	27.2	24.9–33.3 (28.8)	1.5
BD	47.9	47.9–64.3 (56.8)	3.1
HD	34.0	27.3–50.1 (36.4)	4.1
CFBD	13.2	12.4–20.0 (16.5)	1.4
PelES	8.6	8.6–17.8 (14.5)	1.5
PelBS	7.7	7.7–16.9 (14.0)	1.4
PecES	-	0–4.7 (0.2)	0.8
PecBS	-	-	-
Th	?	6.5–12.9 (9.9)	1.2
LDR	14.4	12.0–21.9 (17.7)	1.6
LAR	15.2	14.4–21.0 (18.1)	1.3
% HL			
PreHL	26.5	20.2–36.7 (28.3)	2.4
PosHL	64.2	48.1–64.4 (56.4)	3.2
SnL	33.0	25.1–38.3 (31.2)	2.9
MES	27.3	22.3–39.4 (31.4)	2.8
MBS	19.2	16.9–30.7 (22.2)	2.7
NSD	?	16.1–30.2 (23.5)	2.6
EdV	11.3	7.8–16.1 (11.5)	1.4
DBO	5.4	4.3–11.0 (7.2)	1.4
WO	11.3	9.6–19.8 (14.7)	1.9

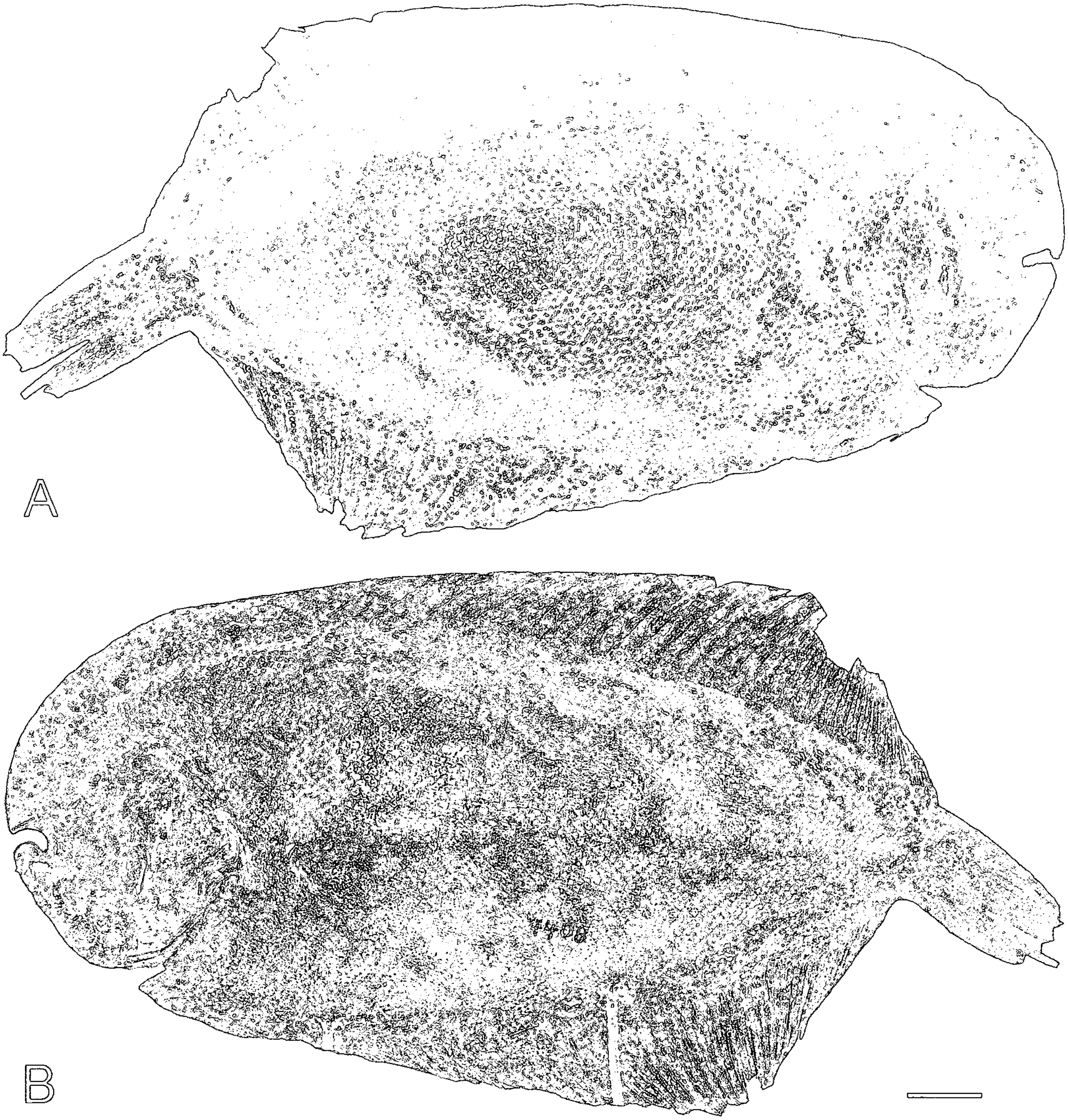


Figure 1.15: Eyed-side (A) and blind-side (B) of the holotype of *Trinectes maculatus*, ZMB 7408, 130.6 mm, location unknown. The scale bar corresponds to 10 mm.

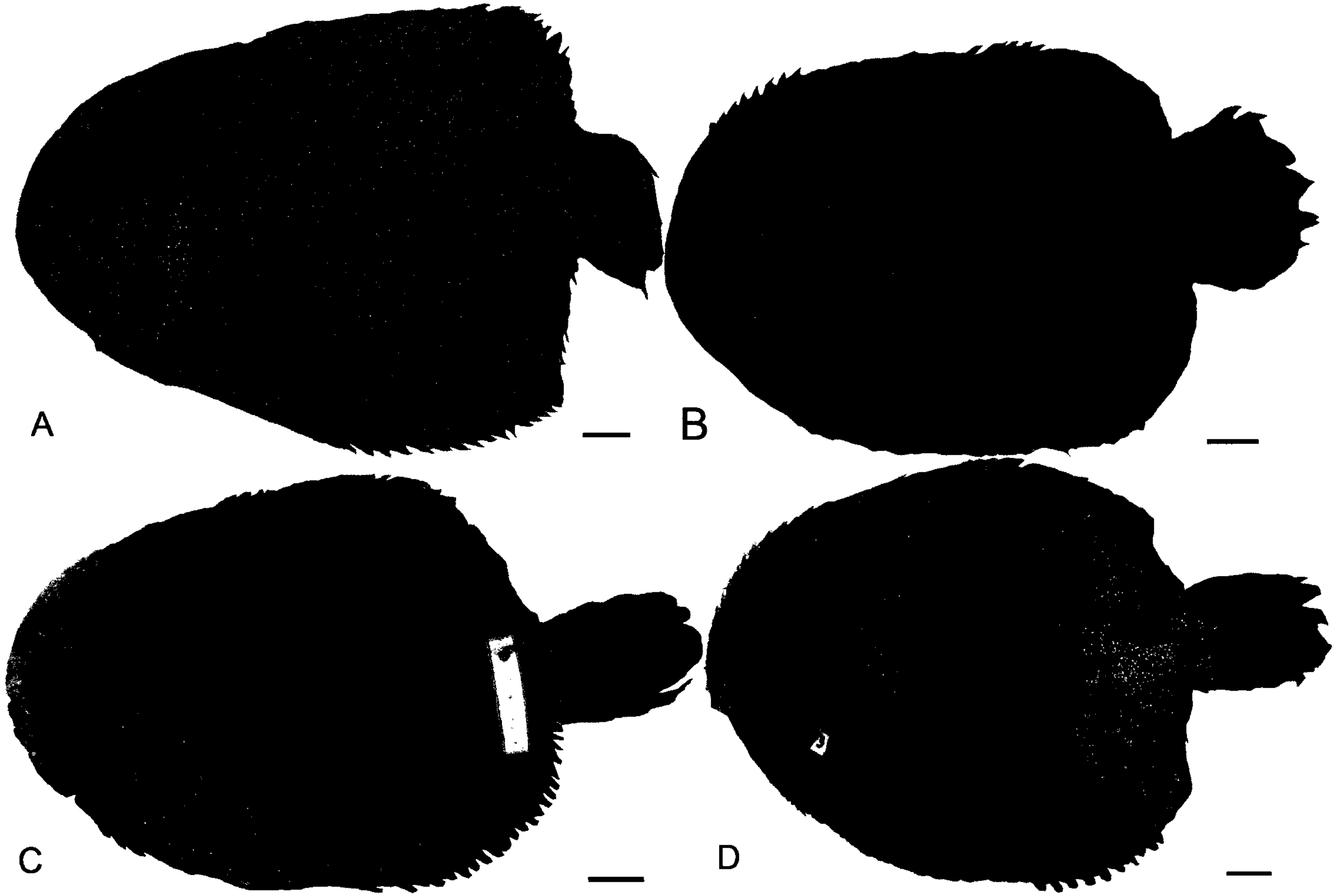


Figure 1.16: Variation in the blind-side pigmentation in *Trinectes maculatus*. (A) USNM 286784, 125.3 mm, U.S.A., Florida; (B) USNM 049053, 74.4 mm, U.S.A., New York; (C) SU 49869, 92.9 mm, U.S.A., Virginia; (D) FMNH 40232, 101.7 mm, U.S.A., Texas.

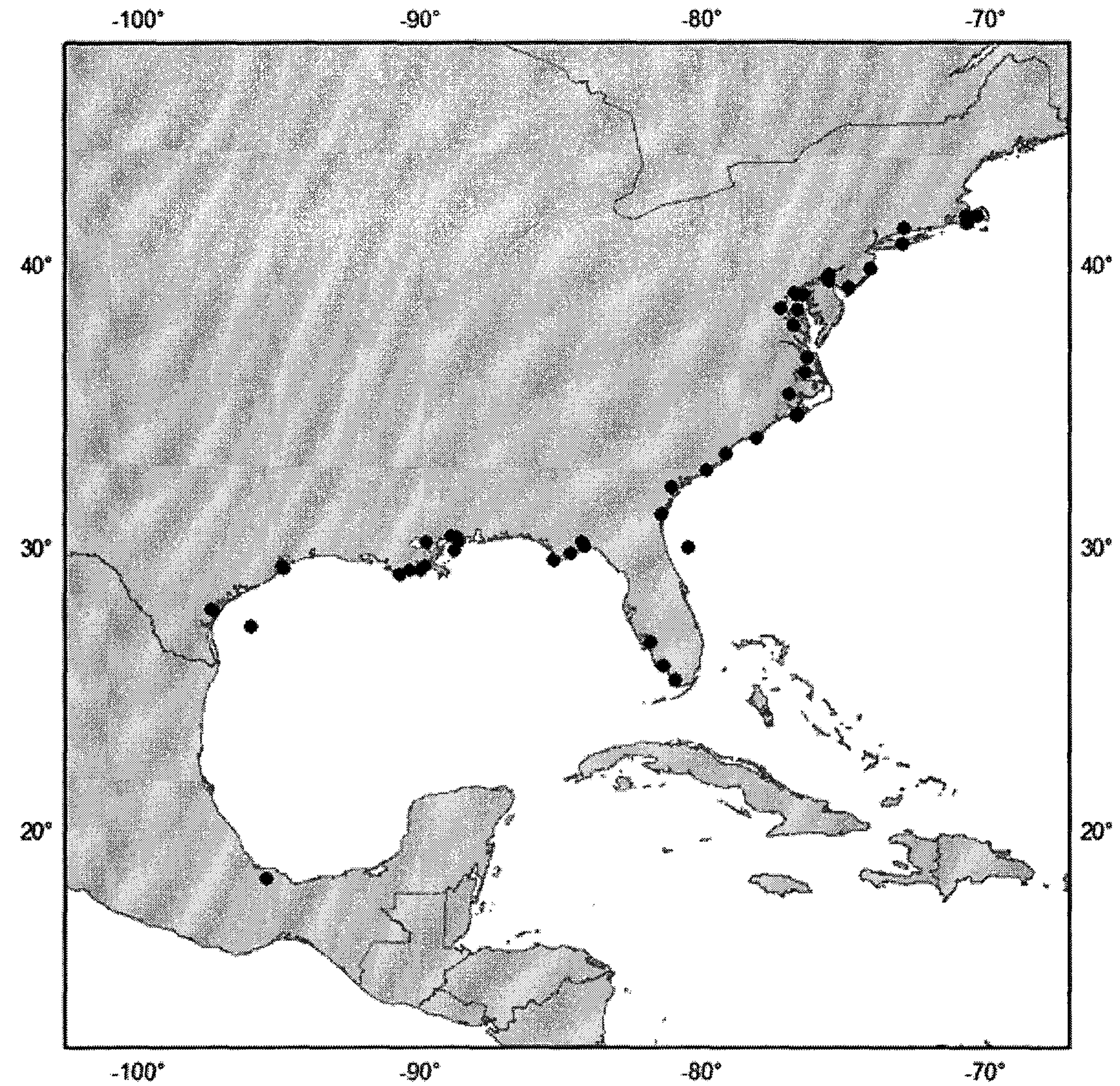


Figure 1.17: Occurrences of *Trinectes maculatus* specimens included in this study.

Trinectes microphthalmus (Chabanaud, 1928)

Figures 1.18–1.19, Tables 1.1–1.4 & 1.10

Synonym(s). —*Achirus microphthalmus* Chabanaud 1928

Common name(s). — Linguado

Materials examined. — **Trinectes microphthalmus**, 100 specimens (27.19–66.10 mm)

Achirus microphthalmus

Holotype: MNHN 0000-3314, 1(66.10 mm), No data.

Other material: ANSP 123712, 14(43.02–55.17 mm), Rio de Janeiro, Brazil; LIUEFS 1524, 1(52.01 mm), Praia de Monte Cristo, Saubara, Brazil; LIUEFS 4964, 2(33.07–51.75 mm), Praia de Saubada, Brazil; LIUEFS 2494, 1(50.07 mm), Praia de Monte Cristo, Saubara, Brazil; LIUEFS 5002, 1(59.80 mm), Praia de Cabucu (Mun. de Saubara, BA), Brazil; LIUEFS 5362, 1(46.92 mm), Brazil; LIUEFS 4930, 3(49.5–60.09 mm), Bahia, Brazil; LIUEFS 4765, 1(41.71 mm), Bahia, Brazil; LIUEFS 0096, 1(36.21 mm), Cacha Pregos, Vera Cruz (BA), Brazil; LIUEFS 2432, 1(47.71 mm), Praia de Monte Cristo, Saubara Remessa (BA), Brazil; MUFAL 1550, 3(45.58–52.72 mm), Praia dea Avenida Maceio, Brazil; MZUSP 72759, 1(56.37 mm), Copacabana, Rio de Janeiro, Brazil; MZUSP 72754, 1(50.33 mm), Guaruja, Sao Paulo, Brazil; MZUSP 4356, 5(43.33–60.45 mm), Atafona Paraiba, Rio de Janeiro, Brazil; MZUSP 62975, 1(38.81 mm), Baia de Santos, Sao Paulo, Brazil; MZUSP 62949, 7(37.64–62.55 mm), Ilha da Moela, Santos, Sao Paulo, Brazil; MZUSP 72753, 2(48.27–55.11 mm), Sao Paulo, Brazil; MZUSP 60896, 1(56.68 mm), Bahia, Brazil; MZUSP 72752, 1(57.96 mm), Alagoas Coqueiro

Seco, Brazil; MZUSP 62973, 2(55.94–57.74 mm), Sao Paulo, Brazil; MZUSP 79875, 1(50.35 mm), Alagoas Maccio, Brazil; MZUSP 62914, 2(57.73–58.94 mm), Sao Paulo, Brazil, MZUSP 72757, 1(33.09 mm), Praia do Itagua, Ubatuba, Sao Paulo, Brazil, MZUSP 62903, 1(27.19 mm), Alagoas Maceio, Brazil; MZUSP 51281, 3(52.80–56.71 mm), Ubatuba, Sao Paulo, Brazil; MZUSP 72760, 1(55.01 mm), Guaraja, Sao Paulo, Brazil, MZUSP 4357, 6(44.9–56.58 mm), Atafona, Rio de Janeiro, Brazil; MZUSP 72756, 1(37.24 mm), Cananeia, Sao Paulo, Brazil; MZUSP 62972, 1(31.65 mm), Cananeia, Sao Paulo, Brazil; MZUSP 74714, 3(39.24–50.45 mm), Bacia de Ribeira, Brazil; MZUSP 62912, 1(63.02 mm), Ao redor da Ilha da Moela, Sao Paulo, Brazil; MZUSP 72755, 1(51.05 mm), Norteste da Ihla Vitoria, Sao Paulo, Brazil; MZUSP 72758, 1(42.99 mm), Ubatuba, Enseada da Fortaleza, Sao Paulo, Brazil; SU 52449, 1(38.14 mm), Ceara, Fortaleza, Mucuripe, Brazil; UFES 130184, 2(37.37–59.73 mm), Praia de Camburi, Vitoria, Brazil; UFPB 6314, 4(36.00–48.15 mm), Praia do Amor, Jacuma, Conde, PB, Brazil; UFPB 3595, 10(47.95–59.49 mm), No data; MZUSP 62974, 2(52.44–60.96 mm), No data; MZUSP 72751, 1(50.93 mm), No data; MZUSP 84514, 2(33.84–38.55 mm), No data.

Diagnosis. — A species of *Trinectes* characterized by the following combination of characters: eyed-side lower lip with numerous, long, highly-branched fimbriae (Fig. 1.4C); ring of cirri around eyed-side anterior nostril aperture (Fig. 1.4C); body very deep, 59.7% to 72.1% (mean = 66.3%); eyes very small, 6.5% to 13.9% (mean = 9.8%) in HL; pectoral fins absent; 47–52 dorsal fin rays; 32–37 anal fin rays; 7 pterygiophores anterior to the neural spine of the third precaudal vertebrae (Fig. 1.3; Fig. 2.4); ethmoid process longer than the width of dorsal orbit (Fig. 2.4AB); angle of urohyal closed (Fig. 2.6A); dorso-posterior process of neural arc pointed (Fig. 1.3);

haemal spine of posteriormost precaudal hemapophysis with posterior wing (Fig. 1.3); haemal arch of anteriormost precaudal vertebrae thick (Fig. 1.3).

