1985

A systematic revision of the South American freshwater stingrays (chondrichthyes: potamotrygonidae) (batoidei, myliobatiformes, phylogeny, biogeography)

Ricardo de Souza Rosa
College of William and Mary - Virginia Institute of Marine Science

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A SYSTEMATIC REVISION OF THE SOUTH AMERICAN FRESHWATER STINGRAYS (CHONDRICHTHYES: POTAMOTRYGONIDAE)

The College of William and Mary in Virginia Ph.D. 1985

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A SYSTEMATIC REVISION
OF THE SOUTH AMERICAN FRESHWATER STINGRAYS
(CHONDRICHTHYES: POTAMOTRYGONIDAE)

A Dissertation

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Doctor of Philosophy

by

Ricardo S. Rosa

1985

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Ricardo S Rosa

Ricardo de Souza Rosa

Approved, March 1985

John A. Musick

John A. Musick, Chairman

George C. Grant

George C. Grant

John D. Boon III

John D. Boon III

J D McEachran

John D. McEachran, Texas A & M University

Stanley H. Weitzman

Stanley H. Weitzman, National Museum of Natural History

To the memory of

Alexandre V. Boffi

my mentor and friend

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ABSTRACT

Three genera are recognized in the family Potamotrygonidae of neotropical freshwater stingrays: Potamotrygon, Paratrygon, and Plesiotrygon, the latter being described as a new genus. Potamotrygon is polytypic, and both Paratrygon and Plesiotrygon are monotypic, as far as known. The family name Potamotrygonidae has priority over Paratrygonidae Gill.

Nineteen previously described species of Potamotrygonidae are recognized: Paratrygon aiereba, Potamotrygon brachyura, P. castexi, P. constellata, P. dumerilii, P. falkneri, P. henlei, P. histrix, P. humerosa, P. leopoldi, P. magdalenae, P. motoro, P. ocellata, P. orbignyi, P. schroederi, P. schuemacheri, P. scobina, P. signata, and P. yepezi. One additional specific name is established as new (Plesiotrygon iwamae). Three of the eighteen recognized species of Potamotrygon are resurrected from synonymy (P. dumerilii, P. henlei, and P. orbignyi), one previously overlooked subspecific name (Trygon histrix ocellata) is erected to specific rank, and one previously overlooked specific name (Taeniura constellata) is placed in the genus Potamotrygon, and treated as a senior synonym of P. circularis. The remaining names previously assigned to the Potamotrygonidae include: eight junior synonyms (Disceus thayeri, Potamotrygon brumi, P. circularis, P. laticeps, P. menchacai, Trygon mulleri, T. reticulatus, and T. strogylopterus), five doubtful names (Elipesurus spinicauda, Potamotrygon africana, P. alba, P. humboldtii, and Trygon garrapa), two invalid names (Potamotrygon labratoris and P. pauckei), two doubtful names corresponding to one unidentified marine species of the family Dasyatididae (Raja ajereba and R. orbicularis), and one freshwater species of Dasyatis (D. garouaensis) originally described in the genus Potamotrygon.

Potamotrygon and Paratrygon are regarded as sister groups, and Plesiotrygon as the primitive potamotrygonid genus, based on a cladistic analysis of stingray characters. Plesiotrygon is restricted to the upper Amazon drainage, and Paratrygon is known from most of the Amazon drainage, occurring also in Rio Orinoco. Eleven species of Potamotrygon have Amazonian distribution (including Rio Tocantins), four of which occur also in other drainages. Four species of Potamotrygon are apparently endemic to Rio Paraguay and lower Rio Paraná drainages (P. brachyura, P. falkneri, P. histrix, and P. schuemacheri); P. yepezi is endemic to the Maracaibo basin in Venezuela; P. magdalenae is endemic to Rio Magdalena and Rio Atrato drainages in Colombia, and P. signata is apparently endemic to Rio Parnaíba drainage in Brazil.

A SYSTEMATIC REVISION
OF THE SOUTH AMERICAN FRESHWATER STINGRAYS
(CHONDRICHTHYES: POTAMOTRYGONIDAE)

INTRODUCTION

The family Potamotrygonidae Garman (1877) comprises freshwater stingrays inhabiting most river systems of tropical South America. Despite their wide distribution and medical importance, their taxonomy and most of their biological aspects are still poorly known.

The Potamotrygonidae are morphologically distinguished from the marine stingrays of the families Urolophidae and Dasyatididae by the presence of a well-developed anteromedian process on the pelvic girdle (Garman, 1877, 1913; Ribeiro, 1907, 1923; Bigelow and Schroeder, 1953; Thorson and Watson, 1975), by the reduction of the rectal gland (Gerst and Thorson, 1977; Thorson et al., 1978; Brooks, Thorson and Mayes, 1981; Thorson, Brooks and Mayes, 1983), and by the reduction of the electroreceptive ampullary organs and associated canals (Szabo et al., 1972; Obara and Bennet, 1972; Bullock, 1973; W. Raschi, pers. comm.). The Potamotrygonidae are physiologically distinguished from all marine elasmobranchs by the low urea content of blood serum and body fluids (Thorson et al., 1967; Junqueira et al., 1968; Brooks, Thorson and Mayes, 1981; Thorson, 1982; Thorson, Brooks and Mayes, 1983), and by their inability to raise urea levels and osmoregulate when exposed to salt water (Thorson, 1970; Griffith et al., 1973; Gerst and Thorson, 1977; Brooks, Thorson and Mayes, 1981; Thorson, Brooks and Mayes, 1983).

Thirty-four post-Linnaean specific names (including two marine forms) and one subspecific name have been assigned to South American freshwater stingrays. One fossil and one extant African species also have been included in the Potamotrygonidae, respectively by Arambourg (1947) and Stauch and Blanc (1962). The chronology of these names is presented in Table 1.

The first species descriptions (Roulin, 1829; Müller and Henle, 1841; Castelnau, 1855; Günther, 1880) were included in marine genera (Pastinaca, Trygon, and Taeniura) of the family Trygonidae (=Dasyatididae). Garman's (1877) subdivision of the Trygonidae into Potamotrygones and Thalassotrygones was the first attempt to separate the potamotrygonids from their marine relatives. Garman (1913) reviewed most of the existing original descriptions, described new species, and included them in a separate family which he named Potamotrygonidae. Most of the early and recent original descriptions were incomplete, and failed to include enough characters for specific diagnoses. The taxonomic status of several species has remained doubtful because their type specimens have been lost.

Since Garman's (1913) review, little taxonomic work has been done in the family, except for descriptions of new species, and two partial reviews of the literature (Fowler, 1948; Castex, 1964b). Several authors have reported or described new species of intestinal parasites of potamotrygonids (Brooks and Thorson, 1976; Rego and Dias, 1976; Mayes et al., 1978, 1981a, 1981b; Brooks et al., 1979; Brooks, Mayes and Thorson, 1981; Deardorff et al., 1981), but they frequently encountered difficulties in the host's identification. Other authors dealing with biolcgical aspects of potamotrygonids (e.g. Mangum et al., 1978) have found similar identification problems.

This paper is a systematic revision of the potamotrygonids, based on external morphology and skeletal anatomy. The study was undertaken to elucidate the taxonomic status of the nominal genera and species of this group, to diagnose and redescribe all valid taxa, and to provide information on their geographic distributions.

TABLE 1

CHRONOLOGY OF SPECIFIC AND SUBSPECIFIC NAMES ASSIGNED TO THE POTAMOTRYGONIDAE. ORIGINAL AUTORSHIP, GENERIC PLACEMENT, AND SPELLING ARE MAINTAINED IN THIS LIST.