Description. — Morphometrics of type and non-type specimens are given in Table 1.10. Body small and round, reaching 66.1 mm (measured specimens). Head short, 27.0% to 34.4% (mean = 30.4%), deep, 36.6% to 55.2% (mean = 45.2%), and rounded. Deep body, body depth 59.7% to 72.1% (mean = 66.3%). Snout forming a fleshy hook. Eyed-side gill opening at least one eye diameter lower than the ventral margin of the ventral eye. Eyed-side anterior nostril moderately-sized with ring of cirri around nostril margin, and cirri around base of nostril. Blind-side posterior nostril wide tube. Blind-side opercular region naked of tentacles; anterior blind-side head with few, short tentacles. Several short tentacles projecting from anteriormost rays of blind-side dorsal fin. Large, round caudal fin with wide base, caudal fin base depth 12.2% to 20.3% (mean = 16.3%). Eyed-side and blind-side pelvic fins of moderate length, 12.7% to 25.4% (mean = 21.5%) and 12.6% to 28.9% (mean = 19.2%). Pectoral fin rays wholly absent on both sides. Body thin, 7.2% to 12.7% (mean = 10.7%). Longest dorsal ray 17.0% to 25.1% (mean = 20.3%), longest anal ray 16.9% to 25.3% (mean = 20.8%). Vertical fins longest at mid-point of body.

Preorbital head relatively long, 25.6% to 36.9% (mean = 32.0%) in HL. Postorbital head long, 35.2% to 61.6% (mean = 54.4%) in HL. Snout of moderate length, 29.8% to 54.0% (mean = 37.1%). Eyed-side mouth long, 27.1% to 44.9% (mean = 35.6%) in HL. Blind-side mouth short, 13.6% to 40.9% (mean = 26.2%) in HL. Posterior corner of mouth on eyed-side reaching quarter of ventral eye. Nostril to snout distance 23.9% to 38.5% (mean = 30.7%) in HL. Eyes very small, ventral eye diameter 6.5% to 13.9% (mean = 9.8%) in HL. Distance between orbits at least the width of one orbit, 5.2% to 32.9% (mean = 10.6%) in HL. Width of orbits narrow, 8.6% to 19.9% (mean = 14.0%) in HL. Eyed-side opercular region occasionally with scaleless patch. Lower eyed-side lip covered with numerous long, highly-branched fimbriae (Fig. 1.4C). Frequency distributions for the following characters are shown in Tables 1.1–1.4: 47–52 dorsal fin rays, 32–37 anal fin rays, 19 caudal vertebrae, 9 precaudal vertebrae, pectoral fins absent, 5 eyed-side pelvic fin rays, and 5 blind-side pelvic fin rays.

Colour of preserved specimens. — Body light beige, usually with darker brown flecks. Approximately 5 to 7 faint transverse bands extending across eyed-side body, from tip of snout to base of caudal fin. Median fins similar in pigmentation to body, lightening near tips. Blind-side usually light beige with no distinct pattern.

Distribution. — *Trinectes microphthalmus* is an Atlantic species that ranges from Trinidad and Tobago to Southern Brazil (Fig. 1.12). It is a coastal species and is often found in brackish water and lagoons.

Remarks. — Original description by Chabanaud (1928), with the holotype collected in Bahia, Brazil. Included in this description are the following characters that are useful for the identification of the species (translated from French): 37 anal fin rays, very small eyes, lower lip with 7 or 8 finely ciliated fimbriae, and gill opening very low (Chabanaud 1928).

Comparison. — *Trinectes microphthalmus* most closely resembles the Pacific species *T. fimbriatus* and *T. opercularis*. It differs from *T. fimbriatus* in having no distinct white spots on its eyed-side body and vertical fins, as well as having a longer (as opposed to shorter) ethmoid process than width of dorsal orbit. *Trinectes microphthalmus* can be distinguished from *T. opercularis* in having 7 as opposed to 8 pterygiophores anterior to the neural spine of the third precaudal vertebra. *Trinectes microphthalmus* can be distinguished from all other congeners in having any of the following characters (single or multiple): 32–37 anal fin rays, long and highly-branched fimbriae on lower eyed-side lip, very deep body, a ring of cirri on the margin of anterior eyed-side nostril, and very small eyes.

Table 1.10: Twenty-two morphometric variables of body shape in *Trinectes microphthalmus* (n = 100). Proportional measurements of both standard length (% SL) and head length (% HL) are included. Measurements for the holotype are shown separately, and combined with non-type specimens under 'All specimens'. Included are the ranges, means (in parentheses), and standard deviations (SD). Measurements and abbreviations are described in Appendix B.

	Holotype of *Trinectes microphthalmus* MNHN 0000-3314	All specimens (n = 100)	SD
SL (mm)	66.1	27.2–66.1 (49.1)	8.3
TL (mm)	87.1	36.4–87.1 (64.7)	10.4
% SL			
HL	29.2	27.0–34.4 (30.4)	1.2
BD	70.0	59.7–72.1 (66.3)	2.9
HD	54.3	36.6–55.2 (45.2)	3.9
CFBD	16.5	12.2–20.3 (16.3)	2.0
PelES	18.6	12.7–25.4 (21.5)	2.0
PelBS	17.6	12.6–28.9 (19.2)	2.0
PecES	-	-	-
PecBS	-	-	-
Th	9.8	7.2–12.7 (10.7)	1.1
LDR	17.7	17.0–25.1 (20.3)	1.7
LAR	18.5	16.9–25.3 (20.8)	1.6
% HL			
PreHL	32.8	25.6–36.9 (32.0)	2.5
PosHL	53.3	35.2–61.6 (54.4)	4.0
SnL	41.5	29.8–54.0 (37.1)	3.0
MES	33.4	27.1–44.9 (35.6)	3.9
MBS	26.6	13.6–40.9 (26.2)	4.4
NSD	30.2	23.9–38.5 (30.7)	3.1
EdV	7.6	6.5–13.9 (9.8)	1.5
DBO	13.7	5.2–32.9 (10.6)	3.3
WO	13.4	8.6–19.9 (14.0)	2.4

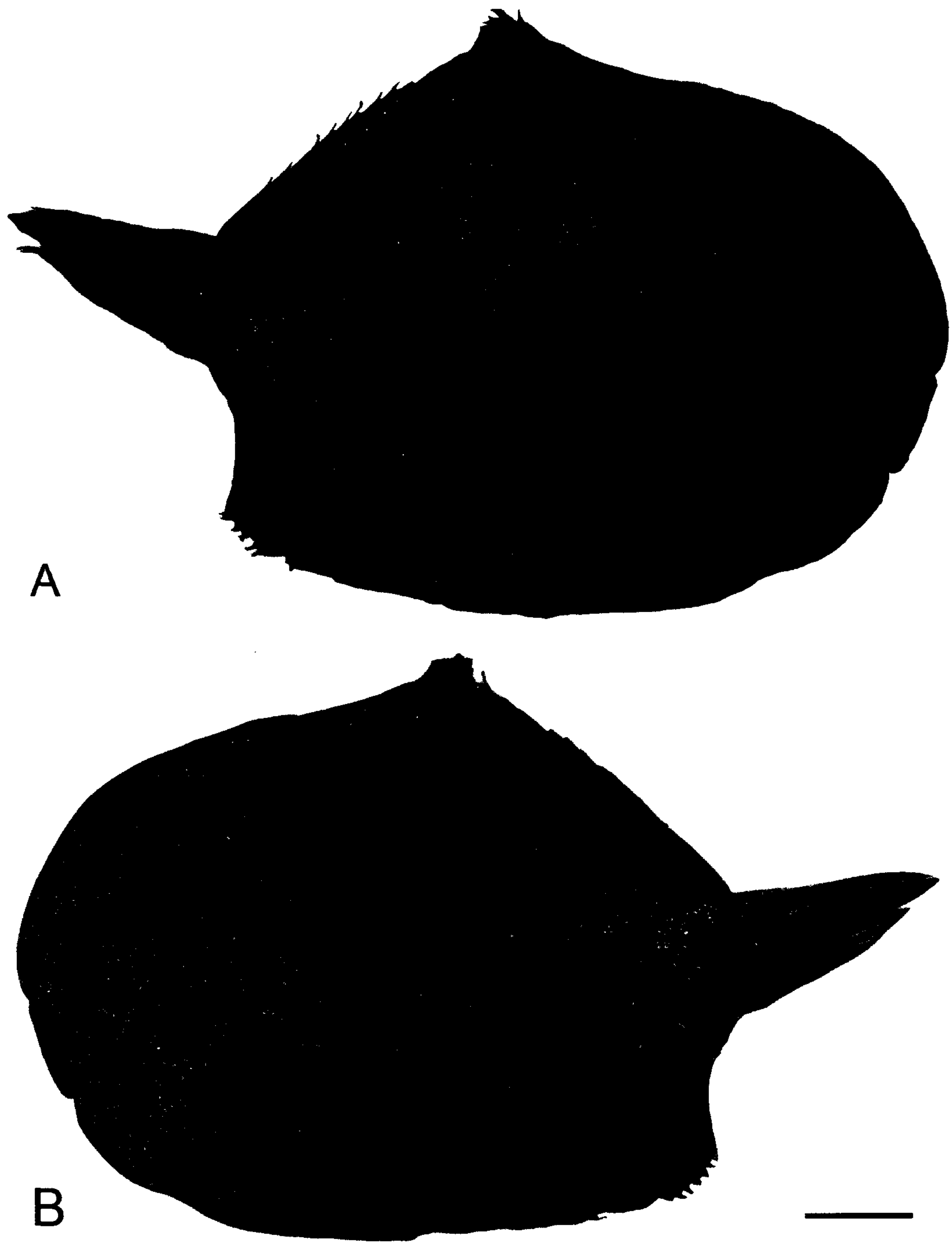


Figure 1.18: Eyed-side (A) and blind-side (B) of the holotype of *Trinectes microphthalmus*, MNHN 0000–3314, 66.1 mm, Bahia, Brazil. The scale bar corresponds to 10 mm.

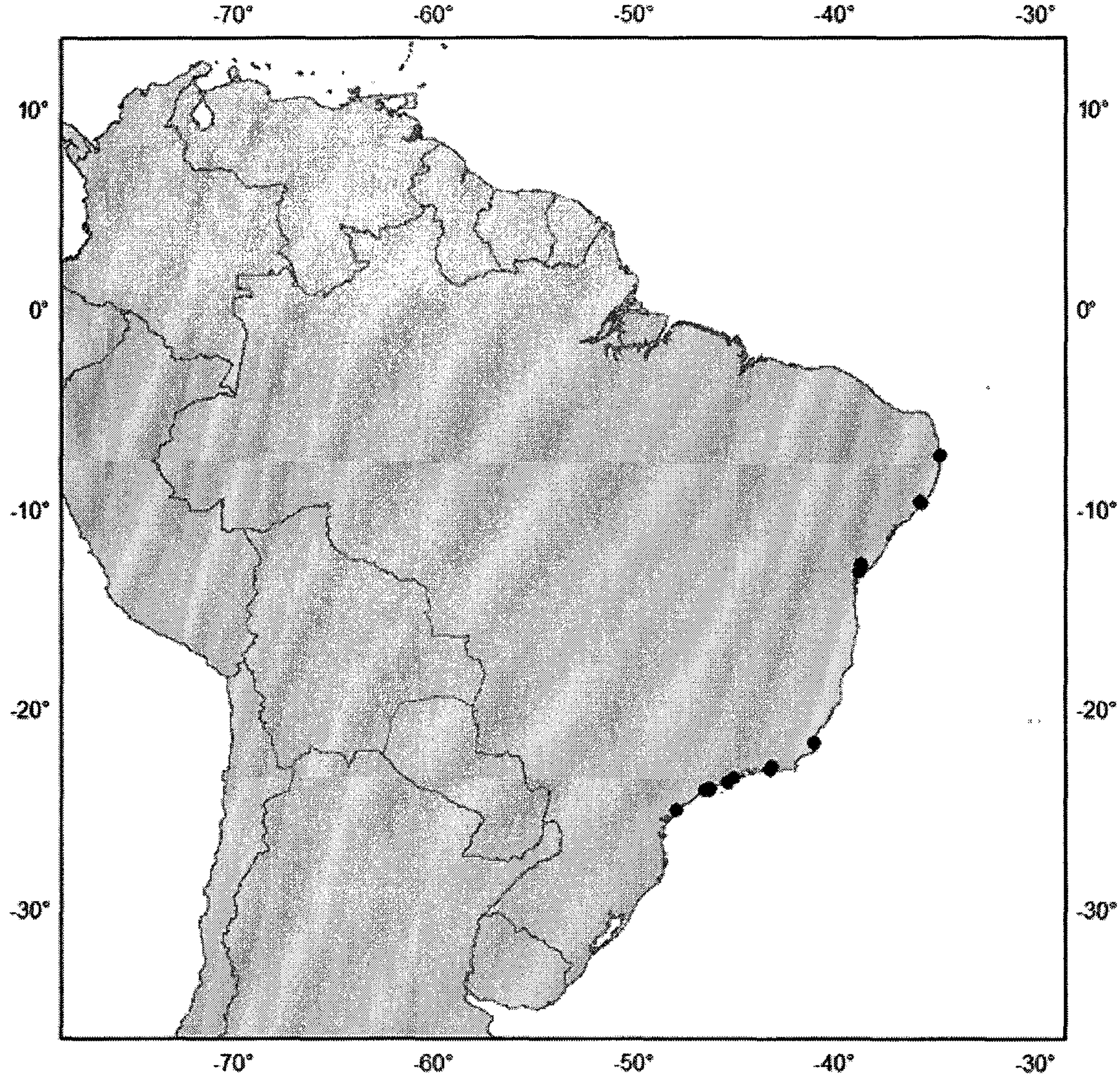


Figure 1.19: Occurrences of *Trinectes microphthalmus* specimens included in this study.

Trinectes opercularis (Nichols & Murphy 1941)

Figures 1.20–1.21, Tables 1.1–1.4 & 1.11

Synonym(s). — *Achirus opercularis* Nichols & Murphy 1941

Common name. — Spottedcheek sole, Sole à joue tachetée, Suela opérculo manchado

Materials examined. — ***Trinectes opercularis***, 15 specimens (29.61–65.29 mm)

Achirus opercularis

Holotype: AMNH 15958, 1(47.28 mm), No data.

Other material: AMNH 35090, 1(29.61 mm), No data, USNM 361517, 6(49.62–56.95 mm), 04°20'--" N 077°28'--" W; 04°18'--" N 077°29'--" W, off Rio Togoroma, Colombia, USNM 361522, 1(51.54 mm), 02°21'--" N 078°39'--" W; 02°23'--" N 078°36'--" W, off Boca San Juan, Colombia, USNM 361523, 3(51.64–53.06 mm), 04°47'--" N 077°22'--" W, Buenaventura, Colombia, USNM 361537, 2(52.29-65.29 mm), 01°39'--" N 079°02'30" W; 01°37'30" N 079°02'00" W, off Cape Manglares, South of Tumaco, Colombia, USNM 361540, 1(51.96 mm), 03°14'--" N 077°34'--" W, Buenaventura, Colombia.

Diagnosis. — A species of *Trinectes* characterized by the following combination of characters: eyed-side lower lip with numerous highly-branched fimbriae (Fig. 1.4C); ring of cirri around eyed-side anterior nostril aperture (Fig. 1.4C); body very deep, 62.0% to 68.8% (mean = 66.3%); ventral eye diameter very small, 5.3% to 10.0% (mean = 7.1%) in HL; pectoral fins absent; 8 pterygiophores anterior to the neural spine of the third precaudal vertebra (Fig. 1.3; Fig. 2.4); 50–

53 dorsal fin rays; 33–37 anal fin rays; ethmoid process longer than width of dorsal orbit (Fig. 2.4AB); angle of urohyal closed (Fig. 2.6A); dorso-posterior process of neural arc pointed (Fig. 1.3), hemal spine of posterior-most precaudal hemapophysis with posterior wing (Fig. 1.3), and hemal arch of anterior-most precaudal vertebrae thick (Fig. 1.3).

Description. — Morphometrics of type and non-type specimens are given in Table 1.11. Body small and round, reaching 65.3 mm (measured specimens). Head short, 31.1% to 34.3% (mean = 32.9%), deep, 38.7% to 51.0% (mean = 46.5%), and rounded. Deep body, body depth 62.0% to 68.8% (mean = 66.3%). Eyed-side gill opening extending at least one eye diameter ventrally to ventral eye. Eyed-side anterior nostril moderately-sized with ring of cirri around margin, as well as cirri around base of nostril. Blind-side posterior nostril wide tube. Blind-side opercular region without tentacles; anterior blind-side head with few, short tentacles. Little to no cirri on eyed-side body. Caudal fin large and round-shaped with wide base, caudal fin base depth 13.3% to 17.3% (mean = 15.2%). Eyed-side and blind-side pelvic fins of moderate length, 18.0% to 25.4% (mean = 21.3%) and 17.3% to 25.1% (mean = 19.8%). Pectoral fins absent. Body thin, 8.5% to 10.3% (mean = 9.4%). Longest dorsal ray 18.0% to 25.0% (mean 19.9%), longest anal ray 16.9% to 25.4% (mean = 20.3%). Vertical fins longest at mid-point of body.

Preorbital head relatively long, 28.2% to 34.7% (mean = 32.1%). Postorbital head long, 50.5% to 58.2% (mean = 54.1%). Snout moderately long, 31.9% to 42.1% (mean = 37.4%) in HL, forming a fleshy hook. Eyed-side mouth long, 28.5% to 42.0% (35.3%) in HL, curving downward at the corner. Posterior corner of mouth on eyed-side reaching quarter of ventral eye. Blind-side mouth short, 20.6% to 29.0% (mean = 23.9%) in HL. Nostril to snout distance 23.9% to 32.5% (mean = 29.0%) in HL. Eyes very small, ventral eye diameter 5.3% to 10.0% (mean =

7.1%) in HL. Interorbital space often with bony ridge, distance between orbits at least the width of one orbit, 6.8% to 13.7% (mean = 10.1%) in HL. Width of orbits narrow, 8.2% to 19.6% (mean = 12.7%). Eyed-side opercular region usually with naked patch; rarely scaly. Lower eyed-side lip covered with numerous long and highly-branched fimbriae (Fig. 1.4C). Frequency distributions for the following meristics are shown in Tables 1.1–1.4: 50–53 dorsal fin rays, 33–37 anal fin rays, 19 caudal vertebrae, 9 precaudal vertebrae, pectoral fins absent, 5 eyed-side pelvic fin rays, and 5 blind-side pelvic fin rays.

Colour of preserved specimens. — Body light beige to brown, occasionally mixing with one another. Approximately 5 to 9 faint transverse bands across eyed-side body, but not vertical fins. Median fins similar in pigmentation near body, lightening near tips. Blind-side light beige.

Distribution. — *Trinectes opercularis* is a Pacific species distributed from Colombia to Panama (Fig. 1.21). It is a coastal species, found on sandy and muddy bottoms (Nichols & Murphy 1941). *Trinectes opercularis* is known to occur in freshwater.

Remarks. — Original description by Nichols & Murphy (1941), with holotype collected at Cuevita Bay, Pacific Colombia. They reported that the holotype was dredged from a green sand and mud bottom at a depth of 10–40 m. Our examination of the holotype showed the following differences from all other *T. opercularis* specimens: 17 caudal fin rays, and a few faint white spots within the scaleless patch on the eyed-side opercular region (see Fig. 1.20A). Included in the original description are the following characters that are useful to the identification of the species: 34 anal fin rays, body deep, eyes small, and pectoral fins absent (Nichols & Murphy

1941). Note that the presence of a "considerable scaleless area" on the opercular region on both sides was found to be too variable to be used taxonomically.

Comparison. — *Trinectes opercularis* most closely resembles the Pacific species *T. fimbriatus* and especially the Atlantic species *T. microphthalmus*. *Trinectes opercularis* differs from *T. fimbriatus* in having no distinct white spots on its eyed-side body and vertical fins, as well as having a longer as opposed to shorter ethmoid process than the width of its dorsal orbit. *Trinectes opercularis* can be distinguished from *T. microphthalmus* in having 8 as opposed to 7 pterygiophores anterior to the neural spine of the third precaudal vertebra. *Trinectes opercularis* can be distinguished from all other congeners, with the exception of *T. fimbriatus* and *T. microphthalmus*, in having any of the following characters (single or multiple): 33–37 anal fin rays, long and highly-branched fimbriae on eyed-side lips, very deep body, a ring of cirri on the margin of anterior eyed-side nostril, and very small eyes.

Table 1.11: Twenty-two morphometric variables of body shape in *Trinectes opercularis* (n = 15). Proportional measurements of both standard length (% SL) and head length (% HL) are included. Measurements for the holotype are shown separately, and combined with non-type specimens under 'All specimens'. Included are the ranges, means (in parentheses), and standard deviations (SD). Measurements and abbreviations are described in Appendix B.

	Holotype of *Trinectes opercularis* AMNH 15958	All specimens (n = 15)	SD
SL (mm)	47.3	29.6–65.3 (52.2)	7.5
TL (mm)	62.5	39.4–84.7 (70.0)	9.9
% SL			
HL	31.7	31.1–34.3 (32.9)	1.0
BD	67.7	62.0–68.8 (66.3)	2.0
HD	46.1	38.7–51.0 (46.5)	3.3
CFBD	17.3	13.3–17.3 (15.2)	0.9
PelES	23.0	18.0–25.4 (21.3)	1.9
PelBS	19.3	17.3–25.1 (19.8)	1.7
PecES	-	-	-
PecBS	-	-	-
Th	9.8	8.5–10.3 (9.4)	0.5
LDR	20.5	18.0–25.0 (19.9)	1.7
LAR	16.9	16.9–25.4 (20.3)	2.1
% HL			
PreHL	32.8	28.2–34.7 (32.1)	1.5
PosHL	53.3	50.5–58.2 (54.1)	2.3
SnL	41.5	31.9–42.1 (37.4)	3.2
MES	33.4	28.5–42.0 (35.3)	3.5
MBS	26.6	20.6–29.0 (23.9)	2.4
NSD	30.2	23.9–32.5 (29.0)	2.4
EdV	7.6	5.3–10.0 (7.1)	1.2
DBO	13.7	6.8–13.7 (10.1)	1.8
WO	13.4	8.2–19.6 (12.7)	2.9

Figure 1.20: Eyed-side (A) and blind-side (B) of the holotype of *Trinectes opercularis*, AMNH 15958, 47.3 mm, Location unknown. The scale bar corresponds to 10 mm.

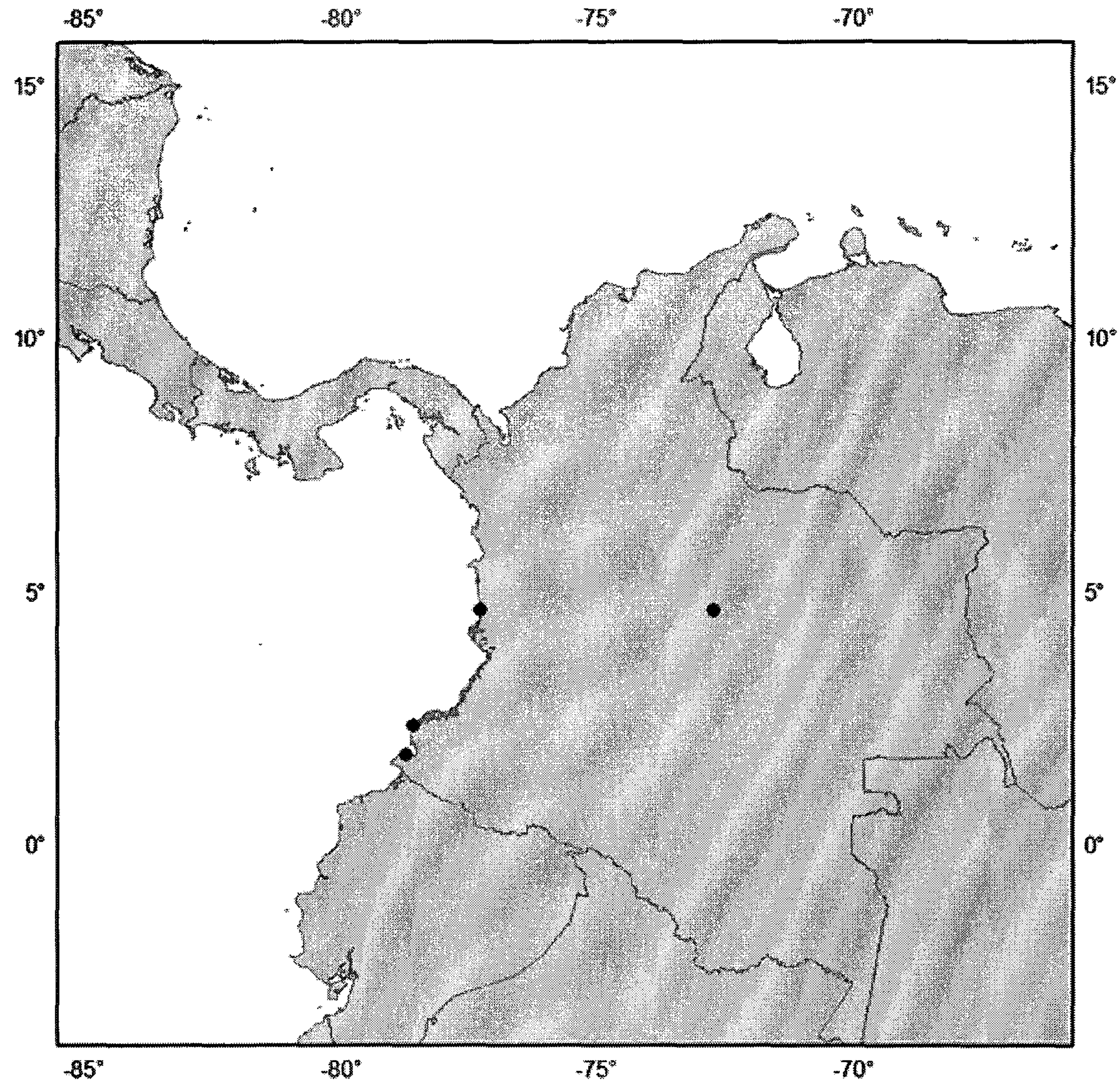


Figure 1.21: Occurrences of *Trinectes opercularis* specimens included in this study.

Trinectes paulistanus (Miranda Ribeiro 1913–15)

Figures 1.22–1.23, Tables 1.1–1.4 & 1.12

Synonym(s). — *Achirus paulistanus* Miranda Ribeiro 1913–15, *Achirus affinis* Steindachner 1915, *Achirus autrinus* Chabanaud 1928

Common name(s). — Slipper sole, Southern hogchoker, Sole pantoufle, Linguado lixa, Solha verdadeira, Tapa, Lenguado Redondo, Suela carioca, Suela chancieta

Materials examined. — ***Trinectes paulistanus***, 126 specimens (18.51–154.70 mm)

Achirus paulistanus

Holotype: MNRJ 1963, 1(117.20 mm), Santos, Sao Paulo, Brazil.

Other material: CAS 47595, 1(92.54 mm), Caribbean Sea, Caratasca lagoon, Honduras, CAS 48709, 1(85.07 mm), French Guiana, CAS 48791, 1(72.93 mm), Brazil, FMNH 79674, 3(87.62–97.12 mm), 06°20'30" N, Coquette sta. 150, Suriname, FMNH 79669, 1(103.74 mm), N. Coppename, N 20 mi. offshore, Suriname, FMNH 79672, 2(73.92–74.32 mm), Sar. River, 15 mi., Suriname, FMNH 65425, 10(78.41–96.56 mm), No data, LBP 1396, 2(81.43–104.72 mm), Branganca, Praia Ajurutena, Brazil, LIUEFS 5000, 6(59.44–73.91 mm), Praia de Cabucu, Brazil, MCP 5656, 1(101.73 mm), Santa Catarina, Brazil, MCP 5653, 1(104.07 mm), Santa Catarina, Brazil, MCP 5651, 1(85.43 mm), Santa Catarina, Brazil, MNHN 0000–3099, 1(57.30 mm), Brazil, MNRJ 1955, 1(106.29 mm), 57°47' W, No data, MNRJ 2470, 1(84.72 mm), Rio de Janeiro, Biaja de Guanabara, Brazil, MRNJ 3157, 1(102.66 mm), 83°54' W, No data, MRNJ 1612, 1(82.83 mm), 47°09'--" W, No data, MRNJ 28303, 1(40.14 mm), No data, MRNJ 5736, 6(80.26–109.93 mm), No data, MRNJ 28302, 3(34.50–41.11 mm), Nova Vicosa, Bahia, Brazil, MRNJ 5737, 6(79.34–118.86 mm), Rio de Janeiro, Brazil, MRNJ 5623, 2(141.42–141.88 mm), Sepetiba, Rio de Janeiro, Brazil, MRNJ 5824, 4(89.70–106.49 mm), Sepetiba, Distrito Federal, Brazil, MZUSP 62969, 5(72.12–102.66 mm), Ponta do Itaipu, Santus Farol da Moela, Sao Paulo, Brazil, SIO 77-376, 5(85.34–101.07 mm), 15°29'--" N, Honduras, SIO 63-459, 1(84.80 mm), 00°27' S, Brazil, SIO 63-460, 7(74.72–87.66 mm), 06°54'--" N, British Guiana, SU 52451, 3(50.89–102.64 mm), Ceara, Fortaleza, Mucuripe, Brazil, UMMZ 146099, 1(63.07 mm), Alta Verapaz, 'El Canal' a diversion of the Rio Polochic ca. 10 river km below Panzos, Guatemala, UMMZ 199548, 1(74.48 mm), lower end of trib to W side of distributary of Rio Patuca, Honduras, UMMZ 197351, 3(45.89–60.71 mm), Izabal, Motagua River at Finca Hopi, 17 km above mouth, Guatemala, USNM 290990, 1(30.46 mm), Caribbean, Salisbury River, between road and mouth, Dominica, USNM 286990, 13(71.17–98.52 mm), 04°26'--" N 050°55'--" W, French Guiana, USNM 121811, 1(75.46 mm), Venez, Lago Maracaibo, 7 km South of Maracibo, Venezuela, USNM 114336, 1(70.38 mm), Lake Izabel, Guatemala, USNM 114340, 3(18.51-39.77 mm), CA Jicotea Cr., Tributary Rio Sarstoon, CA 1/4 mile above mouth, Guatemala, USNM 114281, 1(68.02 mm), Rio Sauce, 2 miles South-West of El Estor at mouth in Lake Yzabel, Guatemala, USNM 159537, 1(96.23 mm), 06°24'--" N 054°54'--" W, Suriname, USNM 290995, 1(76.26 mm), 04°59'--" N 051°58'--" W, French Guiana, USNM 286991, 1(95.89 mm), 04°48'--" N 051°38'--" W, French Guiana, USNM 121810, 5(47.20–92.28 mm), Caribbean, Lago Maracaibo at Yacht club, Venezuela, USNM 286985, 3(69.14–88.14 mm), 04°43'--" N 051°29'--" W, French Guiana.

Achirus affinis

Type: N/A

Non-type: N/A

Achirus austrinus

Syntypes: NMW 8009, 1(112.70 mm), No data, MNHN 3317, 2(80.80–94.00 mm), 84°50'--" W, Brazil, NMW 8101, 1(82.70 mm), No data, NMW 8099(8100?), 2(40.40–47.20 mm), Brazil, NMW 8099, 1(85.30 mm), Demarara.

Diagnosis. — A species of *Trinectes* with the following combination of characteristics: eyed-side body with 8 or fewer thin, unpigmented transverse bands (Fig. 1.22A); 8 pterygiophores anterior to the neural spine of the third precaudal vertebra (Fig. 1.3; Fig. 2.4); 20 caudal vertebrae, eyed-side pectoral fin, when present, with 1 ray; presence of coracoscapular complex on eyed- and blind-side pectoral fins; blind-side head with numerous long fleshy tentacles (Fig 1.22B), and caudal fin unpigmented (Fig. 1.22).

Description. — Morphometrics of type and non-type specimens are given in Table 1.12. Body oblong and oval, reaching 141.9 mm. Head short, 24.9% to 33.9% (mean = 28.6%), deep, head depth 25.5% to 52.6% (mean = 36.9%), and rounded. Body depth 47.5% to 67.6% (mean = 54.6%). Eyed-side gill opening extending ventrally to ventral eye. Eyed-side anterior nostril a large protruding tube, often with cirri around base. Blind-side posterior nostril a wide tube. Blind-side head and operculum with long fleshy tentacles. Many short tentacles projecting from anteriormost rays of blind-side dorsal fin. Caudal fin long and oval-shaped, with deep base, caudal fin base deep 12.3% to 20.5% (mean = 16.4%). Eyed-side and blind-side pelvic fins moderately long, 10.6% to 20.3% (14.2%) and 10.1% to 17.3% (mean = 13.8%), respectively. Eyed-side pectoral fin, when present, rudimentary. Blind-side pectoral fin absent. Body thin, 6.7% to 12.6% (mean = 10.2%). Longest dorsal ray 10.9% to 22.3% (mean = 15.0%), longest anal ray 11.3% to 23.3% (mean = 15.3%). Vertical fins longest in posterior third of body.

Preorbtial head moderate in length, 17.9% to 35.3% (mean = 27.3%) in HL. Postorbital head long, 43.6% to 61.3% (mean = 55.9%) in HL. Snout moderately long, 23.9% to 60.0% (mean = 33.2%) in HL. Eyed-side mouth relatively long, 25.0% to 40.5% (mean = 33.2%) in HL, slightly curving downward. Posterior corner of eyed-side mouth reaching half of ventral eye. Blind-side mouth short, 15.9% to 34.9% (mean = 22.2%) in HL. Nostril to snout distance 13.2% to 28.0% (mean = 22.5%) in HL. Eyes medium-sized, ventral eye diameter 5.5% to 16.5% (mean = 10.7%) in HL. Interorbital space scaly, distance between orbits approximately the width of one orbit, 4.8% to 12.4% (mean = 8.2%) in HL. Width of orbits narrow, 6.8% to 21.7% (mean = 15.6%). Eyed-side operculum scaly. Lower lip covered with short, lightly-branched fimbriae (Fig. 1.4B). Eyed-side body devoid of cirri. Frequency distributions for the following meristics are shown in Tables 1.1–1.4: 53–62 dorsal fin rays, 38–45 anal fin rays, 20 caudal vertebrae, 9 precaudal vertebrae, 0–2 eyed-side pectoral fin rays, blind-side pectoral fin absent, 5 eyed-side pelvic fin rays, and 5 blind-side pelvic fin rays.

Colour of preserved specimens. — Body beige or light brown (rarely dark brown), occasionally with darker blotches throughout body. Body with 8 (or fewer) thin, unpigmented transverse bands extending from base of dorsal fin to base of anal fin, reaching from the caudal fin base to the vertical of the gill opening. Median fins with slightly lighter pigmentation than body. Blind-side pale beige, usually devoid of pigmentation (occasionally with dark blotches).

Distribution. — *Trinectes paulistanus* is an Atlantic species distributed from Southern Mexico (tip of the Yucatan Peninsula) to Southern Brazil (Santa Catarina) (Fig. 1.16). Greenfield & Thomerson (1997) reported finding this species downriver in mangrove channels in Belize. This species is found on shallow soft bottoms, often penetrating freshwater and commonly found in brackish water and estuaries.

Remarks. — Original description by Miranda Ribeiro (1913-15), with the holotype collected in Santos, São Paulo, Brazil. Our analysis of the holotype generally agreed with the non-type specimens (see Table 1.12).

Achirus affinis was originally described by Steindachner 1915. Though five syntypes are supposed to be at the NMW collection (Vienna, Austria) (Eschmeyer 2009), the specimens have since been lost. *Achirus affinis* was first synonymized to *T. paulistanus* by Jordan (1923). The original description mentions the following characters (based on 3 specimens) that suggest that it should be a synonym of *Trinectes paulistanus*: 39–41 anal fin rays, body depth 53–57%, and 77–126 mm (Steindachner 1915). Ratios were calculated based on data provided by Steindachner (1915). Additionally, the specimens were taken from the Itacupim River in Brazil, an area where the only *Trinectes* species known to be found fit the description is *T. paulistanus* (see Fig. 1.23). Therefore, we support the synonymy of *A. affinis* to *T. paulistanus*.

Achirus austrinus was originally described by Chabanaud (1928), with known range to be from Guyana to Rio de Janeiro, Brazil. Analysis of four syntypes of this species indicates that this species is identical to *Trinectes paulistanus*, on the basis of the following diagnostic characters: unpigmented transverse bands, 0–2 eyed-side pectoral fin rays, long tentacles on blind-side head, and body depth 51.2–53.7%. Again, the only *Trinectes* species whose known range overlaps with that of *A. austrinus* that fits the above description is *T. paulistanus* (see Fig. 1.23).

Comparison. — Most closely resembles the Atlantic species *Trinectes maculatus* and the Pacific species *T. fonsecensis* in body shape, size, and general appearance. *Trinectes paulistanus* can be distinguished from *T. maculatus* in having 5 eyed- and blind-side pelvic fin rays as opposed to 4 rays. *Trinectes paulistanus* can be distinguished from *T. fonsecensis* and further distinguished from *T. maculatus* in having the following characters: unpigmented transverse bands on eyed-side body as opposed to pigmented bands, and light beige pigmentation as opposed to brown. *Trinectes paulistanus* can be further distinguished from *T. fonsecensis* in having 6–8 as opposed to 9–11 transverse bands on the eyed-side body. *Trinectes paulistanus* can be distinguished from *T. opercularis*, *T. fimbriatus*, and *T. microphthalmus* in having: short, lightly-branched fimbriae on eyed-side lower lip as opposed to long, highly-branched fimbriae, a shallow body as opposed to a deep body, and a margin devoid of cirri on the eyed-side anterior nostril as opposed to a margin with a ring of cirri. *Trinectes paulistanus* can be distinguished from *T. fluviatilis* and *T. xanthurus* in having: a wider caudal fin base depth, 20 caudal vertebrae as opposed to 21, and smaller eyes. *Trinectes paulistanus* can be distinguished from *T. inscriptus* in having: no reticulating dark lines covering eyed-side body and vertical fins, no blind-side pectoral fin as opposed to a rudimentary fin with 1 ray, and a rudimentary pectoral fin (when present) with 1 ray as opposed to a well-developed eyed-side pectoral fin with 2–4 rays.