Raja ajereba	Walbaum, 1792
Raja orbicularis	Schneider, in Bloch and Schneider, 1801
Trygon histrix	Müller & Henle, in Orbigny, 1834
Trygon aiereba	Müller & Henle, 1841
Taeniura motoro	Natterer, in Müller and Henle, 1841
Trygon garrapa	Schomburgk, 1843
Trygon strogylopterus	Schomburgk, 1843
Elipesurus spinicauda	Schomburgk, 1843
Trygon d'orbignyi	Castelnau, 1855
Trygon dumerilii	Castelnau, 1855
Trygon henlei	Castelnau, 1855
Trygon mulleri	Castelnau, 1855
Pastinaca humboldtii	Roulin, in Duméril, 1865
Taeniura magdalenae	Valenciènnes, in Duméril, 1865
Trygon reticulatus	Günther, 1880
Trygon brachyurus	Günther, 1880
Taeniura constellata	Vaillant, 1880
Trygon hystrix ocellata	Engelhardt, 1912
Potamotrygon circularis	Garman, 1913
Potamotrygon humerosus	Garman, 1913
Potamotrygon laticeps	Garman, 1913
Potamotrygon scobina	Garman, 1913
Potamotrygon signatus	Garman, 1913

TABLE 1

(continued)

Disceus thayeri	Garman, 1913
Potamotrygon brumi	Devicenzi & Teague, 1942
Potamotrygon africana	Arambourg, 1947
Potamotrygon schroederi	Fernández-Yépez, 1957
Potamotrygon garouaensis	Stauch & Blanc, 1962
Potamotrygon labratoris	Castex, 1963
Potamotrygon pauckei	Castex, 1963
Potamotrygon alba	Castex, 1963
Potamotrygon falkneri	Castex & Maciel, in Castex, 1963b
Potamotrygon schühmacheri	Castex, 1964
Potamotrygon menchacai	Achenbach, 1967
Potamotrygon castexi	Castello & Yagolkowsky, 1969
Potamotrygon yepezi	Castex & Castello, 1970
Potamotrygon leopoldi	Castex & Castello, 1970

METHODS AND MATERIALS

Measurements and counts were modified from Devicenzi and Teague (1942), Bigelow and Schroeder (1953), Fernández-Yépez (1957), Hubbs and Ishiyama (1968), Castex and Castello (1970a), Thorson and Watson (1975), Stehmann et al. (1978), Chirichigno and McEachran (1979), and Compagno and Roberts (1982). All measurements are redefined below, and outlined in Figures 1, 2 and 3. Measurements were taken point to point, without projections. Measurements over 150 mm were taken to the nearest millimeter with steel ruler; measurements under 150 mm were taken to the nearest tenth of millimeter, with dial calipers. Measurements are expressed as proportions (percent of disc width), readily accessible to other taxonomists for comparisons. Allometric characters, for which the proportional sample means have little significance, are discussed in the text. Broken tails were disregarded in computing proportional tail length and total length, except where otherwise indicated. Only the largest caudal sting of each specimen was used in computing mean sting length and proportions. Cranial measurements, except for the interorbital distance, were usually taken on radiographs.

Vertebral counts (1 to 6) were made from radiographs. Since the first haemal arch is hardly recognized without dissection or special radiographs, the vertebral column was arbitrarily divided in a precaudal region, anterior to the postero-median margin of pelvic girdle, and a caudal region, posterior to the same point of reference. The counts of pelvic and pectoral-fin radials (7 to 11) were made from radiographs, dissections, or cleared and stained specimens. Primary and secondary branching from basal elements on the anterior portion of the pectoral fin were counted as distinct radials. The anterior pelvic-fin radial, usually enlarged and branched, was counted as two radials; clasper cartilages were excluded from pelvic-fin counts. Tooth counts (Fig. 3) were made under stereomicroscope, and followed the method of Stehmann et al. (1978), with addition of the number of exposed teeth in median row of lower jaw (count 14). Tooth counts are given in the text as dental formulas, the numerator referring to the upper jaw teeth (count 12), and the denominator to the lower jaw teeth (count 13). All measurements and counts are listed below.

List of measurements

1) Disc width- greatest distance between lateral margins of disc; it is the independent variable for all proportional measurements on disc and tail.

2) Disc length- greatest distance from tip of snout to posterior margin of disc.

3) Total length- medial distance from tip of snout to tip of tail.

4) Internal disc length- distance from tip of snout to axil of pectoral fin.

5) Mouth to scapulocoracoid- distance from anterior margin of lower dental plate to anterior margin of coracoid bar, taken medially with mouth closed.

6) Mouth to cloaca- distance from anterior margin of lower dental plate to proximal margin of cloaca, taken medially with mouth closed.

7) Cloaca to caudal sting- distance from posterior margin of cloaca to base of first caudal sting, taken on straightened tail.

8) Tail length- distance from posterior margin of cloaca to tip of tail.

9) Tail width- greatest width of base of tail, excluding lateral spines.

10) Tail width at sting- width of tail taken at origin of first caudal sting.

11) Tail height- greatest height of base of tail, excluding dorsal spines.

12) Pelvic fin width- greatest width on posterior margin of pelvic fin, including inner margin of clasper in males.

13) Pelvic fin length- length of anterior margin of pelvic fin.

14) Clasper length- distance from posterior margin of cloaca to tip of clasper.

15) Sting length- greatest length of exposed portion of caudal

sting.

16) Precloacal length- distance from tip of snout to proximal margin of cloaca.

17) Preoral length- distance from tip of snout to mouth slit, taken medially with mouth closed.

18) Prenarial length- distance from tip of snout to anterior margin of nostril.

19) Branchial basket length- distance between inner margins of first and fifth gill slits.

20) Branchial basket width- distance between inner margins of first pair of gill slits.

21) Mouth width- greatest distance between lateral rims of mouth.

22) Nostril length- distance between anterior and posterior external margins of nostril.

23) Internarial width- distance between anterior margins of nostrils.

24) Eye length- greatest horizontal diameter of exposed portion of eyeball.

25) Spiracle length- greatest oblique diameter of spiracle, between anterior and posterior spiracular margins.

26) Interocular width- distance between midpoints on upper margins of eyeballs.

27) Interspiracular width- distance between posterior margins

of spiracles.

28) Preocular length- distance from tip of snout to anterior margin of eyeball.

29) Cranium length- distance from anterior margin of nasal capsule to occipital condyle.

30) Cranium width- distance between lateral margins of nasal capsules.

31) Preorbital width- distance between external margins of preorbital processes of cranium.

32) Postorbital width- distance between external margins of postorbital processes of cranium.

33) Interorbital width- shortest distance between internal edeges of orbits, taken on clean cranium, or externally by pressing calipers on orbital edges.

34) Fontanelle length- greatest distance between anterior and posterior margins of cranial fontanelle.

35) Fontanelle width- greatest width of cranial fontanelle.

36) Upper dental plate width- greatest width of upper jaw tooth plate.

37) Lower dental plate width- greatest width of lower jaw tooth plate.

Remarks.- All measurements were taken on preserved specimens, which showed a 1.6 to 4.1 percent shrinkage in disc width relative to field measurements of fresh specimens. Disc length and internal disc length were taken obliquely to midline, due to the difficulty of finding large calipers, ichthyometers, or triangles necessary to measure big specimens. The method of drawing the stingray contour on cardboard (Clark, 1926) would avoid the use of special instruments, but it is time-consuming. The deviation from the true paramedial disc length measurements is compensated by using disc width instead of disc length in proportional measurements. Disc width was used as the independent variable for proportional measurements of stingrays by Bigelow and Schroeder (1953, 1962), Fernández-Yépez (1957), Thorson and Watson (1975), and Compagno and Roberts (1982). It has the advantage of being a more stable measurement than total length and disc length, and does not show the bilateral variation of the latter. The use of tail length as the independent variable for other caudal measurements (Castex and Castello, 1970b; Castex and Yagolkowski, 1970) is not recommended, because the distal portion of the tail is usually broken in adult specimens.

List of counts

1) Precaudal vertebrae- from first radiographically distinct vertebral centrum embedded in first synarcual to posterior limit of pelvic girdle.

2) Caudal vertebrae- from posterior margin of pelvic girdle girdle to last radiographically distinct vertebra in the tail; each two diplospondylous centra counted as one

vertebra.

3) Caudal vertebrae to base of sting- from the posterior margin of pelvic girdle to base of first caudal sting; included in count 2.

4) Total vertebrae- the addition of counts 1 and 2.

5) Diplospondylous vertebrae- number of diplospondylous vertebrae in the tail; included in counts 2 and 4.

6) Synarcual vertebrae- number of radiographically distinct centra embedded in the first synarcual; included in counts 1 and 4.

7) Pelvic fin radials- expressed separately for males and females.

8) Propterygial radials- number of pectoral-fin radials articulated with propterygium.

9) Mesopterygial radials- number of pectoral-fin radials articulated with mesopterygium.

10) Metapterygium radials- number of pectoral-fin radials articulated with metapterygium.

11) Total pectoral-fin radials- the addition of counts 8, 9 and 10.

12) Upper tooth rows- number of longitudinal rows in upper dental plate.

13) Lower tooth rows- number of longitudinal rows in lower dental plate.

14) Lower median teeth- number of exposed teeth in median longitudinal row of lower dental plate.

15) Middorsal spines- total number of spines in middorsal series, from posterior disc to tail.

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Synonymies given in the taxonomic section are in short form (author, date, page number), the complete references being found in the literature cited. A period is used between the taxonomic names and references other than the original description. Specific synonymies include original descriptions, and the first usage of new combinations, emendations, misspellings, and misidentifications. Generic synonymies include not only strict synonyms, but also marine genera used in part for South American stingrays. Vernacular names other than the general designation of "raya" (Spanish) and "raia" or "arraia" (Portuguese) are included for each species. Taxonomic accounts on the genera are presented in the hypothesized phylogenetic sequence, those of the species of Potamotrygon in alphabetical order. Additional references following species descriptive accounts are given in alphabetical order. Comments on doubtful species are given chronologically.

Anatomical illustrations were prepared from cleared and/or dissected specimens, under magnification and camera lucida. Outlines of neurocrania were drawn from radiographs. The methodology for staining and clearing specimens followed Dingerkus and Uhler (1977). Illustrations and photographs were prepared by the author, except where other credits are given.

Nomenclature of skeletal elements followed El-Toubi and Hamdy (1969a) for neurocrania, El-Toubi and Hamdy (1969b) and Heemstra and Smith (1980) for branchial skeleton, and Compagno and Roberts (1982) for pelvic girdle. Nomenclature of clasper elements followed Compagno and Roberts (1982), with exception of the dorsal terminal 2 cartilage (=ventral terminal of Compagno and Roberts, 1982) and the ventral pseudosiphon (=pseudopera of Compagno and Roberts, 1982), which followed J. D. McEachran (pers. comm.). Other descriptive terms are listed below.

Sting- used for the barbed spine on the tail, to distinguish this structure from other spines or thorns occurring on tail or disc. Corresponding terms in the South American literature are "espina, aguijón, púa" (Spanish), and "espinho, esporão, agulhão, dardo, ferrão" (Portuguese).

Denticle- used for small skin investments (dermal denticles), usually with stellate crowns, and occurring on the dorsal surface of disc and tail. Corresponding terms in the South American literature are "dentículo" and "formación estelar" (Castex, 1967c).

Spine- vertically enlarged denticle derivative, with a projecting crown, found on middorsal surface of disc and tail, and on the sides of tail.

Tuberclc- horizontally enlarged denticle derivative, with a rounded crown, and usually a slightly projecting center, found dorsally near disc margins or over the pectoral girdle.

Abbreviations used in figures and text are given in Table 2. Specific methods for phylogenetic analysis are presented in the respective section.

Study material was obtained mainly from museum collections. Privately owned specimens were also examined, from Dr. T. B. Thorson's collection (cited as TBT field numbers), housed at University of Nebraska-Lincoln, and from Dr. M. Goulding's collection housed at INPA, Manaus. Institutional abbreviations are given in Table 3. Lists of specimens examined and localities are given in Appendix A.

FIG. 1

Graphic representation of dorsal measurements taken on specimens of Potamotrygonidae. Numbers on figure refer to those of the list of measurements.

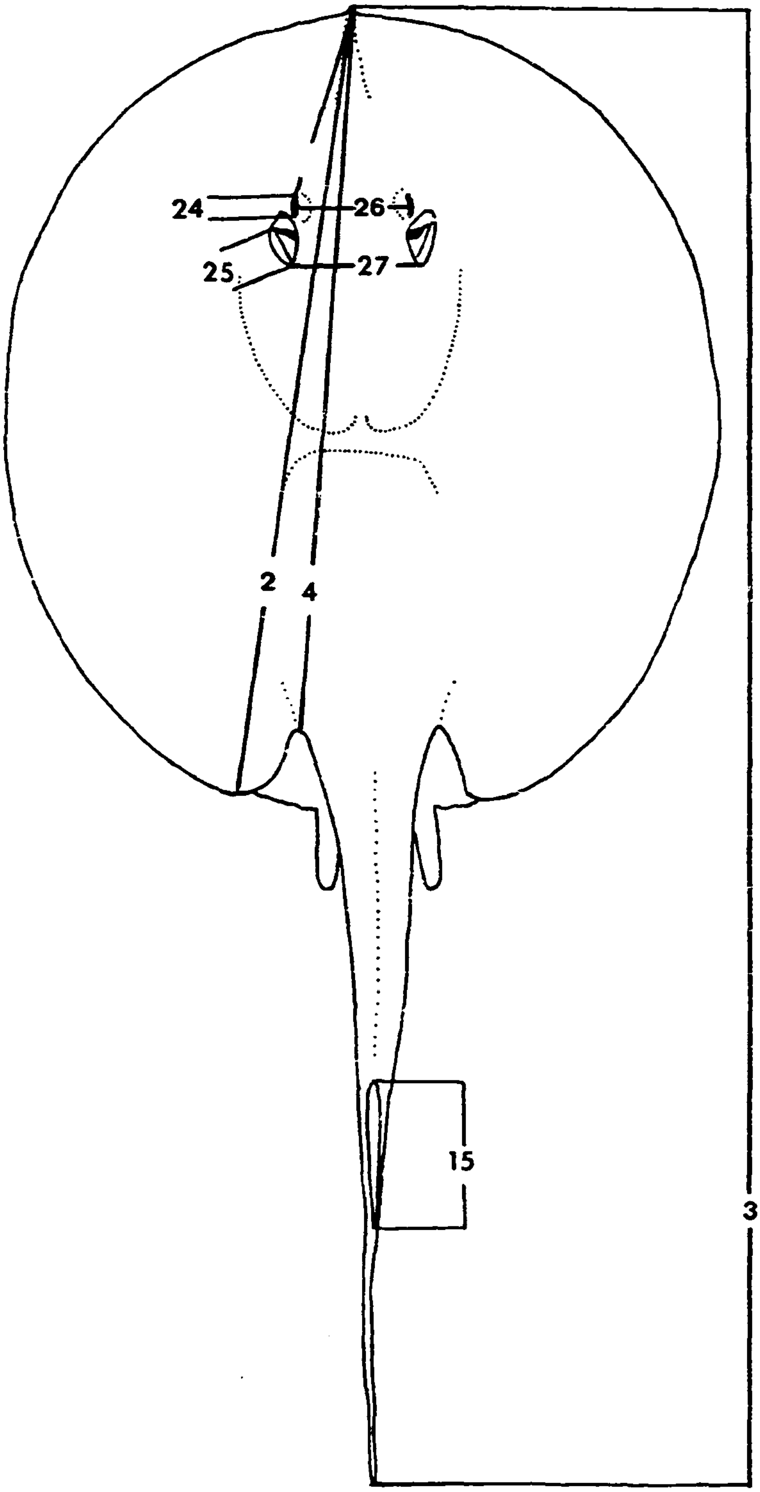
24
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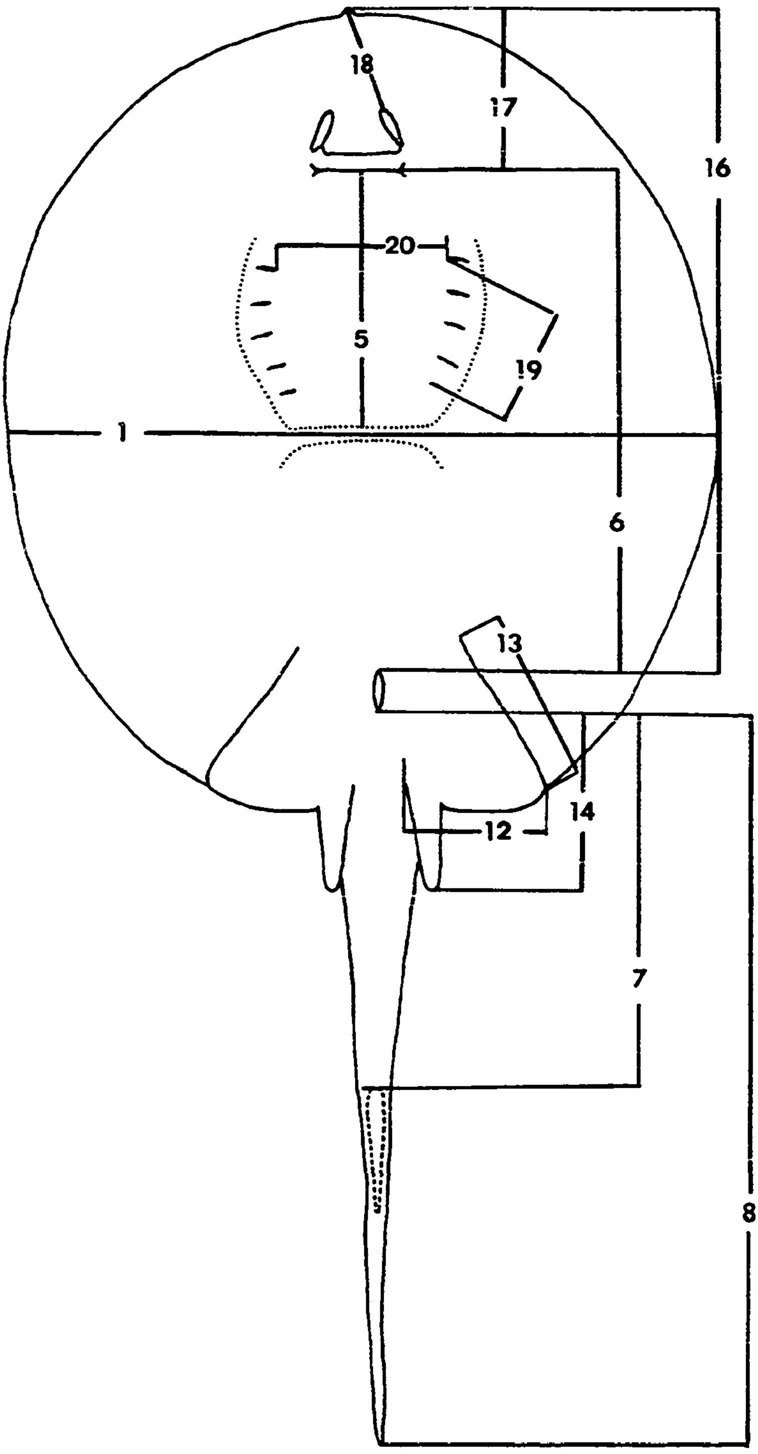
FIG. 2