Table 1.12: Twenty-two morphometric variables of body shape in *Trinectes paulistanus* (n = 126). Proportional measurements of both standard length (% SL) and head length (% HL) are included. Measurements for the syntypes for *Achirus austrinus* (three lots) and the holotype for *Achirus paulistanus* are shown separately, and combined with non-type specimens under 'All specimens'. Included are the ranges, means (in parentheses), and standard deviations (SD). Measurements and abbreviations are described in Appendix B.

	Syntype of *Achirus austrinus* NMW 8009	Syntype of *Achirus austrinus* MNHN 8089	Syntypes of *Achirus austrinus* MNHN 3317 (n = 2)	Holotype of *Achirus paulistanus* MNRJ 1963	All specimens (n = 126)	SD
SL (mm)	112.7	85.3	80.8–94.0	117.2	18.5–141.9 (72.2)	20.9
TL (mm)	146.1	105.6	105.1–121.7	?	25.0–191.8 (106.6)	27.4
% SL						
HL	26.6	25.1	26.5–27.1	27.8	24.9–33.9 (28.6)	1.7
BD	53.6	51.2	53.7	57.1	47.5–67.6 (54.6)	2.8
HD	40.3	30.2	42.0–52.6	44.2	25.5–52.6 (36.9)	3.2
CFBD	17.9	14.8	17.3–15.6	17.5	12.3–20.5 (16.4)	1.2
PelES	14.0	13.0	13.3–15.8	12.9	10.6–20.3 (14.2)	1.7
PelBS	13.9	10.7	13.0–12.9	12.3	10.1–17.3 (13.8)	1.4
PecES	1.7	1.9	0–2.8	1.4	0–11.2 (1.6)	2.1
PecBS	-	-	-	-	-	-
Th	9.0	8.7	7.4–8.4	10.0	6.7–12.6 (10.2)	1.1
LDR	14.6	10.9	13.9–14.8	13.0	10.9–22.3 (15.0)	1.7
LAR	15.3	11.2	15.4	12.6	11.3–23.3 (15.3)	1.7
% HL						
PreHL	24.3	25.2	21.3–25.1	32.7	17.9–35.3 (27.3)	2.8
PosHL	61.3	57.9	52.6–53.9	59.8	43.6–61.3 (55.9)	2.9
SnL	60.0	29.9	27.7–32.9	?	23.9–60.0 (33.2)	3.7
MES	31.3	33.6	31.7–35.6	39.1	25.0–40.5 (33.2)	2.8
MBS	26.0	20.1	23.3–23.7	33.4	15.9–34.9 (22.2)	3.2
NSD	18.3	20.1	14.9–18.7	19.8	13.2–28.0 (22.5)	2.8
EdV	11.0	10.8	11.0–13.6	9.8	5.5–16.5 (10.7)	2.0
DBO	7.7	7.9	6.8–7.2	8.1	4.8–12.4 (8.2)	1.5
WO	13.0	20.5	14.6–18.9	15.1	6.8–21.7 (15.6)	2.8

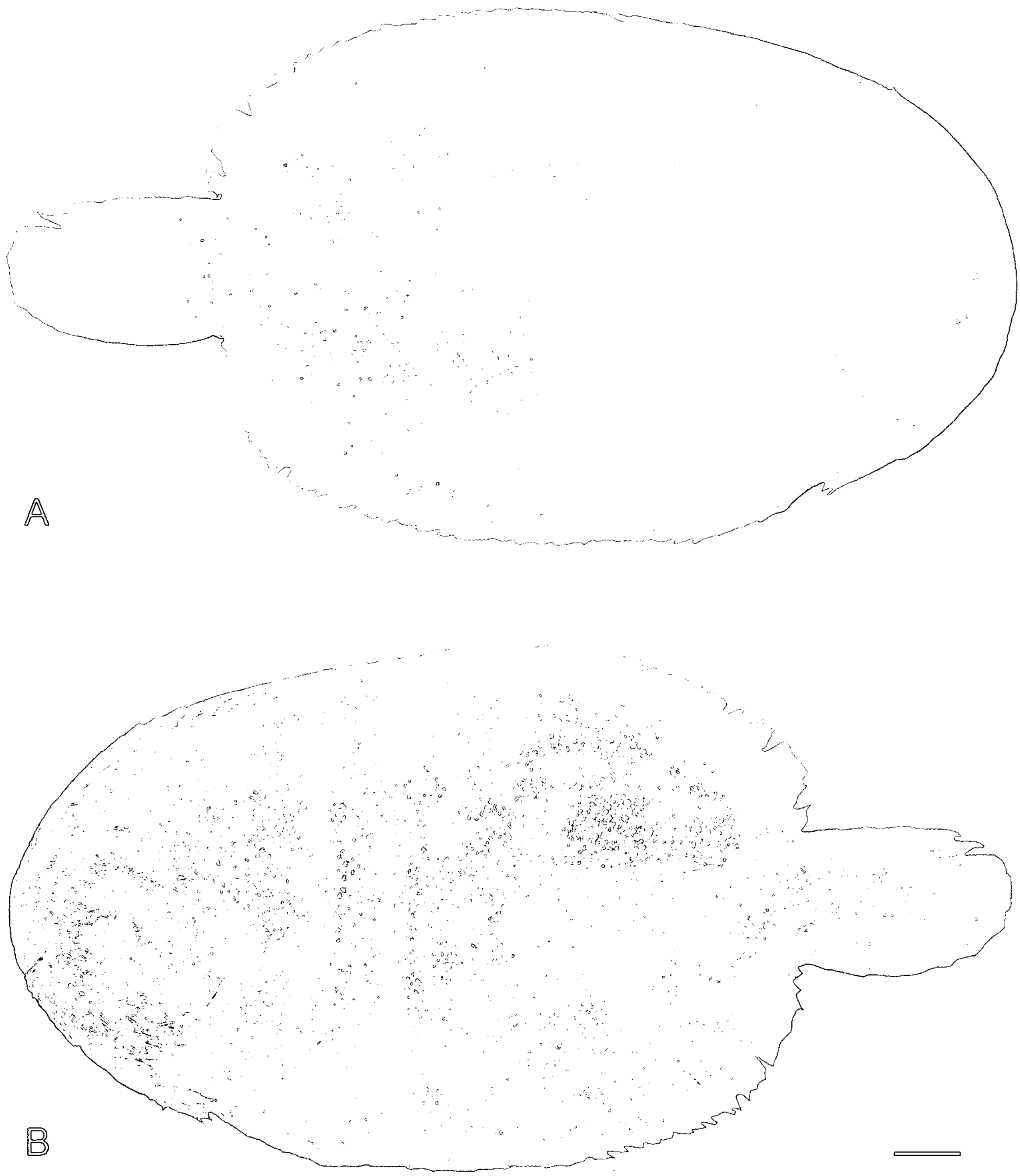


Figure 1.22: Eyed-side (A) and blind-side (B) of the holotype of *T. paulistanus*, MNRJ 1963, 117.2 mm, Brazil (São Paulo, Santos). The scale bar corresponds to 10 mm.

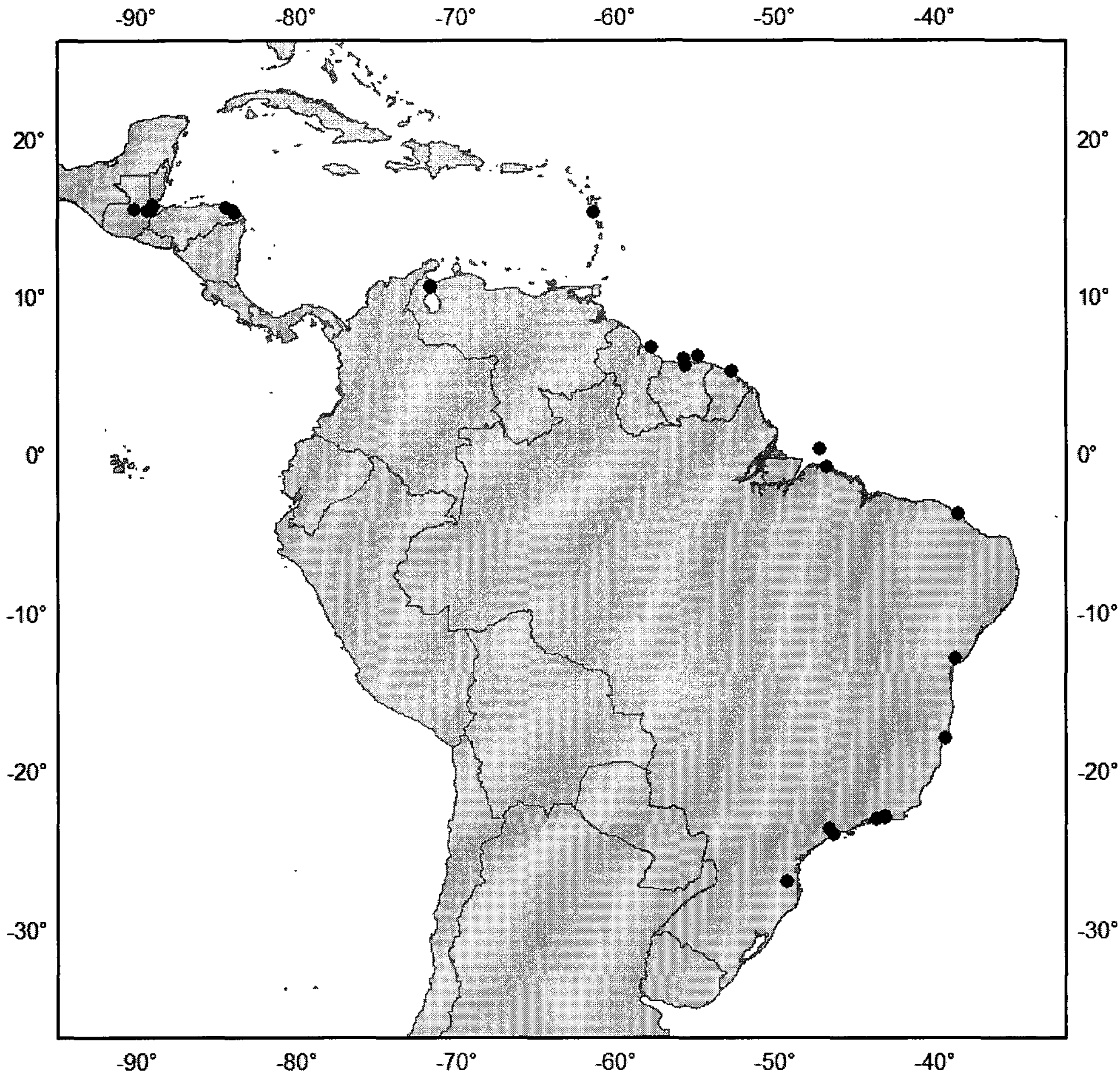


Figure 1.23: Occurrences of *Trinectes paulistanus* specimens included in this study.

Trinectes xanthurus Walker & Bollinger 2001

Figures 1.24–1.25, Tables 1.1–1.4 & 1.13

Synonym(s). — N/A

Common name(s). — N/A

Materials examined. — ***Trinectes xanthurus***, 56 specimens (54.34–83.61 mm)

Trinectes xanthurus

Paratypes: SIO 63–293, 23(60.28–83.60 mm), LACM 33805–27, 6(67.52–77.29 mm), Puntarenas, Gulf of Nicoya, Boca de Barrancas, Costa Rica, SIO 73–276, (56.59–59.15 mm), El Salvador, LACM 49189–2, 1(71.85 mm) Punta Chame, Panama.

Other material: CAS 32542–6, 2(63.30–64.65 mm), Puntarenas, South of Panta Uvita to Isla Ballena, Costa Rica, LACM 33806–101, 2(65.48–65.65 mm), No data, SIO 82–15, 11(54.34–74.70 mm), No data, USNM 361532, 1(62.50 mm), 3°32'--" N 77°22'15" W, Tortugas Grounds, South of Buenaventura, Colombia, USNM 361534, 1(69.70 mm), 2°22'--" N 78°37' W, off Boca San Juan (San Juan Del Sur), Colombia, USNM 361536, 1(69.96 mm), 1°38'15" N 79°02'15" W, Pacific, off Cape Manglares, South of Tumaco, Colombia, USNM 361539, 2(61.96–66.66 mm), Market Buenaventura, Colombia, USNM 361541, 4(69.70–83.61 mm), 3°14'--" N 77°33'--" W, Buenaventura, Colombia.

Diagnosis. — A species of *Trinectes* characterized by the following combination of characteristics: vertical fins more darkly pigmented than body (Fig. 1.24); caudal fin yellow, widening posteriorly (Fig. 1.24); eyes large, 11.7% to 19.2% (mean = 16.0%) in HL; fimbriae on lower lip unbranched (Fig. 1.4A); 21 precaudal vertebrae; blind-side head with numerous distinct tufts of short tentacles (Fig. 1.24B); narrow caudal fin base, 11.9% to 14.8% (mean = 13.3%); 9 pterygiophores anterior to the neural spine of the third precaudal vertebra (Fig. 1.3; Fig. 2.4).

Description. — Morphometrics of type and non-type specimens are given in Table 1.13. Body oblong and oval, reaching 95.0 mm (Walker & Bollinger 2001). Head short, 28.1% to 39.6% (mean = 31.2%), deep, 31.4% to 45.6% (mean = 40.5%), and rounded. Body moderately deep, 51.5% to 64.8% (mean = 58.9%). Eyed-side gill opening slightly ventral to ventral eye. Eyed-side anterior nostril large protruding tube, with smooth aperture and no cirri around its base. Blind-side posterior nostril wide tube. Opercular region bare of cirri on both sides, blind-side head covered with distinct tufts of short tentacles. Caudal fin long with very narrow base, 11.9% to 14.8% (mean = 13.3%) and flaring at tip. Eyed-side and blind-side pelvic fins moderate to long, 13.5% to 18.7% (16.4%) and 13.0% to 17.3% (mean = 15.2%), respectively. Pectoral fins wholly absent. Body thin, 8.0% to 11.4% (mean = 9.5%). Longest dorsal ray 14.9% to 21.7% (mean = 18.4%), longest anal ray 16.6% to 21.9% (mean = 18.0%). Dorsal and anal fins longest at mid-point to posterior end of body.

Preorbital head moderate in length, 15.9% to 33.7% (mean = 26.8%) in HL. Postorbital head moderate, 39.7% to 61.3% (mean = 51.0%) in HL. Snout of moderate length, 23.3% to 40.1% (mean = 33.4%) in HL, with distinct fleshy hook. Eyed-side mouth moderate in length, 23.2% to 36.5% (mean = 31.0%) in HL, with pronounced downward curve. Posterior corner of mouth on eyed-side reaching quarter of ventral eye. Blind-side mouth short, 18.6% to 30.8% (mean = 23.4%) in HL. Nostril to snout distance 12.9% to 32.0% (mean = 25.0%) in HL. Eyes large, ventral eye diameter 11.7% to 19.2% (mean = 16.0%) in HL. Interorbital space scaly, approximately one half the width of one orbit, distance between orbits 6.4% to 12.1% (mean = 8.6%). Width of orbits large, 14.5% to 27.2% (mean = 21.7%) in HL. Lower lip with short, unbranched fimbriae (Fig. 1.4A). Body absent of cirri. Frequency distributions for the following meristics are shown in Tables 1.1–1.4: 54–61 dorsal fin rays, 41–45 anal fin rays, 21 caudal vertebrae, 9 precaudal vertebrae, pectoral fins absent, 5 eyed-side pelvic fin rays, and 5 blind-side pelvic fin rays.

Colour of preserved specimens. — Body brown, with 7 to 8 unpigmented transverse bands. Median fins distinctly darker brown than body (on both sides), caudal fin light beige to yellow. Blind-side without pigmentation, occasionally with posterior half dark brown.

Distribution. — *Trinectes xanthurus* is a Pacific species distributed from the Gulf of Fonseca, El Salvador ca. 13°06'N, 87°59'W to the mouth of the Orapu River, Colombia ca. 43°4'N, 77°20'W (Fig. 1.25) (Walker & Bollinger 2001). It is a coastal species and is often found on sand or muddy bottoms in rivers, dwelling in waters of 2–40 m, but usually less than 18 m (Walker & Bollinger 2001).

Remarks. — Original description by Walker & Bollinger (2001), with the holotype collected in Bahia San Miguel, Panama. Walker & Bollinger's (2001) description of the holotype specimen contains all the diagnostic characteristics listed in this description of the species. Additionally, counts of anal and dorsal fin rays of the holotype, shown in Tables 1.2–1.5, also fall in range of *T. xanthurus* specimens analyzed in this study.

Comparison. — *Trinectes xanthurus* can be distinguished from all congeners in having: vertical fins that are more darkly pigmented than the body (both sides) as opposed to vertical fins with lighter or similar pigmentation as body, distinct tufts of tentacles on the blind-side head as opposed to no or scattered tentacles, a yellow caudal fin with a flaring posterior edge as opposed to a caudal fin that is not yellow and circular or rectangular in shape. *Trinectes xanthurus* can be further distinguished from all congeners, except *T. fluviatilis*, in having: unbranched as opposed to branched fimbriae on eyed-side lower lip, large (mean >15% HL) as opposed to small (mean <15% HL) eyes, a narrow (mean >14%) as opposed to wide (mean <14%) caudal fin base depth, and 21 as opposed to less than 21 caudal vertebrae.

Table 1.13: Twenty-two morphometric variables of body shape in *Trinectes xanthurus* (n = 56). Proportional measurements of both standard length (% SL) and head length (% HL) are included. Measurements for the paratypes (four lots) are shown separately, and combined with non-type specimens under 'All specimens'. Included are the ranges, means (in parentheses), and standard deviations (SD). Measurements and abbreviations are described in Appendix B.

	Paratype of *Trinectes xanthurus* LACM 49189–2	Paratypes of *Trinectes xanthurus* LACM 33805–27 (n = 6)	Paratypes of *Trinectes xanthurus* SIO 63–293 (n = 23)	Paratypes of *Trinectes xanthurus* SIO 73–276 (n = 2)	All specimens (n = 56)	SD
SL (mm)	71.8	67.5–77.3	60.3–83.6	56.6–59.2	54.3–83.6 (68.6)	6.0
TL (mm)	96.6	91.1–104.2	81.9–109.5	78.4–80.6	73.2–109.5 (92.1)	7.4
% SL						
HL	30.7	30.8–33.1	28.1–39.6	33.8–34.1	28.1–39.6 (31.2)	1.7
BD	57.0	61.0–63.3	54.6–61.9	59.3–63.9	51.5–64.8 (58.9)	2.8
HD	39.3	40.1–42.7	31.4–42.3	42.5–42.8	31.4–45.6 (40.5)	2.6
CFBD	12.8	11.9–13.3	12.8–14.8	12.5–13.9	11.9–14.8 (13.3)	0.5
PelES	15.5	16.4–17.5	13.5–18.0	16.7–17.0	13.5–18.7 (16.4)	1.2
PelBS	14.7	14.6–15.8	13.1–17.1	15.4–15.9	13.0–17.3 (15.2)	1.1
PecES	-	-	-	-	-	-
PecBS	-	-	-	-	-	-
Th	10.2	8.9–10.4	8.0–11.4	10.3–10.6	8.0–11.4 (9.5)	0.6
LDR	17.4	17.3–19.4	16.6–21.7	18.6–19.4	14.9–21.7 (18.4)	1.1
LAR	20.4	17.4–19.5	17.0–20.6	18.8–21.1	16.6–21.9 (18.9)	1.1
% HL						
PreHL	26.0	25.3–27.4	21.5–32.3	25.5–27.8	15.9–33.7 (26.8)	3.0
PosHL	53.0	52.2–55.4	39.7–58.0	51.6–53.7	39.7–61.3 (51.0)	3.6
SnL	29.7	30.5–37.7	23.3–38.3	32.2–36.3	23.3–40.1 (33.4)	3.2
MES	29.4	31.4–34.3	26.1–34.2	30.0–31.4	23.2–36.5 (31.0)	2.2
MBS	23.2	21.4–25.3	18.6–29.7	19.2–19.7	18.6–30.8 (23.4)	2.6
NSD	23.5	22.8–27.9	18.5–32.0	19.7–20.3	12.9–32.0 (25.0)	3.5
EdV	16.2	14.0–16.8	11.7–18.6	14.2–15.3	11.7–19.2 (16.0)	1.7
DBO	8.1	6.9–9.2	7.0–12.1	6.4–10.2	6.4–12.1 (8.6)	1.2
WO	21.2	16.9–23.9	14.5–26.8	22.0–22.7	14.5–27.2 (21.7)	2.7

Figure 1.24: Eyed-side (A) and blind-side (B) of a paratype of *Trinectes xanthurus*, LACM 33805–27, 74.6 mm, Colombia (Buenaventura). The scale bar corresponds to 10 mm.

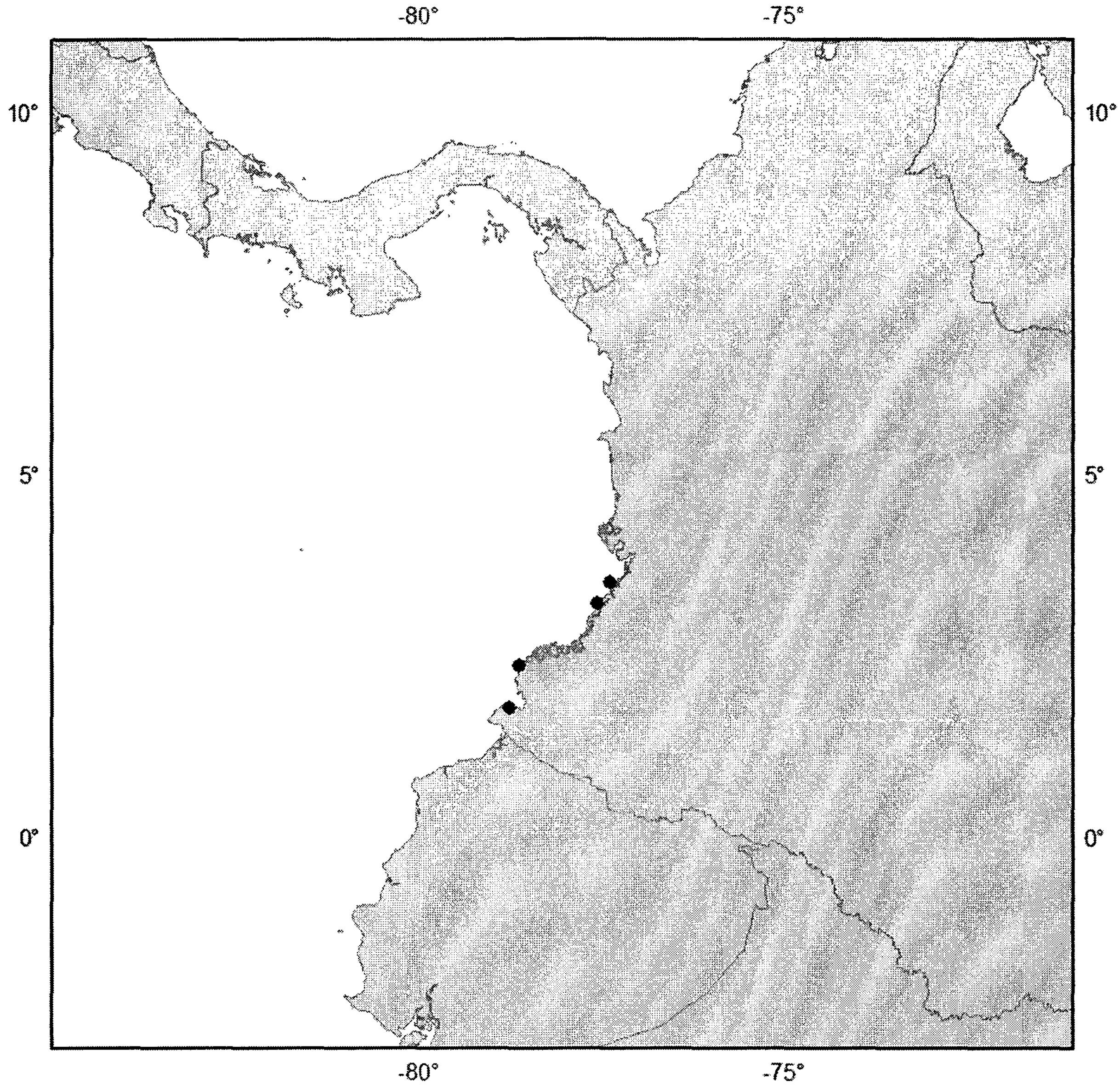


Figure 1.25: Occurrences of *Trinectes xanthurus* specimens included in this study.

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APPENDIX A

Nominal species list

Nominal Species Author/Year	Current Status	Designated By	Nominal Reference	Type Specimen(s)	Comments
Pleuronectes maculatus Bloch & Schneider 1801	Valid as *Trinectes maculatus*	Hubbs (1932)	Bloch, M. E. & J. G. Schneider (1801) M. E. Blochii, Systema Ichthyologiae iconibus cx illustratum. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit Jo. Gottlob Schneider, Saxo. Berolini. Sumtibus Auctoris Impressum et Bibliopolio Sanderiano Commissum. Systema Ichthyol.: i-lx + 1-584, Pls. 1-110.	Holotype ZMB 7408 (stuffed)	Examined
Achirus fasciatus Lacepède 1802	Synonym of *Trinectes maculatus*	Jordan (1923)	Lacepède, B. G. E. (1802) Histoire naturelle des poissons. Tome Quatrième. A Paris, chez Plassan, Imprimeur-libraire, Rue de Vaugirard, No 1195, 728 pp.	No types known	-
Pleuronectes mollis Mitchill 1814	Synonym of *Trinectes maculatus*	Smith (1986)	Mitchill, S. L. (1814) Report, in part, of Samuel L. Mitchill, M. D., Professor of Natural History, etc., on the fishes of New York, New York. *In*: Gill, T. (Ed), *Report, in part, of Samuel L. Mitchill, M. D., Professor of Natural History, etc., on the fishes of New York*. Printed for the Editor, 1898, P. 1–28.	No types known	-
Trinectes scabra Rafinesque 1832	Synonym of *Trinectes maculatus*	Hubbs (1932)	Rafinesque, C. S. (1832) Extracts from a second series of zoological letters written to Baron Cuvier of Paris, by Prof. Rafinesque in 1831. *Atlantic Journal Friend Knowledge*, 1(1), pp. 19-22.	No types known	-
Monochirus inscriptus Gosse 1851	Valid as *Trinectes inscriptus*	Myers (1929)	Gosse, P. H. (1851) *A naturalist's sojourn in Jamaica*. London. Sojourn Jamaica: i-xxiv + 1-508.	Holotype BMNH 1846.10.28.24	Examined
Monochir reticulatus Poey 1860	Synonym of *Trinectes inscriptus*		Poey, F. (1860) Memorias sobra la historia natural de la Isla de Cuba, acompañadas de sumarios Latinos y extractos en Francés. V. 2, Imprenta de la Viuda de Barcina, Calle de la Reina Num. 6, pp. 97–336.	No types known	-
Solea fimbriata	Valid as	Jordan (1923)	Jordan, D. S. (1923) On the family of Achiridae or	Holotype BMNH	Examined

Günther 1862	*Trinectes fimbriatus*		Broad-Soles, with description of a new species *Achirus barnharti* from California, *University of California Publications in Zoology*, 26(1), pp. 1–14.	1848.3.18.184	
Solea fonsecensis Günther 1862	Valid as *Trinectes fonsecensis*	Meek & Hildebrand (1928)	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.* Catalog of Fishes 4(i-xxi), 534 pp.	Holotype BMNH 1848.3.18.189	Examined
Solea panamensis Setindachner 1876	Synonym of *Trinectes fonsecensis*	Castro-Aguirre 1999	Steindachner, F. (1876) Ichthyologische Beiträge (V). Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe, 74(1) pp. 49-240, Pls. 1-15.	Holotype NMW 8023	Examined
Achirus paulistanus Miranda Ribeiro 1915	Valid as *Trinectes paulistanus*		Miranda Ribeiro, A. de 1913-15. Fauna brasiliense. Peixes. Tomo V. [Eleutherobranchios aspirophoros]. Physoclisti. [A summary and index appeared in Miranda-Ribeiro 1918, ref. 20859; Serranidae, Haemulidae and Sciaenidae published in 1913]. Arq. Mus. Nac. Rio de Janeiro v. 17: [1-679], 30 pls. [Issued in parts by family(ies). Not continuously paginated, plates unnumbered. Dates established from ref. 20859.]	Holotype MNRJ 1963	Examined
Achirus affinis Steindachner 1915	Synonym of *Trinectes paulistanus*	Miranda Ribeiro (1915)	Steindachner, F. (1915) Ichthyologische Beiträge (XVIII). Anzeiger der Akademie der Wissenschaften in Wien, 52 (27), pp. 346-349.	Syntypes (5) NMW	Not examined: specimens lost
Achirus microphthalmus Chabanaud 1928	Valid as *Trinectes microphthalmus*	Myers (1929)	Chabanaud, P. (1928) 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 Océanographique*, Monaco, No. 523, pp. 1–53.	Holotype MNHN 0000–3314	Examined
Achirus austrinus Chabanaud 1928	Synonym of *Trinectes paulistanus*	Miranda Ribeiro (1915)	Chabanaud, P. (1928) 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 Océanographique*, Monaco, No. 523, pp. 1–53.	Syntypes: (13) BMNH; NMW 8009 (1), 8089 (1), 8100 (2), 8101 (1); MNHN 0000–3099 (1), MNHN 0000–3317 (2)	Examined: NMW 8009, 8089, 8100 (2), 8101 (1), MNHN 0000-3099 (1)
Achirus fluviatilis	Valid as	Meek &	Meek, S. E. & S. F. Hildebrand (1928) The marine	Holotype USNM	Examined:

Meek & Hildebrand 1928	*Trinectes fluviatilis*	Hildebrand (1928)	fishes of Panama. Part III. Field *Museum of Natural History Publ. Zool. Ser.*, 15 (publ. 249): xxv-xxxi + 709-1045, Pls. 72-102.	81667; Paratypes and non-types: FMNH 18204–09 (0, 1, 1, 1, 1, 1), 18210–44 (total 45); USNM 81668 (now 18), 85768 (10, not found in 1980), 165536 (6); MNHN 1976–0405 (1)	USNM 81668 (9)
Achirus opercularis Nichols & Murphy 1944	Valid as *Trinectes opercularis*	Nichols	Nichols, J. T. & R. C. Murphy (1944) A collection of fishes from the Panama Bight, Pacific Ocean. *Bulletin of the American Museum of Natural History*, 83(4), pp. 217-260, Pls. 15-18.	Holotype AMNH 15958	Examined
Trinectes xanthurus Walker & Bollinger 2001	Valid as *Trinectes xanthurus*	Walker & Bollinger (2001)	Walker H. J. & J. Bollinger (2001) A new species of Trinectes (Pleuronectiformes: Achiridae), with comments on the other eastern Pacific species of the genus. *Revista de Biología Tropical*, 49(1), pp. 177-185.	Holotype: SIO 63–292; Paratypes GCRL V72-9100 (1), V72-9101 (2), V72-9106 (1); LACM W53-33 1(1); SIO 63-292 (30), 63-293 (23), 63-295 (1), 64-965 (3), 69-386 (5), 73-276 (2); UCLA 9754-14 (1), 30714-14 (3), 30715-4 (1), 30716-6 (1), 30745-4 (3), 32542-6 (2), 33805-27 (6), W53-20 (1), W53-275 (28), W53-317 (4), W58-55 (3), W58-304 (41), W58-305 (40); UCR 136.083 (3), 296.007 (7), 360-005 (1), 970.005 (12), 1216.002 (1); USNM 361978 (3)	Examined: SIO 63-293 (23), 73-276 (2), LACM 33805-27 (6), 49189-2 (1)

APPENDIX B

Morphological measurements

Standard length (SL) (Table 1.1; 1.6–1.13): Horizontal distance from tip of snout to posteriormost edge of hypural plate.

Total length (TL): Length from tip of snout to tip of longest caudal fin ray.

% SL

Head length (HL): Length from tip of snout to posterior edge of operculum.

Body depth (BD): Distance from base of the dorsal fin to base of the anal fin.

Head depth (HD): Distance from base of the dorsal fin to base of the anal fin in line with posterior edge of posteriormost eye.

Caudal fin base depth (CFBD): Smallest distance from dorsalmost edge to analmost edge of juncture between body and caudal fin.

Length of eyed-side pelvic fin (PelES): Distance between base of anteriormost eyed-side pelvic fin ray to tip of posteriormost eyed-side pelvic fin ray.

Length of blind-side pelvic fin (PelBS): Distance between base of anteriormost blind-side pelvic fin ray to tip of posteriormost blind-side pelvic fin ray.

Length of eyed-side pectoral fin (PecES): Distance between anteriormost edge of eyed-side pectoral fin to tip of posteriormost eyed-side pectoral fin ray.

Length of blind-side pectoral fin (PecBS): Distance between anteriormost edge of blind-side pectoral fin to tip of posteriormost blind-side pectoral fin ray.

Thickness (Th): Distance from posterior edge of eyed-side operculum to posterior edge of blind-side operculum.

Longest dorsal ray (LDR): Length from base to tip of longest dorsal fin ray.

Longest anal ray (LAR): Length from base to tip of longest anal fin ray.

% HL

Preorbital head length (PreHL): Horizontal distance from anteriormost edge of anteriormost eye to tip of snout.

Postorbital head length (PosHL): Horizontal distance from posteriormost edge of posteriormost eye to posteriormost edge of eyed-side operculum.

Snout length (SnL): Horizontal distance from anterior-most edge of ventral eye to tip of snout.

Mouth length on eyed-side (MES): Distance from posteriormost point to anterior most point inside eyed-side mouth.

Mouth blind-side length (MBS): Distance from posteriormost point to anterior most point inside blind-side mouth.

Nostril to snout distance (NSD): Distance from posterior eyed-side nostril to tip of snout.

Ventral eye diameter (EdV): Horizontal distance from posteriormost edge to anteriormost edge of ventral eye, inclusive of margin.

Dorsal eye diameter (EdD): Horizontal distance from posteriormost edge to anteriormost edge of dorsal eye, inclusive of margin.

Distance between orbits (DBO): Shortest distance between ventral and dorsal eyes.

Width of orbits (WO): Greatest horizontal distance between the posteriormost margin of the posteriormost eye to the anteriormost margin of the anteriormost eye.

Meristic measurements

Dorsal fin rays (Table 1.2): Number of dorsal fin rays.

Anal fin rays (Table 1.2): Number of anal fin rays.

Caudal vertebrae (Table 1.3): Number of caudal vertebrae.

Precaudal vertebrae (Table 1.3): Number of precaudal vertebrae.

Pectoral fin rays ES and BS (Table 1.4): Number of eyed-side and blind-side pectoral fin rays, respectively.

Pelvic fin rays ES and BS (Table 1.5): Number of eyed-side and blind-side pelvic fin rays, respectively.

Caudal fin rays (CFR): Number of caudal fin rays.

Supracranium: Number of pterygiophores anterior to the neural spine of the third precaudal vertebra (Fig. 1.3).

Qualitative characters

Length of ethmoid (Fig. 1.3): Length of the ethmoid process.

Margin of anterior eyed-side nostril (Fig. 1.4): Margin with ring of cirri or without ring (smooth).

Dorso-posterior process of neural arc (Fig. 1.3): Rounded or pointed.

Angle of urohyal (Fig. 2.6): Open or closed.

Hemal spine of posteriormost precaudal hemapophysis (Fig. 1.3): With or without posterior wing.

Hemal arch of anteriormost precaudal vertebrae (Fig. 1.3): Thick or thin.

APPENDIX C

Glossary

Anal fin rays (AFR) (Fig. 1.3B): Includes all rays projecting from the anal fin, which extends from the anus to the base of the caudal fin.

Apomorphy: Derived character state.

Autapomorphy: A derived trait that is unique to a given taxon.

Bremer Index: Estimate of support for a given branch on a cladogram. Values correspond to the number of steps required to break the branch; therefore the higher the number, the stronger the support. Also known as Bremer support values or Decay Index.

Caudal fin rays (CFR) (Fig. 1.3A): Includes all rays projecting from the caudal skeleton.

Caudal vertebrae: Vertebrae with hemapophyses that fully extend to the anal fin.

Centrum: The central portion of a vertebra.

Cirri: Plural of cirrus, meaning a bundle or tuft of cilia found on the eyed-side body or head of flatfish.

Clade: Monophyletic group, consisting of a single common ancestor and all its descendents.