Graphic representation of ventral measurements taken on specimens of Potamotrygonidae. Numbers on figure refer to those of the list of measurements.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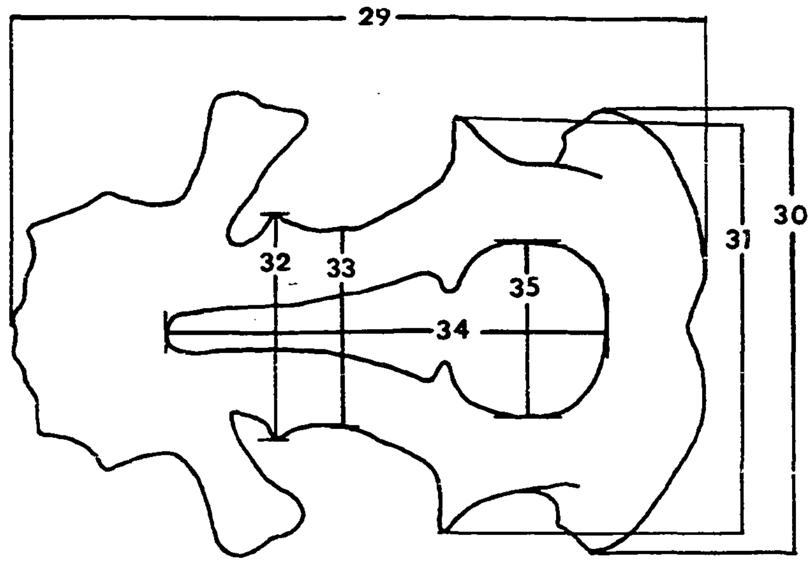
8

FIG. 3

A.- Graphic representation of cranial measurements taken on specimens of Potamotrygonidae. Numbers refer to those of the list of measurements. B.- Graphic representation of tooth counts made on specimens of Potamotrygonidae: a- upper jaw tooth rows; b- lower jaw tooth rows; c- exposed teeth in median row of lower jaw. Dashed line on lower dental plate indicates the limit of the buccal integument covering the inner series of teeth.



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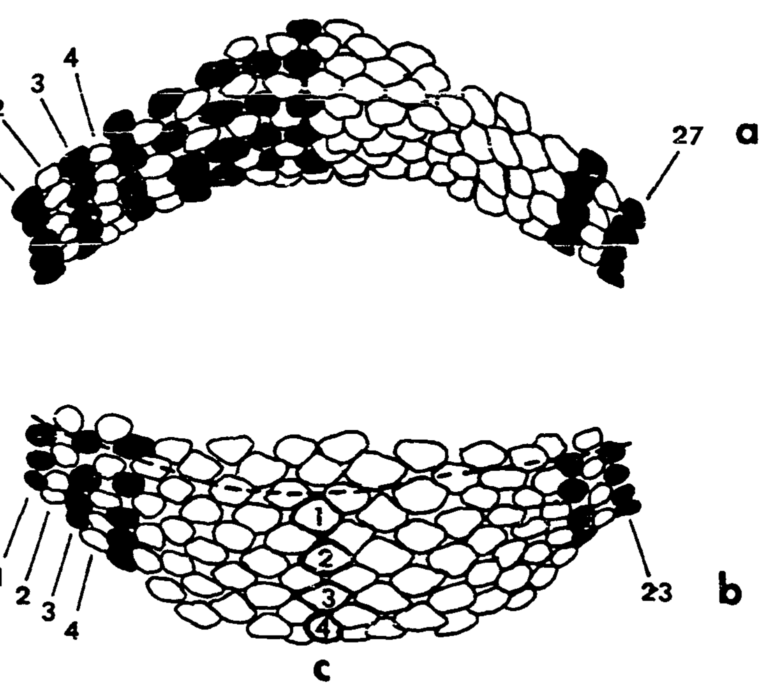

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TABLE 2

ABBREVIATIONS USED IN TEXT AND FIGURES

Af.-	Anterior cranial fontanelle
An.-	Angular cartilage
Ao.-	Antorbital cartilage
Ap.-	Apopyle
Ax.-	Axial cartilage
B1-B2.-	Basal segments of clasper axis
Bb.-	Basibranchial plate
Be.-	Beta cartilage
Bh.-	Basihyal
Cb1-Cb5.-	Ceratobranchials one to five
Cg.-	Clasper groove
Coll.-	Collected by
DL.-	Disc length
Dmg.-	Dorsal marginal cartilage
Dps.-	Dorsal pseudosiphon
Dt 1.-	Dorsal terminal 1 cartilage
Dt 2.-	Dorsal terminal 2 cartilage
DW.-	Disc width
Ef.-	Endolinfatic foramen
Fm.-	Foramen magnun
Hb.-	Hypobranchial cartilage
Hm.-	Hyomandibular
Hp.-	Hypopyle
ICZN.-	International Code of Zoological Nomenclature

TABLE 2

(continued)

Ip.-	Iliac process
Isp.-	Ischial process
Mc.-	Meckel's cartilage
Ms.-	Mesopterygium
Mt.-	Metapterygium
Na.-	Nasal aperture
Nc.-	Nasal capsule
Ne.-	Neurocranium
Oc.-	Occipital condyle
Of.-	Obturator foramen
Pb.-	Puboschiadic (or ischiopubic) bar
Pf.-	Posterior cranial fontanelle
Ph.-	Pseudohyoid
Po.-	Propterygium
Pp.-	Prepubic process
Pq.-	Palatoquadrate
Pr.-	Preorbital process
Pt.-	Postorbital process
Ptr.-	Pectoral-fin radial
Pvr.-	Pelvic-fin radial
Sa.-	Scapulocoracoid
Sc.-	Spiracular cartilage
Soc.-	Supraotic crest
V.-	Ventral covering piece
Vmg.-	Ventral marginal cartilage
Vps.-	Ventral pseudosiphon

TABLE 3

INSTITUTIONAL ABBREVIATIONS

AMNH.-	American Museum of Natural History, New York.
ANSP.-	Academy of Natural Sciences of Philadelphia, Philadelphia.
BMNH.-	British Museum (Natural History), London.
FMNH.-	Field Museum of Natural History, Chicago.
FSM.-	Florida State Museum, Gainesville.
ILAFIR.-	Instituto Latinoamericano de Fisiologia Reprodutiva, Universidad del Salvador, San Miguel (collection discontinued).
INPA.-	Instituto Nacional de Pesquisas da Amazônia, Manaus.
IRSNB.-	Institut Royal des Sciences Naturelles de Belgique,Bruxelles.
IUM.-	Indiana University Museum (specimens currently housed at CAS).
LACM.-	Natural History Museum of Los Angeles County, Los Angeles.
MACN.-	Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires.
MBUCV.-	Museo de Biologia, Universidad Central de Venezuela, Caracas.
MCNG.-	Museo de Ciencias Naturales de Guanare, Guanare.
MCZ.-	Museum of Comparative Zoology, Harvard University, Cambridge.
NNM. -	Museo de Historia Natural de Montevideo, Montevideo.
MNHN.-	Museum National d'Histoire Naturelle, Paris.
MNRJ.-	Museu Nacional, Rio de Janeiro.
MFA.-	Museo Provincial de Ciências Naturales Florentino Ameghino, Santa Fe.
MZUSP.-	Museu de Zoologia, Universidade de São Paulo, São Paulo.
RMNH.-	Rijksmuseum van Natuurlijke Historie, Leiden.
SOSC.-	Smithsonian Institution Oceanographic Sorting Center, Washington D.C.
SU.-	Stanford University (specimens currently housed at CAS).
UFPB.-	Universidade Federal da Paraíba, João Pessoa.