Coracoscapular complex: Assemblage of cartilage and bones associated with the cleithrum and supporting the pectoral fin rays.

Dorsal fin rays (DFR) (Fig. 1.3DE): Includes all rays projecting from the dorsal fin, which extends from the tip of the snout dorsally to the base of the caudal fin.

Dorso-posterior process of vertebral centrum (DPP) (Fig. 1.3E): Small dorso-posterior projection of a centrum.

Epural (EP) (Fig. 1.3A): Free bone of caudal skeleton inserted between hypural 5 and the last neural spine.

Ethmoid (ET) (Fig. 1.3D): Unpaired bone on anterior part of skull that forms part of the nasal cavity and extending anterior to the dorsal orbit.

Fimbriae (Fig. 1.4): Fleshy extensions projecting from the lips.

Hemal spine 1 (HS1) (Fig. 1.3B): First spine of the caudal region.

Penultimate hemal spine and antepenultimate hemal spine (PenHS & AHS) (Fig. 1.3A): Hemal spine of the penultimate (second-to-last) and antepenultimate (third-to-last) caudal vertebrae, occasionally supporting caudal fin rays.

Hemapophysis (HMP) (Fig. 1.3E): Ventral projection of the centrum of a precaudal vertebra; fused in the caudal region to form a hemal arch bearing a spine.

Hypural plates (HP) (Fig. 1.3A): Series of 5 bones articulating or attached to the last caudal centrum.

Median fins: Dorsal, anal, and caudal fins.

Last neural spine (LNS) (Fig. 1.3A): Neural spine of the penultimate centrum.

Parhypural (PH) (Fig. 1.3A): Free bone inserted between the last hemal spine and the hypural complex.

Pectoral fin: Fins that project from the cleithrum of both the eyed- and blind-sides.

Pelvic fin: Fins that project ventral to the pelvic girdle on both the eyed- and blind sides.

Penultimate caudal vertebrae (PenCV) (Fig. 1.3AE): Posteriormost caudal vertebrae

Plesiomorphic: Ancestral character state.

Precaudal vertebrae (PCV) (Fig. 1.3E): Vertebrae in the abdominal region, anterior to the first caudal vertebrae which bears a modified hemal spine (hemal spine 1).

Pterygiophore (PTR) (Fig. 1.3BD): Bone that supports the median fin rays.

Supracranium (Fig. 1.3D): Area dorsal to the cranium.

Tentacle: Fleshy projections on the blind-side head and opercular regions.

Transverse band: Bands that extend vertically throughout the body, from the base of the dorsal fin to the base of the anal fin.

Type specimen(s): Specimen(s) used in the original description of a given species: this/these specimen(s) fix(es) a name to a taxon.

Urohyal (UR) (Fig. 1.3C): U-shaped bone in the hyoid arch.

Urostyle (US) (Fig. 1.3A): Last visible centrum of the vertebral column.

Vertical fins: Dorsal and anal fins.

CHAPTER 2

Phylogenetic relationships within *Trinectes* (Pleuronectiformes: Achiridae)

ABSTRACT

The phylogenetic relationships of the nine valid species of the flatfish genus *Trinectes* (Pleuronectiformes: Achiridae) were hypothesized based on a cladistic analysis of 22 morphological, meristic and osteological characters. The analysis resulted in one most parsimonious tree with a length of 39 steps (CI = 0.69; RI = 0.79). *Trinectes* is monophyletic based on two synapomorphies: the unpierced interbranchial septum, and the presence of seven or more pterygiophores anterior to the neural spine of the third precaudal vertebra. Our analysis indicates that *T. inscriptus* is the most plesiomorphic species of the genus. All other species form a monophyletic group subdivided in two clades. The first clade contained (most plesiomorphic to most recent): *T. paulistanus*, *T. fonsecensis*, and the clade of *T. fluviatilis*-*T. xanthurus*, the latter clade being strongly supported by five synapomorphies. The second clade included (most plesiomorphic to most recent): *T. maculatus*, *T. opercularis* and the clade *T. fimbriatus*-*T. microphthalmus*. The clade that includes *T. opercularis, T. fimbriatus,* and *T. microphthalmus* is strongly supported with 12 synapomorphies. The resulting cladogram depicts a sequence of speciation events and provides an opportunity to propose a biogeograhical hypothesis on the evolution of the species in the genus.

RÉSUMÉ

Les relations phylogénétiques des neuf espèces valides du genre de poisson plat *Trinectes* (Pleuronectiformes: Achiridae) sont examinées par une analyse cladistique de 22 caractères morphologiques, méristiques, et ostéologiques. L'analyse visant la découverte de l'arbre le plus parcimonieux a résulté en un seul arbre avec 39 transformations de caractères (IC = 0.69; IR = 0.79). La monophylie de *Trinectes* est fondée sur deux synapomorphies : septum interbranchial entier, et au moins sept ptérygiophores de la nageoire dorsale antérieurs à l'épine neurale de la troisième vertèbre pré-caudale. Nos résultats indiquent que *T. inscriptus* est la plus plésiomorphique espèce du genre, les autres espèces formant un groupe monophylétique subdivisé en deux clades. Le premier clade (en ordre d'ancienneté) contient *T. paulistanus*, *T. fonsecensis*, ainsi que le clade *T. fluviatilis*-*T. xanthurus*, fondée sur cinq synapomorphies. Le deuxième clade contient *T. maculatus, T. opercularis* et le clade *T. fimbriatus*-*T. microphthalmus*. La monophylie du clade qui inclut *T. opercularis*, *T. fimbriatus* et *T. microphthalmus* est corroborée par 12 synapomorphies. Le cladogramme démontre une séquence de spéciation qui se prête à l'élaboration d'une hypothèse biogéographique sur l'évolution des espèces de ce genre.

INTRODUCTION

Family Achiridae

The family Achiridae includes approximately 31+ valid species in nine genera of dextral amphi-american flatfishes (Munroe 2005). The monophyletic status of the family was established by Chapleau & Keast (1988) in their phylogenetic assessment of the family Soleidae. They determined that the family Soleidae was not monophyletic because one of its subfamilies, the Soleinae was more closely related to the family Cynoglossidae than to the other soleid subfamily, the Achirinae (Chapleau & Keast 1988). To ensure that their classification was an accurate reflection of phylogeny, Chapleau & Keast (1988) elevated both soleid subfamilies to the familial level, thus creating the Achiridae and Soleidae (*sensu novo*). The Achiridae were found to be monophyletic based on five characters (Chapleau & Keast 1988): (1) the smaller eyed-side suspensorium (excluding opercular bones); (2) the ascending process of eyed-side premaxilla modified to accommodate ventral margin of the rostral cartilage; (3) the large ethmoid forming anterior and anteroventral margins of upper eye (except in *Gymnachirus*); (4) the concave dorsal margin of blind-side lateral ethmoid; (5) and the presence of a large foramen through the lateral surface of first basibranchial.

Ramos (1998), in his unpublished thesis on the Achiridae, added eight synapomorphies in support of the monophyly of the family. Recently, Azevedo *et al.* (2008) conducted a molecular phylogenetic analysis using sequences of 12S and 16S mitochondrial rRNA genes on several pleuronectiform species, which included five achirid species belonging to four genera (*Trinectes*, *Achirus*, *Catathyridium* and *Hypoclinemus).* Their analysis indicated that the five species formed a monophyletic group, corroborating previous hypotheses of monophyly for the Achiridae.

Genus Trinectes

Trinectes Rafinesque 1832 is a genus of the family Achiridae inhabiting temperate to warm waters of both the Atlantic and Pacific coasts of North, Central, and South America. *Trinectes* was revised in Chapter 1 and comprises nine valid species: *T. maculatus*, *T. inscriptus*, *T. microphthalmus*, and *T. paulistanus* are found in the Atlantic from Maine, USA, to Rio de Janeiro, Brazil, and *T. fonsecensis*, *T. fimbriatus*, *T. fluviatilis*, *T. opercularis*, and *T. xanthurus* are found in the Pacific from the Gulf of California, Mexico, to Southern Peru. Although primarily marine, *Trinectes* often occur in estuaries and in freshwater, with one species, *T. fluviatilis*, occuring almost exclusively in freshwater.

Rafinesque (1832) was the first to use the generic name *Trinectes* in his short description of *T. scabra*, which simply reads (translated from French) "A new genus of fish near to *Achirus*, found in the River Schuylkill; it has only three fins, dorsal, and anal and caudal." Hubbs (1932) later confirmed the synonymy between *T. scabra* and *Achirus fasciatus* Lacépède 1802, and subsequently between *A. fasciatus* and *Pleuronectes maculatus* Bloch & Schneider 1801. Based on these observations, Hubbs (1932) determined the scientific name of this species (and new genus) should stand as *T. maculatus* (Bloch & Schneider 1801), which is still currently recognized as the type species of the genus (Chapter 1).

The objective of this study is to conduct a phylogenetic analysis of all valid *Trinectes* species, based on morphometric and osteological characters. Comments on the biogeography and speciation patterns of *Trinectes* are also provided.

MATERIALS AND METHODS

Data acquisition

The phylogenetic analysis was based on 22 morphological, meristic, and osteological characters of nine terminal taxa. These characters are described in Appendix #. Autapomorphies of each species were not included in the character matrix. All data for character states were obtained from whole preserved specimens, radiographs, and/or cleared and stained (C&S) specimens. All morphological characters were taken from the eyed-side except for characters 8 (blind-side operculum) and 12 (caudal fin base depth), which were taken on the blind-side.

C&S specimens were prepared according to Taylor & Van Dyke (1985). Terminology of bones follows Cooper & Chapleau (1998). Institutional abbreviations follow Leviton *et al.* 1985. Morphological measurements were taken with an electronic caliper, sensitive to the nearest hundredth (0.01) mm, but rounded to the nearest tenth (0.1) of a mm for analyses.

Table 2.1: Data matrix for 22 characters of the valid *Trinectes* species. *Achirus lineatus*, *Catathyridium jenynsi*, and *Hypoclinemus mentalis* were used as outgroups. The presence of polymorphism in a taxon is indicated by 0/1. States that could not be scored due to character absence are represented by (?). List of characters, along with descriptions, can be found in the Materials and Methods.

	Character																					
Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**
Achirus lineatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Catathyridium jenynsi	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	2	0	0/1
Hypoclinemus mentalis	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	?	0	0/1	0	0
Trinectes fimbriatus	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	1	0	1	1	2	0	1
T. fluviatilis	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	2	2	0	0	2	1	3
T. fonsecensis	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0/1	0	1	0	0	1	0	3
T. inscriptus	1	0	0	0	0	0	0	0	0	0/1	0	0	0	0	1	0	0	0	0	0	0	1
T. maculatus	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1	2	0	2
T. microphthalmus	1	1	1	1	1	1	1	1	1	0	0	0	0/1	0	0	1	0	1	1	2	0	1
T. opercularis	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	2	0	2
T. paulistanus	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	1	0	2
T. xanthurus	1	0	0	0	0	0	0	0	0	1	0	1	1	1	1	2	2	1	1	2	1	3

Data analysis

Mesquite version 2.7 (Maddison & Maddison 2009) was used to build the character matrix (see Table 2.1) and to save it in the nexus format (.nex). The matrix was then opened in PAUP version 4.0a (Swofford 2003), where the phylogenetic analysis was performed. The branch and bound analysis using parsimony was selected, where all characters were unordered, unweighted, and accelerated character optimization (ACCTRAN) was selected as the reconstruction method.

The tree file (.tre) that was generated from the analysis using PAUP was saved, and along with the nexus file was opened under MacClade version 4.08 (Maddison & Maddison 2009). MacClade was used to trace characters along the tree, manipulate the cladogram, and generate the correlation and retention indices (CI and RI, respectively) (Fig. 2.7). The CI is calculated by taking *m/s*, where *m* is equal to the minimum possible number of times a character appears on the tree and *s* is the observed number of times it appears on the tree (Maddison & Maddison 2009). The RI is calculated as (g-s)/(g-m), where m and s represent the same as that for the CI, but g represents the maximum possible number of times a character appears on the tree. In other words, the CI, a number between 0 and 1, is an indication of the amount of homoplasy in a cladogram. The closer to 0, the higher amount of homoplasy. The RI, on the other hand, is an indication of the amount of synapomorphy that is in the cladogram. The closer to 1, the higher the amount of synapomorphy. Bremer support values (Bremer 1988) were calculated using TreeRot version 3 (Sorensen 2007). The methodology in obtaining these values, taken from Sorensen (2007), is shown in Appendix E. The Bremer's index, also known as the decay index, represents the number of steps required to break down a given branch. In other words, they are a measure of the amount of support a given branch has: the higher the number, the stronger the support.

Outgroup selection

Chapleau (1986, *unpublished data*) hypothesized that the achirid genera *Achirus* and *Catathyridium* were plesiomorphic taxa within the Achiridae and that *Trinectes*, *Hypoclinemus*, *Apionichthys*, *Soleonasus*, and *Gymnachirus* formed a monophyletic group (Fig. 2.1). However, this hypothesis was not strongly supported (one synapomorphy).

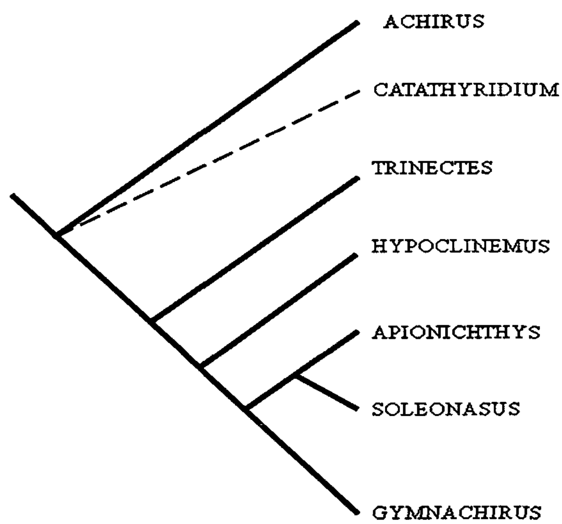

Figure 2.1: Topology of the cladogram presented by Chapleau (1986, *unpublished data*) showing the phylogenetic relationships within Achiridae based on osteological data.

Ramos (1998, *unpublished data*) designated the genus *Hypoclinemus* as the most plesiomorphic achirid genus (Fig. 2.2). In his analysis, Ramos (1998) placed the genera *Apionichthys* and *Hypoclinemus* as sister groups to *Trinectes*. However, this relationship was weakly supported by a single character: the on node "J". The clade of *Gymnachirus*-*Apionichthys*, on the other hand, is strongly supported by sharing seven exclusive characters. Furthermore, in Chapleau's (1986) assessment of *Gymnachirus* and *Apionichthys*, it was established that these two genera are highly derived groups within the family, and differ considerably from all other achirids. Such differences are depicted in *Gymnachirus* lacking any scales, and *Apionichthys* having an eyed-side cranium that is highly reduced to a single process (Chapleau 1986). However, Ramos' (1998; *unpublished data*) placement of *Achirus* and *Catathyridium* as closely related to *Trinectes* was in agreement with Chapleau's (1986; *unpublished data*) conclusion.

Although the study of Azevedo *et al.* (2008) included only a few achirid species, their analysis generated two achirid clades: *Catathyridium-Trinectes* and *Hypoclinemus-Achirus* (Fig. 2.3).

With our current state of knowledge of intrarelationships in the Achiridae, it appears reasonable to consider *Achirus*, *Catathyridium*, and *Hypoclinemus* as outgroups for a study dealing with species intrarelationships of *Trinectes*. For the scope of this study, it was decided to exclude the genera *Gymnachirus* and *Apionichthys* as outgroups. The inclusion of these genera in our phylogenetic analysis would undoubtedly create confusion in character polarization, as they differ so clearly from all other achirids. *Achirus* was represented by *A. lineatus*, *Catathyridium* by *C. jenynsi*, and *Hypoclinemus* by *H. mentalis*.

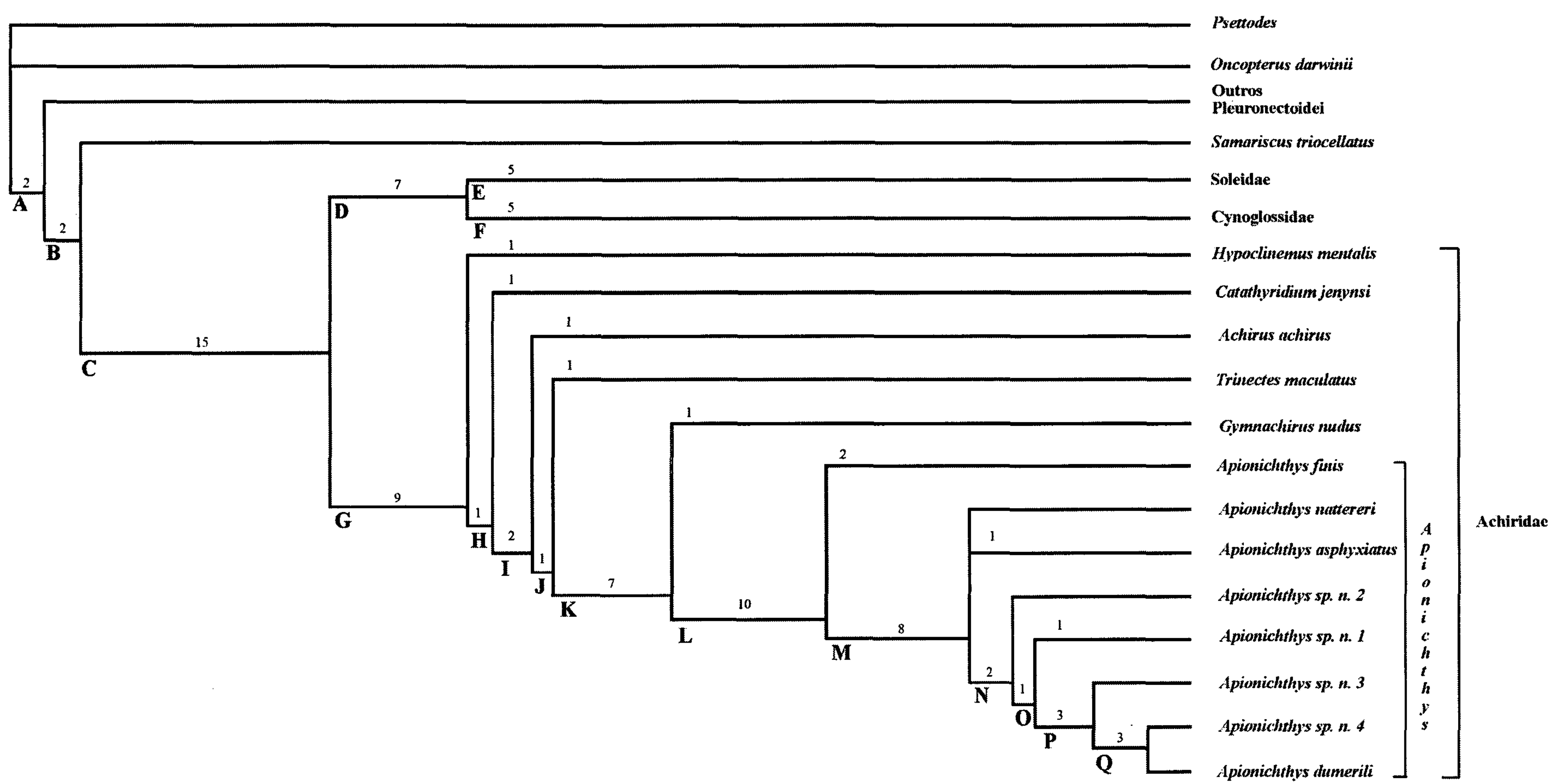

Figure 2.2: Topology of the cladogram presented by Ramos (1998, *unpublished data*) showing the phylogenetic relationships within the Achiridae based on osteological data. Cladogram has been modified to show the number of characters supporting each clade.

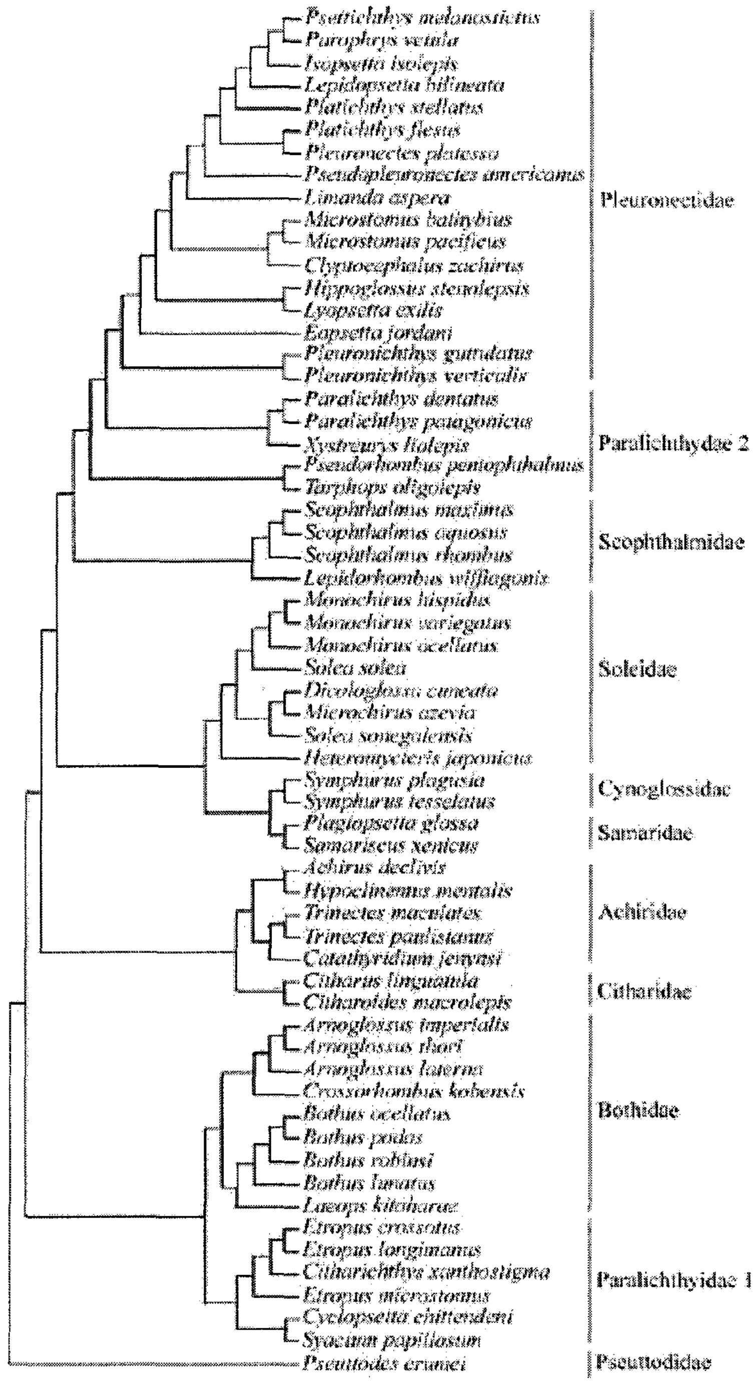

Figure 2.3: Topology of the cladogram by Azevedo *et al.* (2008) showing phylogenetic relationships within Pleuronectiformes based on molecular evidence.

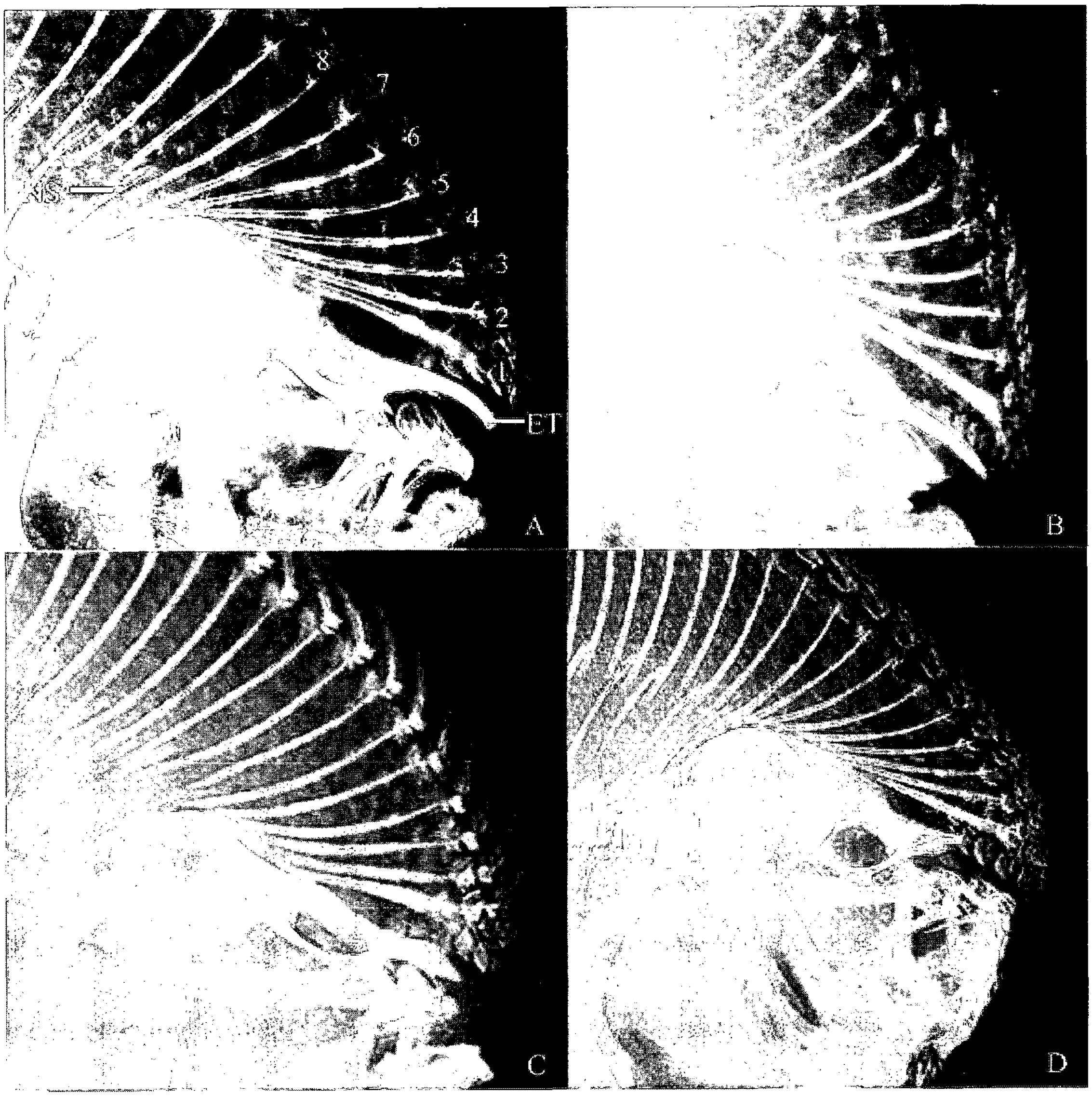

Figure 2.4: Radiographs of the head region, showing variability of the length of the ethmoid process (ET, character 14), and the supracranial complex of the dorsal fin (numbers 1–8, character 22) in: (A) *Trinectes maculatus* (USNM 022621); (B) *T. microphthalmus* (LIUEFS 51065); (C) *Achirus lineatus* (USNM 087774); and (D) *T. xanthurus* (USNM 361532). The ethmoid process is either long (A, B), reaching the distal end of the first dorsal fin ray, or short (C, D), reaching no further than the anteriormost point of the upper maxillary (UM). The supracranial complex of the dorsal fin can be made of 6 (C), 7 (B), 8 (A), or 9 (D) pterygiophores anterior to the neural spine (NS) of the third precaudal vertebra.

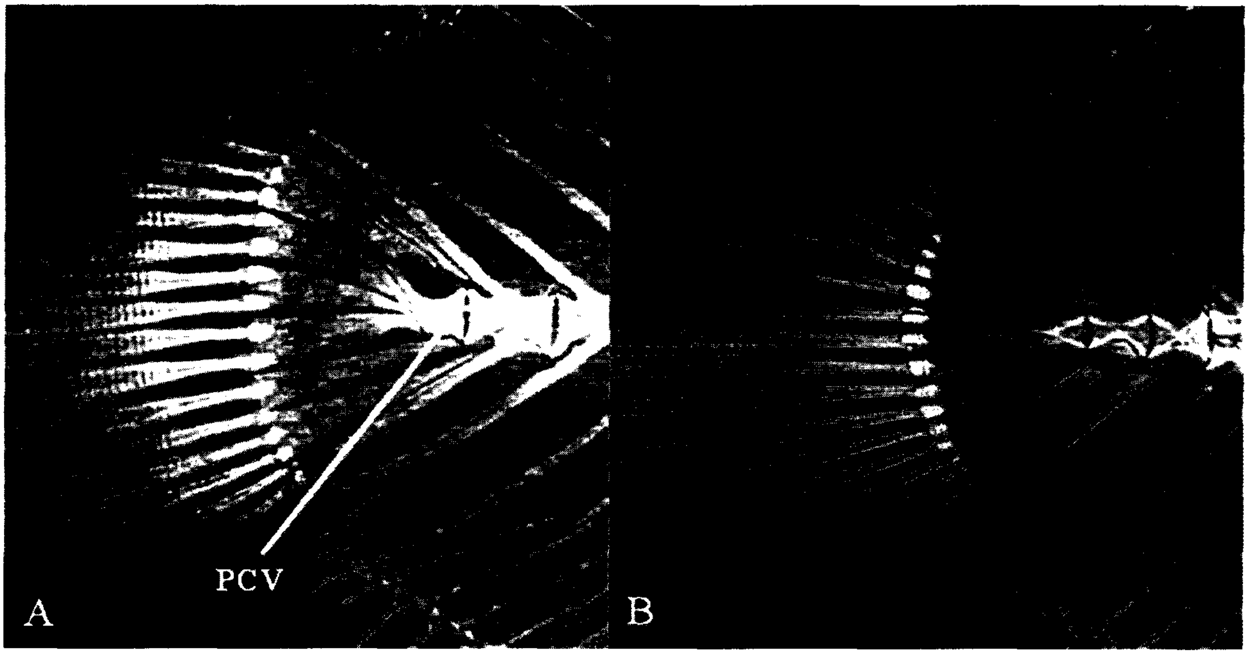

Figure 2.5: Radiographs of the caudal region, showing the connections between the hypural plates 2, 3, and 4 to the posteriormost caudal vertebra (PCV) (character 15) in *Trinectes paulistanus* (A, USNM 286986), and *T. opercularis* (B, USNM 361517). These hypural plates can either be separate (A), or fused (B) to the last centrum of the vertebral column.

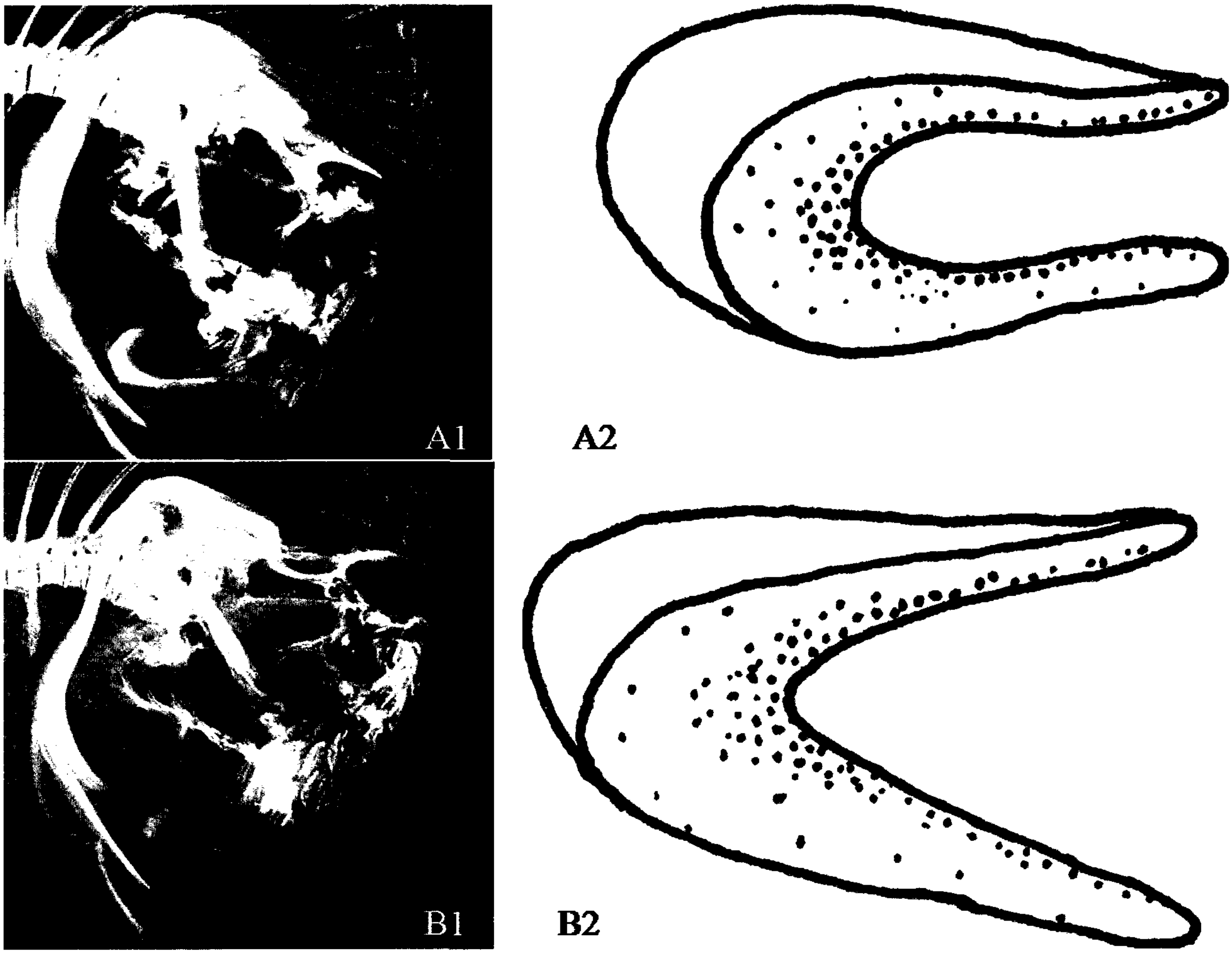

Figure 2.6: Two states of the angle of the urohyal (UR) (character 4), shown in *Trinectes opercularis* (A1, USNM 361517) and *Trinectes maculatus* (B1, USNM 118881). The angle can either be closed (A2, state 1) or open (B2, state 0).

MATERIALS EXAMINED

Trinectes fimbriatus: LACM 33806–38, 2 c&s SIO 94–132, 1 c&s (67.10 mm), 9°47.8'N 84°40.3'W, Costa Rica, Puntarenas, Gulf of Nicoya, Pacific; UMMZ 194671, 1 c&s (59.02 mm), 9°53'--"N 84°50'--"W, Costa Rica, Puntarenas, Gulf of Nicoya, Pacific; USNM 85767, 1(51.40 mm), Chame Point, Panama; USNM 361523, No data; ***T. fluviatilis***: USNM 293639, 2(23.51–26.18 mm), Rio Tuira Drain, between Calle Larga + Pinogarna above El Real; USNM 081669, 2(29.97–40.62 mm), Rio Culebra, Panama; USNM 293387, No data; USNM 293385 1 c&s, No data; ***T. fonsecensis***: USNM 361527, 1(128.51 mm), 06°58'--" N 077°41'--" W, Buenaventura, Colombia; USNM 361525, 1(89.31 mm), 06°58'--" N 077°41'--" W, Buenaventura, Colombia; USNM 361521, 1(152.75 mm), Buenaventura, Colombia; LACM 33806–102, 2(93.55–131.44 mm), Puntarenas, Costa Rica; UMMZ 192147, 2 c&s (52.01–53.12 mm), 21°50'--"N 105°10'--"W, Mexico, Nayarit, Rio Grande de Santiago, Pacific; USNM 050332, 1(120.62 mm), Panama; ***T. inscriptus***: FMNH 65426, 1 c&s (66.88 mm), 18°30'00"N 065°55'00"W, Caribbean Sea, Oregon Station 2603; CAS 11994, 2 c&s (38.47–39.29 mm), Cuba, Matanzas, Rio Yumuri drainage, outlet to ocean at Matanzan, below freshwater; SU 18587, 1 c&s (58.92 mm), Panama, Rio Portogandi, Mosquito Point; USNM 125476, 2(70.23–71.55 mm), Caribbean Sea, Puerto Rico; USNM 035001, No data; USNM 44120, 1(55.04 mm), No data; ***T. maculatus***: ANSP 86613, 2 c&s (70.08–66.75 mm), USA, Delaware, New Castle, Delaware River; ANSP 140013, 2 c&s (65.97–76.04 mm), USA, New Jersey, Dennis Cove; USNM 197444, 2(81.09–91.75 mm), Arkansas Bay, Gulf of Mexico, Texas, USA; USNM 049012, No data; USNM 022621, No data; USNM 118474, No data; ***T. microphthalmus***: ANSP 123712, 2 c&s (51.07–52.28 mm), Brazil, Rio de Janeiro, Atafona; LIUEFS 2733, No data; LIUEFS 51065, No data; UFPB 3595, 10(47.95–59.49 mm), No data; ***T. opercularis***: USNM 361523, 3(51.64–53.06 mm), 04°47'--" N 077°22'--" W, Buenaventura, Colombia; USNM 361540, 1(51.96 mm), 03°14'--" N 077°34'--" W, Buenaventura, Colombia; USNM 361517, 6(49.62–56.95 mm), 04°20'--" N 077°28'--" W; 04°18'--" N 077°29'--" W, off Rio Togoroma, Colombia; AMNH 15958, holotype (47.28 mm), No data; ***T. paulistanus***: SIO 63-460, 2 c&s(74.72–87.66 mm), 06°54'--" N, British Guiana, USNM 114281, 1(68.02 mm), Rio Sauce, 2 miles South-West of El Estor at mouth in Lake Yzabel, Guatemala; USNM 121810, 5(47.20–92.28 mm), Caribbean, Lago Maracaibo at Yacht club, Venezuela; USNM 286986, No data; USNM 290995, 1(76.26 mm), 04°59'--" N 051°58'--" W, French Guiana; ***T. xanthurus***: LACM 33806–101, 2 c&s (65.48–65.65 mm), Costa Rica, Puntarenas; SIO 73–276, paratype (56.59–59.15 mm), El Salvador; SIO 82–15, 2 c&s (65.68–74.42 mm), No data; USNM 361532, 1(62.50 mm), 3°32'--" N 77°22'15" W, Tortugas Grounds, South of Buenaventura, Colombia; USNM 361541, 4(69.70–83.61 mm), 3°14'--" N 77°33'--" W, Buenaventura, Colombia; ***Achirus lineatus***: AMNH 21827, 2 c&s, No data; FMNH 51012, No data; USNM 087774, No data; ***Catathyridium jenynsi***; MZ 16042, 1 c&s, No data; USNM 47662, No data; USNM 55583, 2, No data; USNM 181499, No data; USNM 181526; No data; ***Hypoclinemus mentalis***: USNM 094671, No data; USNM 167720, No data; USNM 176006, No data; USNM 191555, No data; USNM 217644, No data; USNM 368740, No data.