TABLE 3

(continued)

UMMZ.-	University of Michigan Museum of Zoology, Ann Arbor.
USNM.-	U.S. National Museum of Natural History, Smithsonian Institution, Washington D.C.
VIMS.-	Virginia Institute of Marine Science, Gloucester Point.
ZMB.-	Zoologisches Museum der Humboldt-Universität, Berlin.
ZMH.-	Zoologisches Institut und Zoologisches Museum, Hamburg.
ZUEC.-	Departamento de Zoologia, Universidade Estadual de Campinas, Campinas

STINGRAYS AND MAN

Stingrays and indians

Native indians of South America probably were the first humans affected by the neotropical freshwater stingrays. The first written accounts on these fishes by missionaries and early explorers revealed that several indian tribes had names for stingrays in their vocabularies, and that they called some rivers as "stingray-river" by their abundance of these fishes (Vellard, 1931; Castex, 1963b, 1963e; Carvalho, 1964; Ferreira, 1972). The indians used freshwater stingrays as food, and the isolated caudal stings as arrow heads, adornments, or as instruments for tatooing and other forms of self-mutilation, like puncturing their legs, arms, ears, and tongue (Roulin, 1829; Schomburgk, 1843; Müller and Troschel, 1848; Vellard, 1931; Fonseca, 1949; Castex, 1963a, 1963b, 1963e). Stingrays are still fished, and their stings used as arrow heads, by indians of the Amazon and central Brazil.

The indians probably developed the method of wading in the streams by dragging the feet on the bottom, to avoid stepping on stingrays and eliciting their stinging response. They also developed the first natural treatments for stingray-caused injuries, usually prepared from plants. Examples of these treatments are given by Schomburgk (1843), Castex (1963b) and Carvalho (1964).

The venomous properties

Most of the early accounts on freshwater stingrays (Gumilia, 1791; Dobrizhoffer, 1822; Roulin, 1829; Spix and Agassiz, 1829; Schomburgk, 1843; Orbigny, 1844, 1845; Müller and Troschel, 1848; Linden, 1875; Labrador, 1968) mentioned the danger and fear of stingray-caused wounds among natives and explorers, and some reported accidents, including fatal cases.

Despite several statements on the absence of a special venom-secreting organ in stingrays (Hargreaves, 1904; Daniel, 1928; Jorg, 1935), Porta (1905) described venom glands from marine stingrays. Devicenzi (1925) included the stingrays among the fishes having a venom secreting and inoculating apparatus. Phisalix (1922) and Vellard (1931) described the apparatus as consisting of two glands associated with the caudal sting, and experimentally confirmed the toxicity of their secretion. Vellard observed neurotoxic and proteolytic activities if the venom.

Fleury (1950) described in detail the venom-secreting tissues of two marine stingrays (Dasyatis and Myliobatis). Halstead (1970, 1971) reviewed the general anatomy of the venom apparatus of stingrays, and described the venom secreting organs as monocellular-type glads, bilaterally positioned along the ventral surface of the sting, in ventrolateral grooves. The glands are covered by an epidermal sheath, which extends dorsally on the sting and secretes mucus, probably aiding in the transmission of the venom (Castex and Loza, 1964). The loss of the integumentary sheath in traumatized stings is apparently compensated by an increase of secretory activity of the remaining glandular tissue in the ventrolateral grooves. The dorsal portion of the tail at the base of the sting, named the cuneiform area, also secretes venom (Halstead, 1970). The histology of the venom apparatus of several species of Potamotrygon was described by Castex and Loza (1964), who considered the glands similar to those of marine stingrays, but reported differences in the epithelial sheath which contained many more mucus-secreting cells. Castex (1967b) mentioned that there are still questions about the exact position of the secretory cells, and about the mechanisms of secretion. He suggested that the epidermis and its invaginations might contain most of the venom cells.

The sting is composed of vitrodentin, externally covered by a thin layer of enamel (Halstead, 1970). Serrations on the lateral margins of the sting usually cause further traumatism upon its removal from wounded tissues. The serrations are usually covered by epidermis in intact stings (Castex and Loza, 1964; Halstead, 1970). Despite statements on the contrary, the sting has little mobility, being inserted in fibrous connective tissue of the tail. The only muscular fibers in contact with the sting are associated with the glands, possibly aiding the release of the secretion (Castex and Loza, 1964).

The stinging mechanism was described by Castex and Loza (1964). The response is elicited by pressure on the dorsal surface of the disc, and accidents with humans are usually caused by stepping on burried stingrays. Upon the contact, the tail is thrust forward in curve (Fig. 4), with the sting pointing to the stimulated area. The power is enough to drive the sting into wood, thus rubber boots cannot provide effective protection (Castex and Loza, 1964). No active attacks by stingrays are known, and the stinging behavior probably evolved as a defense mechanism. Therefore, most of the accidents can be avoided by probing the way with a stick when wading in shallow water, or simply by dragging the feet on the bottom, thus avoiding stepping on stingrays (Halstead, 1971; Caras, 1975). Accidents may also be caused by removing the stingrays from the water, when they swirl the tail in all directions. It may be difficult to elicit the stinging behavior in captive animals, and sometimes it is necessary to remove them from the water in order to obtain a response (Castex and Loza, 1964).

Nature of the venom

The physical and chemical characteristics of the venom of potamotrygonids have not been studied (Castex, 1967b). Venom extracts from marine species contained thirty percent of proteins, with ten different amino acids. Their toxic component probably is a protein with a molecular weight exceeding 100,000 (Rodrigues, 1972). Castex (1967b) pointed that one of the major difficulties for these biochemical studies is to obtain enough specimens of stingrays. Once available, the data on the composition of the venom could be used in interpreting the interspecific variation of toxicity, and also in systematics.

Clinical aspects

Several of the early explorers of the South American rivers (Spix and Agassiz, 1829; Schomburgk, 1843; Orbigny, 1844) reported on the symptoms following stingray injuries. The lesions usually occur on the victim's leg, ankle, or foot (Vellard, 1931; Halstead, 1970). The pain is extreme, and may be accompanied by spasms or cramps (Vellard, 1931; Myers, 1947; Castex and Loza, 1964; Castex, 1967b; Halstead, 1970, 1971). Other symptoms that may follow are: fall in blood pressure, arrythmia, hyperthermia, sweating, paralysis, vomiting, diarrhea, and lack of appetite. The pain may persist up to ten days following the injury (Mello-Leitão, 1948; Lermond, 1966; Castex, 1967b; Halstead, 1970, 1971; Rodrigues, 1972). Death of the victim is occasional to rare, and it is usually due to the puncture of vital organs or secondary gangrene, and not by the direct action of the venom. Death immediately following the injury has been reported for a man suffering from heart disease. One case of abortion following the injury was personally reported to the author, for a woman in the third month of pregnancy. Healing is slow, taking around one month, or up to five months, usually leaving a scar (Castex 1967b; Castello and Pinedo, 1978).

Castex and Loza (1964) named the pathology of freshwater stingray injuries as the paratrygonic syndrome, as opposed to the trygonic syndrome defined by Fleury (1950) for marine stingrays. The paratrygonic syndrome differs from the other by its stronger local effects, like edema, chronic ulceration and necrosis, and fewer generalized symptoms. The effect of the venom seems to be less important, and the healing process much slower than in the trygonic syndrome (Castex, 1967b; Halstead, 1970).

No good statistics exist for the number of accidents and fatal cases caused by freshwater stingray injuries in South America. The most frequent victims are obviously fishermen, islanders, and their family members. One individual in Piauí State (Northern Brazil) showed fourteen scars on his legs, resulting from stingray injuries. Most of the victims in inhospitable regions cannot seek medical assistance, and must rely on the folk medicine and natural healing.

Treatment

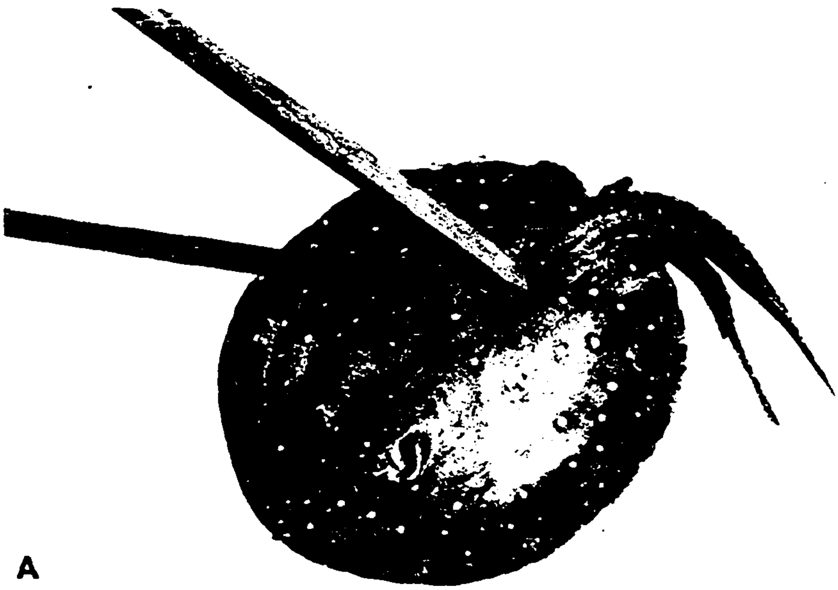
Several plants are used, both internally and externally, in popular medicine for the treatment of freshwater stingray injuries. Some examples include chewed tobacco, mashed "ba-

baçu" coconuts, and several kinds of roots, all with questionable results (Castex, 1963b; Carvalho, 1964; pers. observation in Brazil). Extracts of stingray livers are taken internally as treatment for the injuries, and as a regular vitamin source (pers. observation in Brazil).

Adequate medical treatment following the injury has been summarized by Castex (1967b), Halstead (1970), Dahl (1971), and Castello (1972). It should start with cleaning the wound in cold water. Subsequent immersion in hot water possibly diminishes the toxic action of the venom. Appropriate medication may include pain relievers, antihistaminic, antitetanic, and antibiotic agents, and corticoids. A treatment with vitamin B complex possibly accelerates the healing process. The cardiovascular function should be monitored after the injury. Castex does not recommend the suture of the wound.

FIG. 4

Stinging behavior in Potamotrygon motoro, experimentally elicited out of the water. A.- Stimulation with stick. B.- Stinging response by forward thrusting of the tail. Photographed by G. M. Achenbach, from MFA files.



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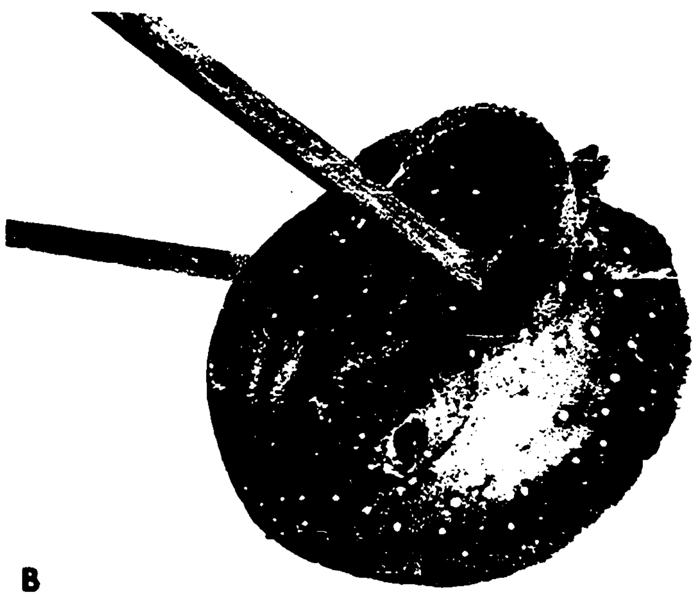


B

TAXONOMIC HISTORY

The earliest known descriptive account and illustration of a South American freshwater stingray appeared in the early seventeenth century, under the native name "yabeburapeni", in a manuscript by the Jesuit Cristóvão de Lisboa (História dos animais e árvores do Maranhão, MSS), preserved in Arquivo Histórico Colonial, Lisbon (Carvalho, 1964). Other manuscript accounts on several species of stingrays from Río Paraguay were written by the Jesuit Sanchez Labrador, in the mid eighteenth century (El Paraguay católico, MSS, Labrador, 1767). Gumilia (1791) mentioned the presence of stingrays in Río Orinoco. Dobrizhoffer (1822) published one illustration of a stingray from the lower Río Paraná drainage. The manuscripts of Alexandre Rodrigues Ferreira, from the late eighteenth century, recorded a freshwater stingray from Pará, Brazil, under the native name "arraia-iaueira" (Ferreira, 1972). Other early vernacular accounts on freshwater stingrays, especially from Río Paraná and Río Paraguay drainages, were treated in detail by Castex (1963a, 1963b, 1963e).

The first published species description of a freshwater stingray, Pastenague de Humboldt (Roulin, 1829), still did not follow strictly binominal nomenclature. The binominal taxonomic history of potamotrygonids started in 1834, with the publication of the plate of *Trygon histrix* by Orbigny. Müller and Henle (1841) provided descriptions for *T. histrix* and for two new species from Brazil, *Trygon motoro* and *Trygon aiereba*, which were not illustrated. Schomburgk (1843) described and illustrated the new species *Trygon garrapa*, *Trygon strogylopterus*, and the new genus and species *Elipesurus spinicauda*, all from Rio Branco, Brazil. Castelnau (1855) described and illustrated four new species from Brazil: *Trygon dumerilii* from Rio Araguaia, *Trygon mulleri* from Rio Crixas and Rio Araguaia, *Trygon henlei* from Rio Tocantins, and *Trygon d'orbignyi*, also from Rio Tocantins.

Duméril (1865) established the new subgenus *Paratrygon* for *T. aiereba* Müller & Henle, and credited to Valenciennes the description of a new species, *Taeniura magdalenae*, from Río Magdalena in Colombia. Garman (1877) established two new genera, *Potamotrygon* and *Disceus*, to include all South American freshwater stingrays. Garman also presented a key to the species of *Potamotrygon*. Günther (1880) described two new species, *Trygon brachyurus* from Buenos Aires, and *Trygon reticulatus* from Surinam. Vaillant (1880) described the new species *Taeniura constellata* from Rio Amazonas, Brazil. Larrazet (1886), based only on fossil tubercles, described from Río Paraná three species of the fossil genus *Dynatobatis*, which later was improperly placed in the synonymy of *Potamotrygon* by Garman (1913).

Ribeiro (1908) published a key to the Brazilian species of freshwater stingrays, with redescriptions and two illustrations. Ribeiro placed all these species in the genus Elipesurus, and in the family Dasyatidae. Garman (1913) reviewed the previous descriptions of potamotrygonids, but overlooked T. constellata Vaillant and T. histrix ocellata, a subspecies described by Engelhardt (1912) from the mouth of Rio Amazonas. Garman (1913) also described five new species of Potamotrygon (P. circularis, P. humerosus, P. laticeps, P. scobina, and P. signata) from Brazil, one of them being a junior synonym of T. constellata. Although Garman's descriptions and redescriptions lacked precise measurements and diagnoses, his work with potamotrygonids was the most complete at that time, including anatomical illustrations and keys to the genera and species.

Devicenzi and Teague (1942) described the new species Potamotrygon brumi from Río Uruguay. Arambourg (1947) described a new fossil species, Potamotrygon africana, from lacustrine paleo-environments in Nanoropus, Ethiopia, based on a series of caudal stings. Fowler (1948) reviewed the Brazilian species of potamotrygonids, based on a compilation of the literature. He altered the nomenclature of the group by using the genus Paratrygon as a senior synonym of Potamotrygon, and by adopting the family name Paratrygonidae, indicating it as a new name, although the authorship stemmed from Gill (1893). Fowler (1948) misidentified the marine Raja ajereba Walbaum (see remarks under Paratrygon and comments on doubtful species later in the text) as a freshwater species, and placed it as the type species of Paratrygon.

After Fowler's (1948) review, the taxonomic work on potamotrygonids was undertaken by South American authors, but was restricted to descriptions of new species of *Potamotrygon* (Fernández-Yépez, 1957; Castex, 1963d, 1963e, 1964a; Castex, Maciel and Achenbach, 1963; Achenbach, 1967; Castello and Yagolkowski, 1969; Castex and Castello, 1970a, 1970b), and another partial compilation of the literature (Castex, 1964b). Stauch and Blanc (1962) described a new species, *Potamotrygon garouaensis*, from the Bénoué River in Nigeria. This species was later assigned to the genus *Dasyatis* by Castello (1973) and Thorson and Watson (1975).

Several species of potamotrygonids were based on a single, sometimes imperfect specimen, and some have been known only from their poor original description or illustration. The taxonomy of potamotrygonids has reached a complicated and confused state, so that a major revision is necessary (Devicenzi and Teague, 1942; Castex, 1964b, 1966, 1967b; Thorson and Watson, 1975; Fink and Fink, 1979; Brooks, Mayes and Thorson, 1981; Brooks, Thorson and Mayes, 1981; Thorson, Brooks and Mayes, 1983). Nomenclatural problems were found at the specific, generic and familial levels, demanding a review of all nominal taxa prior to the taxonomic clarification attempted in this paper.

Potamotrygonidae Garman, 1877

Trygonidae [in part]. Günther, 1870: 471; Garman, 1877: 208; Steindachner, 1878: 72.

Potamotrygones Garman, 1877: 208.

Paratrygoninae Gill, 1893: 130.

Dasyatidae [in part]. Jordan, 1887: 557; Ribeiro, 1907: 39; Bertoni, 1914: 6; Bertin, 1939: 21.

Dasybatidae [in part]. Berg, 1895: 15; Berg, 1897: 263.

Potamotrygonidae Garman, 1913: 415.

Elipesuridae. Jordan, 1923: 104.

Paratrygonidae. Fowler, 1948: 4; Fowler, 1970: 42.