RESULTS

Branch and bound analysis resulted in one most parsimonious tree with 39 steps, a consistency Index (CI) = 0.69, a retention Index (RI) = 0.79, and 12 of 22 characters with CI = 1.00 (Fig. 2.7).

Trinectes is monophyletic based on two synapomorphies: unpierced interbranchial septum (Fig. 1.1; character 1), and seven or more pterygiophores anterior to the neural spine of the third precaudal vertebra (character 22) (Fig. 2.4).

The most plesiomophic taxon of the genus is *Trinectes inscriptus* (Fig. 2.7, node A). All other *Trinectes* species form a monophyletic clade on the basis of two synapomorphies: the presence of eight or more pterygiophores anterior to the neural spine of the third precaudal vertebra (character 22) (Fig. 2.4), and the absence of rays on the eyed-side pectoral fin (character 20), with a reversal in *T. fonsecensis* to one to two rays.

These eight species branch into two four-species clades (Fig. 2.7, node B). The first clade (Fig. 2.7, node D) contains *T. paulistanus*, *T. fonsecensis*, *T. fluviatilis*, and *T. xanthurus*, and is monophyletic on the basis of two synapomorphies: little to no cirri on eyed-side body (character 13; a reversal), and 20 to 21 caudal vertebrae (character 17). Within this clade, *fonsecensis-fluviatilis-inscriptus* form a monophyletic group based on having 9 pterygiophores anterior to the neural spine of the third precaudal vertebra (character 22) (Fig. 2.4). Finally, *fluviatilis-xanthurus* form a monophyletic clade based on five synapomorphies: narrow caudal fin base (character 12), short ethmoid process (character 14) (Fig. 2.4), fimbriae on the lower lip unbranched (character 16), 21 caudal vertebrae (character 17), and a large ventral eye diameter (character 21).

The second clade (Fig. 2.7, node C) contains *Trinectes fimbriatus*, *T. microphthalmus*, *T. opercularis*, and *T. maculatus*, and is based on two synapomorphies: the blind-side coracoscapular complex on the pectoral fin girdle is absent (character 18; a reversal), and the eyed-side coracoscapular complex on the pectoral fin girdle is absent (character 19; a reversal). Within this clade, *fimbriatus-microphthalmus-opercularis* form a monophyletic group on the basis of twelve synapomorphies: 32–36 anal fin rays (character 2); fringe of cirri around margin of eyed-side anterior naris (character 3); urohyal closed (Fig. 2.6A; character 4); dorso-posterior process of neural arc rounded (character 5); haemal spine of posteriormost precaudal haemapophysis with posterior wing (character 6); thick haemal arch (character 7); blind-side operculum with scaleless patch (character 8); interorbital distance at least width of ventral eye diameter (character 9); narrow body (character 10); pigmentation associated with transverse bands (character 11); the second, third, and fourth hypural plates are fused to the posteriormost caudal vertebrae (Fig. 2.5; character 15); and highly-branched fimbriae on the eyed-side lower lip (Fig. 1.4C; character 16). Within this clade, *fimbriatus-microphthalmus* form a monophyletic clade based on the presence of seven pterygiophores anterior to the neural spine of the third precaudal vertebra (character 22; a reversal) (Fig. 2.5).

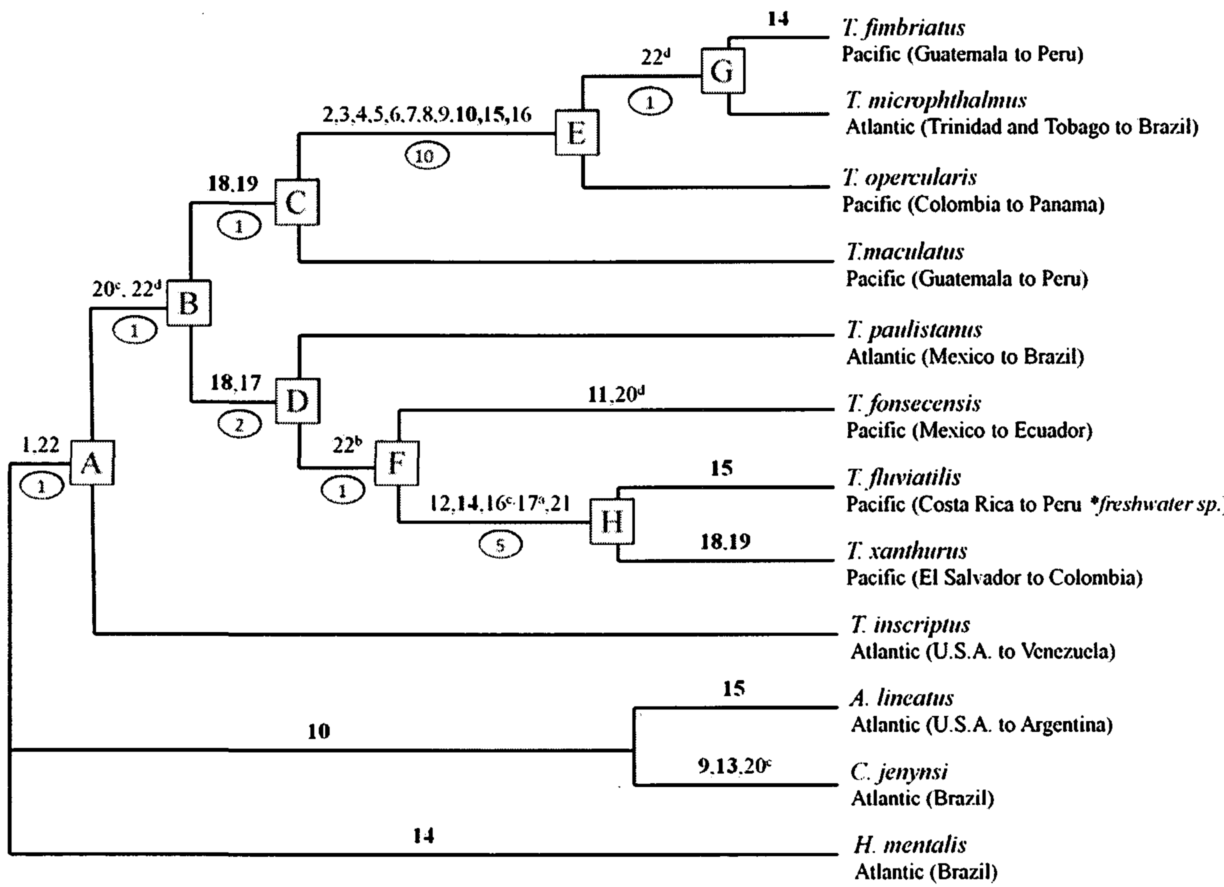

Figure 2.7: Cladogram from an analysis of 22 characters for nine ingroup species of *Trinectes (Achirus lineatus, Cathathyridium jenynsii* and *Hypoclinemus mentalis* were used as outgroups). Character change is 0→1 except a: 1→2, b: 2→3, c: 0→2, d: 2→1; bold: convergence. Letters represent nodes; Bremer's support values are circled under branches.

DISCUSSION

This thesis provides the first analysis of intrarelationships in the genus *Trinectes* (Pleuronectiformes; Achiridae). One fully-resolved tree was obtained from an analysis of 22 characters for 9 internal taxa.

Based on phylogenetic evidence, it is hypothesized that the evolution of *Trinectes* species occurred initially in the Atlantic Ocean (Fig. 2.7, nodes A and B). This is supported by the fact that the most plesiomorphic species of the genus, *T. inscriptus*, is an Atlantic species and that the most plesiomorphic species of both four-species clades (Fig. 2.7, node D and C), *T. paulistanus* and *T. maculatus*, are also Atlantic species.

Within the four-species clade derived from node D (Fig. 2.7), the speciation event that resulted in the ancestor of the clade *fonsecensis-fluviatilis-xanthurus* and the Atlantic *paulistanus* could have been triggered by the formation of an Atlantic-Pacific or East-West barrier. One such barrier that may explain this speciation event is the rise of the Isthmus of Panama, which closed the connection between the Caribbean and the eastern Pacific, approximately 3 million years ago (Coates & Obando 1996). It represents a complete, recent barrier across what was once a large, neotropical environment (Farrell *et al.* 1995; Coates & Obando 1996; Knowlton & Weigt 1998). Assuming that the closure of the Isthmus of Panama was the last Atlantic-Pacific barrier to occur, I hypothesize that this event may have been the driving force behind the speciation event of node D.

The post-isthmus speciation events within the *fonsecensis-fluviatilis-xanthurus* species group resulted from barriers that separated the ancestral Pacific distribution (likely North-South) with subsequent dispersal to explain the overlapping distributions. The nature of these barriers remains unknown. Of interest is the speciation event that resulted in the evolution of *T. fluviatilis* and *T. xanthurus*. *T. fluviatilis* is an almost exclusively freshwater species, whereas *T. xanthurus* occurs mainly in marine waters. It could be argued that this speciation event was accompanied, or possibly triggered, by a difference in salinity requirements.

Similarly to node D, the speciation event that first occurred within the four-species clade derived from node C (Fig. 2.7) that resulted in the ancestor to the clade *opercularis-microphthalmus-fimbriatus* and the Atlantic *maculatus* may have been triggered by the formation of an East-West barrier. However, if it again assumed that the closure of the Isthmus of Panama was the lattest such barrier to occur, the barrier that drove the speciation event of node C likely predated this event. Although the most plesiomorphic species of the *opercularis-microphthalmus-fimbriatus* species group is a Pacific species and *maculatus* is an Atlantic species, the more apomorphic species within the clade derived from node D (i.e. *fimbriatus* and *microphtalmus*) also show an Atlantic-Pacific speciation event (Fig. 2.7). It is therefore hypothesized that the *fimbriatus-microphthalmus* species group was associated with the closure of the Isthmus of Panama.

These results suggest that *Trinectes* had a saltwater origin, particularly in the Atlantic Ocean. However, additional characters (particularly osteological) need to be discovered and incorporated in the analysis to provide a more robust cladogram. Such a cladogram would allow for further verification of the intraspecific biogeographical hypotheses of *Trinectes*.

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APPENDIX D

Characters 1–22

1. INTERBRANCHIAL SEPTUM (CI=1.00; RI=1.00): Tissue layer located underneath the operculum, which separates both opercular chambers. **State 0** – pierced by foramen; **State 1** – not pierced by foramen.
2. ANAL FIN RAYS (CI=1.00; RI=1.00): Rays projecting from the anal fin. **State 0** – 39–45 rays; **State 1** – 32–36 rays.
3. ANTERIOR EYED-SIDE NOSTRIL (CI=1.00; RI=1.00): Nostril located anterior to the ventral eye, just posterior to the tip of the snout. **State 0** – naked margin; **State 1** – ring of cirri on margin.
4. ANGLE OF UROHYAL (CI=1.00; RI=1.00): Angle of the urohyal bone. **State 0** – open; **State 1** – closed.
5. DORSO-POSTERIOR PROCESS OF THE NEURAL ARC (CI=1.00; RI=1.00): Dorsal projection of the vertebral centrum (Fig. 1.3). **State 0** – pointed; **State 1** – rounded.
6. HEMAL SPINE OF POSTERIOR-MOST PRECAUDAL HEMAPOPHYSIS (CI=1.00; RI=1.00): Hemal spine projecting from first, or posterior-most, precaudal hemapophysis, which projects from the posterior-most precaudal vertebra (Fig. 1.3). **State 0** – without wing; **State 1** – or with wing.
7. HEMAL ARCH (CI=1.00; RI=1.00): Hemal spine of anterior-most caudal vertebrae (Fig. #). **State 0** – thin; **State 1** – thick.

8. BLIND-SIDE OPERCULUM (CI=1.00; RI=1.00): State of the opercular region on the blind-side. **State 0** – covered with scales; **State 1** – with scaleless patch.
9. INTERORBITAL SPACE (CI=0.50; RI=0.67): Space between the eyes. **State 0** – less than ventral eye diameter; **State 1** – more than ventral eye diameter.
10. BODY DEPTH (CI=0.50; RI=0.75): Greatest distance from the base of the dorsal fin to the base of the anal fin. **State 0** – narrow, less than 62%; **State 1** – deep, more than 62%.
11. EYED-SIDE TRANSVERSE BANDS (CI=0.50; RI=0.0): Vertical bands on body and head. **State 0** – without pigmentation; **State 1** – with pigmentation.
12. CAUDAL FIN BASE DEPTH (CI=1.00; RI=1.00): Narrowest vertical distance at the base of the caudal fin. **State 0** – deep; **State 1** – narrow.
13. CIRRI ON EYED-SIDE BODY (CI=0.50; RI=0.75): Hair-like cilia on eyed-side body. **State 0** – little to no cirri; **State 1** – abundant.
14. LENGTH OF ETHMOID PROCESS (CI=0.33; RI=0.33): Bone projecting anteriorly from dorsal orbit. **State 0** – long, reaching the distal end of the first dorsal fin ray; **State 1** – only reaching the anteriormost point of the upper maxillary.
15. HYPURAL PLATES (CI=0.33; RI=0.50): Connection between hypural plates (2,3,4) and last centrum of the vertebral column (Fig. 2.5). **State 0** – fused; **State 1** – separate.
16. FIMBRIAE ON LOWER EYED-SIDE LIP (CI=1.00; RI=1.00): Degree of branching in fimbriae projecting from the lower lip (Fig. 1.3). **State 0** – lightly-branched, with a few extensions; **State 1** – highly-branched, with numerous extensions; **State 2** – unbranched, with no extensions.

17. CAUDAL VERTEBRAE (CI=1.00; RI=1.00): Number of vertebrae with haemal spines that extend fully to the anal fin. **State 0** – usually 19 or fewer; **State 1** – usually 20; **State 2** – usually 21.

18. BLIND-SIDE PECTORAL FIN GIRDLE (CI=0.50; RI=0.75): Presence of the coracoscapular complex on the blind-side pectoral fin girdle. **State 0** – absent; **State 1** – present.

19. EYED-SIDE PECTORAL FIN GIRDLE (CI=0.50; RI=0.75): Presence of the coracoscapular complex on the eyed-side pectoral fin girdle. **State 0** – absent; **State 1** – present.

20. EYED-SIDE PECTORAL FIN RAYS (CI=0.67; RI=0.50): Number of rays on the eyed-side pectoral fin. State 0 – 3 or more rays; State 1 – 1–2 rays, no rays (**state 0**).

21. VENTRAL EYE DIAMETER (CI=1.00; RI=1.00): Small (<15% HL) (**state 0**), or large (>15% HL) (**state 1**).

22. SUPRACRANIAL COMPLEX (CI=0.75; RI=0/80): Number of pterygiphores anterior to the neural spine of the third precaudal vertebra. **State 0** – 6; **State 1** – 7; **State 2** – 8; **State 3** – 9.

GENERAL CONCLUSION

In Chapter 1, the first taxonomic review of all 16 nominal species within the flatfish genus *Trinectes* (Pleuronectiformes: Achiridae) was done. It was determined that the following nine nominal species of *Trinectes* are valid: *T. fimbriatus*, *T. fluviatilis*, *T. fonsecensis*, *T. inscriptus*, *T. maculatus*, *T. microphthalmus*, *T. opercularis*, *T. paulistanus*, and *T. xanthurus*. The revision was based on a detailed examination of morphological characters on 647 type and non-type specimens. Additionally, the first identification key of all valid species of *Trinectes* was constructed.

Determining species validity was needed to conduct a proper phylogenetic analysis of *Trinectes* (Chapter 2). The monophyly of *Trinectes* was clearly established on the basis of two characters (Appendix E, char. 1 and char. 22). The analysis of all nine species was based on a total of 22 characters and resulted in a single most-parsimonious cladogram of 39 steps (CI=0.69; RI=0.79) (Fig. 2.7). Representatives of three genera of achirids (*Achirus*, *Cathathyridium*, *Hypoclinemus*) were used as outgroups in the analysis. The cladogram showed that *T. inscriptus* was the most plesiomorphic species within the genus, followed by the following two four-species clades (from most-plesiomorphic to most-apomorphic): (1) *T. maculatus* and the three-species group of *T. opercularis*-*T. microphthalmus*-*T. fimbriatus*, and (2) *T. paulistanus*, *T. fonsecensis*, and the two-species group of *T. fluviatilis*-*T. xanthurus*.

The cladogram showing the intrarelationships within *Trinectes* provided an opportunity to hypothesize the patterns of speciation within the group. The evidence suggested a saltwater origin for the genus, specifically in the Atlantic Ocean. The emergence of East-West barriers, such as the closure of the Isthmus of Panama, may have played an integral role in the speciation process within the two large clades of the group (Fig. 2.7, nodes C and D). Nodes within the cladogram that were not strongly supported by derived characters will require further research and testing to produce a more robust hypothesis of intrarelationship within the genus.