Type genus: Potamotrygon Garman, 1877.

Remarks.- Garman (1877) established the first family-group name (the suprageneric collective Potamotrygones) exclusive for the South American freshwater stingrays. Potamotrygones forms the basonim, and gives its original date and authorship to the family name Potamotrygonidae [see article 11(e) of the ICZN]. Gill (1893) cited the original date and authorship of the family-group name Paratrygoninae as Gill 1892, without giving the appropriate bibliographic reference. No citation of Paratrygoninae was found in his earlier papers.

Most of the recent classifications of elasmobranch fishes (Jordan, 1923; White, 1936; Berg, 1940; Compagno, 1973; Lindberg, 1974; Nelson, 1976) recognized independent familial status for the South American freshwater stingrays, by using the family name Potamotrygonidae. The same treatment has been given in most of the recent taxonomic literature, including nomenclatural papers, catalogues, reviews, and textbooks (Garman, 1913; Eigenmann, 1921; Miles, 1947; Fowler, 1948, 1970 (as Paratrygonidae); Buen, 1950; Bigelow and Schroeder, 1953; Nikol'skii, 1954; Ribeiro, 1959; Ringuelet and Arambu-ru, 1961 (as Paratrygonidae); Castex, 1964b, 1968; Ringuelet et al., 1967; Wheeler, 1975; Starck, 1978). The Potamotrygonidae also have received familial status in the recent biological and medical literature.

Still after Garman's (1877) proposal of the family-group name, some authors (Gill, 1893; Eigenmann, 1912, 1922; Norman, 1966; Bailey, 1969) treated the potamotrygonids as a subfamily of Dasyatididae. Other authors (Jordan, 1887; Berg, 1895, 1897; Ribeiro, 1907, 1923; Starks, 1913; Bertoni, 1914; Bertin, 1939; Fowler, 1941, 1945a, 1945b; Schultz, 1949) included the potamotrygonid genera in the Dasyatididae, without a subfamilial recognition. As discussed later in the chapter on phylogenetic relationships, the inclusion of the potamotrygonids in the Dasyatididae should be avoided in phylogenetic classifications, as it results in a paraphyletic taxon.

THE GENERA OF POTAMOTRYGONIDAE

Four post-Linnaean nominal genera (Elipesurus, Paratrygon, Potamotrygon and Disceus) have been used exclusively for South American freshwater stingrays, and four other generic names (Pastinaca, Trygon, Taeniura and Himantura) both for freshwater and marine stingrays. Most of the recent authors consider that only two genera of potamotrygonids should be valid, corresponding with the two distinct morphotypes found in the group (excluding the new genus described in this paper). Garman's genera Potamotrygon and Disceus have been widely accepted, while Elipesurus and Paratrygon have been considered valid or doubtful, according to different authors.

Duméril (1865) emended Elipesurus to Ellipesurus, and was followed by Günther (1870), Eigenmann and Eigenmann (1891), Ribeiro (1907, 1918, 1920, 1923), and Bridge (1910). Steindachner (1878) and Ihering (1897) suggested that Taeniura should have priority over Potamotrygon, but failed to recognize that the former genus had been established for a marine species (type species Taeniura lymma). Garman (1880) indicated that Taeniura is anatomically distinct from Potamotrygon. Jordan (1887), Eigenmann and Eigenmann (1891), and Eigenmann (1910, 1912) considered Paratrygon as a senior synonym of Disceus. Eigenmann (1912) mistakenly named Raja orbicularis (=Dasyatis orbicularis nomen dubium; see comments on doubtful species), a marine species based on Aiereba Marcgrave (1648), as the type species of Paratrygon. Ribeiro (1907, 1923) used Elipesurus (emended to Ellipesurus) as a senior synonym of Potamotrygon, and included in the former all the Brazilian species of freshwater stingrays.

Garman (1913) used the genera Disceus and Potamotrygon in his revision, and like several previous authors, he cited Elipesurus as doubtful. Bertin (1939) and Fowler (1948, 1970) mistakenly synonymized Paratrygon and Potamotrygon. Fowler (1948, 1970) and Castex (1968) again mistakenly selected a marine species (Raja ajereba) based on Aiereba Marcgrave, as the type species of Paratrygon. Their designation was not only a misidentification like the previous one by Eigenmann (1912), but also an erroneous taxonomic action, because Raja ajereba was not originally cited in Paratrygon when the generic name was established. Besides the major alteration in the generic nomenclature by using Paratrygon as a senior synonym of Potamotrygon, Fowler (1948, 1970) also maintained both Elipesurus and Disceus as valid genera in his classification.

Castex (1968, 1969b) considered Potamotrygon and Disceus as the valid genera, and recommended the rejection of Elipesurus as a doubtful name. His proposals were criticized by Bailey (1969), who considered that Elipesurus should be used as the senior synonym of Disceus. The genus Elipesurus and its type species E. spinicauda were based on a single specimen, with a very short tail, lacking the caudal sting (or stings) normally found in other species of the family. Several authors (Garman, 1877, 1913; Vaillant, 1880; Eigenmann and Eigenmann, 1891; Castex, 1964b, 1968, 1969b; Castex and Castello, 1969; Bailey, 1969) regarded these morphological conditions as the probable result of a mutilation of the tail. The type specimen of E. spinicauda apparently was not preserved, and no similar specimens have been collected since the original description. The poor original description and illustration of E. spinicauda do not contain diagnostic characters other than the tail condition, therefore the generic and specific identities have remained uncertain (Castex, 1964b, 1968).

One additional potamotrygonid genus was discovered by H. P. Castello while examining specimens at Museu de Zoologia, Universidade de São Paulo. The description of the new genus (Plesiotrygon) has been independently submitted for publication by the present author, with coauthors H. P. Castello and T. B. Thorson. The chronology and taxonomic status of the generic names of Potamotrygonidae is presented in Table 4.

TABLE 4

NOMINAL GENERA OF POTAMOTRYGONIDAE

GENUS	AUTHOR	STATUS
Elipesurus	Schomburgk, 1843	doubtful
Paratrygon	Duméril, 1865	valid
Potamotrygon	Garman, 1877	valid
Disceus	Garman, 1877	junior synonym
Plesiotrygon	Rosa, Castello and Thorson	new genus, submitted for publication

KEY TO THE GENERA OF POTAMOTRYGONIDAE

1A. Distance from mouth to anterior margin of disc relatively long, 2.6 to 3.3 times in disc width; a knob-shaped process on external margin of spiracles...*Paratrygon* Duméril

1B. Distance from mouth to anterior margin of disc relatively short, 3.6 to 5.6 times in disc width; external spiracle process absent.. 2

2A. Tail relatively short, less than two times disc width; tail with dorsal and ventral finfolds................... ....*Potamotrygon* Garman

2B. Tail relatively long and filiform, more than two times disc width in intact specimens; only a ventral finfold on tail..............................*Plesiotrygon* new genus

Plesiotrygon new genus

Type species: Plesiotrygon iwamae Rosa, Castello and Thorson (submitted for publication) by monotypy.

Etymology: Plesiotrygon (from Greek = close to Trygon) in the sense of phylogenetic systematics (Hennig, 1966), to the hypothesized most primitive genus of neotropical freshwater stingrays.

Diagnosis.- A presently monotypic genus of Potamotrygonidae, diagnosed by the following combination of characters: tail very long and distally filiform, more than two times DW in length, with one or more rows of spines posterior to caudal sting; no dorsal finfold on tail; eyes very small, non-pedunculate; pelvic fins broadly exposed behind posterior margin of disc; ceratobranchials one and two not fused to each other; 78 to 82 pectoral fin radials.

Plesiotrygon iwamae n. sp.

(Figs. 5 - 17)

Holotype: MZUSP 10153, male, coll. H. Britski for Expedição Permanente da Amazônia.

Type locality: Rio Solimões above Tefé, Amazonas, Brazil.

Remarks.- Specimens of Plesiotrygon iwamae have been misidentified in label and catalogue of ZMH (as Paratrygon aiereba), and in the literature by Ribeiro (1959, as Elipesurus strogylopterus) and by Taniuchi (1982, as Potamotrygon scobina).

Diagnosis.- See generic diagnosis.

Description.- Measurements and counts are given in Table 5. Disc subelliptic, disc length 1.01-1.08 times DW; anterior margin of disc convex with median prominence. Tail very long (broken on holotype), distally filiform; tail length 2.01-5.45 times DW. Ventral membranous finfold present on tail, its height 2.2-3.0 in tail height; dorsal finfold absent. One to three relatively long caudal stings (Fig. 9), sting length 3.6-6.5 in DW, 1.5-2.5 times tail width. Distance from posterior margin of cloaca to insertion of caudal sting relatively long, 1.6-1.9 in DW. Eyes minute, non-pedunculate, their horizontal diameter 4.4-5.7 in interorbital distance, 6.3-7.3 in interocular distance; preocular distance 3.2-3.5 in DW. Spiracles relatively large, their oblique diameter 2.3-3.9 in interspiracular distance, 2.3-3.6 times eye diameter. Mouth relatively small, its width 7.8-8.5 percent of DW. Three to five minute papillae on floor of buccal cavity, or papillae absent in young specimens. No longitudinal tegumentary ridges in buccal cavity. Teeth white, closely crowded in quincunx, in 26/27 to 62/66 rows, and five to ten exposed teeth in median row of lower jaw. Teeth sexually dimorphic (Figs. 10, 11, 12), adult males with pointed teeth in both jaws, females and juvenile males with blunt teeth. No monognathic heterodonty in both sexes, except for tooth size gradient, increasing from mouth corners towards symphysis, and lack of pointed cusps in extreme lateral teeth of adult males. Individual teeth (Fig. 12) with laterally expanded bilobed roots, high triangular crowns in adult males, and blunt cuspless crowns in females. Fourteen spiral valve folds in single specimen examined for this character. Nostrils parallel to midline, relatively short, 1.6-2.3 in internarial distance. Branchial basket relatively wide and long, distance between first gill slits 4.0-4.8 in DW, distance between first and fifth gill slits 7.7-8.5 in DW.

Anterior subpleural portion of lateral line system nonreticulate; suborbital canal with anterior loop pointing forward, and posterior loop reaching transverse level of first pair of gill slits. Pleural canal ventrally with fifteen terminal branches towards anterior margin of disc.

Neurocranium (Figs. 13, 14) relatively long, cranium length 3.8-4.4 in DW. Nasal capsules transversely elliptic, with median indentation between them. Preorbital processes short, preorbital width less than cranium width at nasal capsules. Postorbital processes short, postorbital width 2.6-3.2 in cranium length. Cranial fontanelle long and broad, with transverse constriction at orbital level.

Anterior portion of vertebral column with coalescent vertebrae forming two synarcual plates. Distal portion of vertebral column with eleven to fourteen diplospondylous vertebrae in juvenile specimens, none in adults.

Branchial skeleton (Fig. 15) with segmented basihyal, hypobranchial entire and long, pseudohyoid fused ventrally to first ceratobranchial, other ceratobranchials not fused to each other. Basibranchial plate with blunt anterior margin, posterior margin pointed and long, reaching pectoral girdle. Scapulocoracoid relatively narrow, its maximum width less than distance from mouth to coracoid bar. Lateral face of scapulocoracoid with large anteroventral and postventral fenestrae. Coracoid bar relatively thin, its maximum diameter in median cross section about two times in maximum distance between mesocondyle and metacondyle.

Pelvic girdle (Fig. 15) thick, with long prepubic process, three iliac obturator foramina, and one iliac process on each side. Internal margin of pelvic girdle nearly semicircular, anterior margins concave, with abrupt angle towards lateral margins, lacking prepelvic processes.

Pectoral fin plesodic, with 78 to 82 segmented radials (mode 80). Propterygium arched, anteriorly reaching level of nasal capsules. Anterior segment of propterygium with four to six branching radials. Antorbital cartilage elongate, triangular in dorsal view. Mesopterygium cuneiform in dorsal view, with fourteen to seventeen radials. Metapterygium distally segmented, with 23 to 30 radials. Pelvic fin with 27 or 28 radial (left and right sides) in adult female, and 22 to 24 radials in males.

Claspers moderately elongate (Figs. 16, 17), their length 19.3-21.6 percent of DW in mature males. Clasper arched in lateral view, with concave ventral profile. Clasper groove anteriorly oblique and distally parallel to midline. Dorsal pseudosiphon oblique to midline, its length nearly half of clasper width at level of terminal cartilages. Clasper axial cartilage arched in dorsal view and cylindrical, articulated with pelvic basipterygium by two basal elements. Beta cartilage proximally triangular in cross section and articulated with first basal element, distally depressed, not reaching dorsal marginal cartilage. Dorsal marginal cartilage trapezoidal in dorsal view, slightly arched in cross section forming roof of clasper groove. Ventral marginal cartilage laterally attached to axial cartilage forming floor of clasper groove. Dorsal terminal 1 cartilage arched in dorsal view, proximally attached to dorsal marginal cartilage. Dorsal terminal 2 cartilage fusiform in dorsal view, proximally attached to ventral marginal cartilage, arched in cross section forming roof of ventral pseudosiphon. Ventral covering piece fusiform in lateral view, distally attached to axial and dorsal terminals 1 and 2 cartilages.

Dorsal surface of disc yellowish-brown to grayish-brown, with few scattered small black spots, and many small white spots grouped in rosettes, which decrease in size towards disc margins. Dorsal surface of tail and pelvic fins with same pattern as disc, except distal portion of tail white with scattered dark spots. Ventral surface white, posterior margins of disc and pelvic fins brown. Tail ventrally white, with irregular dark figures and brown finfold. Juveniles with lighter dorsal surface, with relatively larger white spots, not forming rosettes. Sides of tail in juveniles with distinct alternate white and dark bars from insertion of sting to filiform portion.

Geographic distribution.- Upper to mid Amazon drainage (see Fig. 99), from Río Napo in Ecuador to Rio Solimões, in the vicinity of Manaus, Brazil.

Etymology.- The specific name is a posthumous honor to Satoko Iwamae, a Brazilian zoologist who passed in early age.

Remarks.- The description of Plesiotrygon iwamae, along with miscellaneous biological data has been independently submitted for publication in Copeia, with coauthors H. P. Castello and T. B. Thorson.

TABLE 5

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Plesiotrygon iwamae*

	HOLOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	579	6	-	-	208 - 579
DISC LENGTH (mm)	601	6	-	-	215 - 601
DISC LENGTH (%)	103.7	6	104.4	2.5	101.4-108.6
INTERNAL DL (%)	93.7	6	94.6	2.6	92.3-99.5
MOUTH TO SCAPULOCORACOID(%)	30.9	5	30.6	1.5	27.3-31.2
MOUTH TO CLOACA (%)	65.2	6	64.2	2.5	60.6-67.3
CLOACA TO STING (%)	53.3	5	57.6	4.1	53.3-62.9
TAIL LENGTH (%)	150.0*	3	368.1	-	201.4-545.1
TAIL WIDTH (%)	8.8	6	10.5	1.0	8.8-11.5
TAIL WIDTH AT STING BASE(%)	3.7	5	4.4	0.5	3.7- 5.2
TAIL HEIGHT (%)	5.3	6	5.5	0.9	3.9- 6.4
PELVIC FIN WIDTH (%)	26.7	6	27.6	2.6	24.6-30.9
PELVIC FIN LENGTH (%)	25.0	6	25.1	4.9	20.9-34.7
CLASPER LENGTH (%)	19.3	5	15.3	4.7	11.3-21.6
STING LENGTH (%)	17.8	5	19.7	5.9	15.3-27.8
PRECLOACAL LENGTH (%)	88.7	6	90.2	2.9	85.8-93.7
PREORAL LENGTH (%)	24.0	6	25.4	1.2	24.0-27.6
PRENARIAL LENGTH (%)	19.5	6	20.0	1.2	18.0-21.2
BRANCHIAL BASKET LENGTH (%)	12.1	6	12.1	0.4	11.7-12.9
BRANCHIAL BASKET WIDTH (%)	23.7	6	22.7	1.4	20.6-24.6

*Tail broken on holotype.

TABLE 5

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
MOUTH WIDTH (%)	8.5	6	8.1	0.3	7.8- 8.5
NOSTRIL LENGTH (%)	3.9	6	4.3	0.6	3.5- 5.3
INTERNARIAL WIDTH (%)	9.1	6	8.4	1.0	6.7- 9.4
EYE LENGTH (%)	1.5	5	1.5	0.2	1.3- 1.9
SPIRACLE LENGTH (%)	5.1	6	5.0	0.7	4.4- 6.5
INTEROCULAR WIDTH (%)	10.9	3	11.3	-	10.9-12.0
INTERSPIRACULAR WIDTH (%)	13.2	6	15.0	1.3	13.2-17.2
PREOCULAR LENGTH (%)	29.1	5	29.8	1.0	28.9-31.2
CRANIUM LENGTH (%)	25.7	6	24.9	1.3	22.8-26.2
GRANIUM WIDTH (%)	16.0	6	15.7	0.8	14.7-16.6
PREORBITAL WIDTH (%)	12.8	6	13.0	0.7	12.0-13.9
POSTORBITAL WIDTH (%)	7.9	5	8.8	0.8	7.9-10.1
INTERORBITAL WIDTH (%)	7.6	5	8.3	0.5	7.6- 9.1
FONTANELLE LENGTH (%)	14.9	4	14.4	1.4	12.3-15.3
FONTANELLE WIDTH (%)	7.1	6	7.3	1.2	6.6- 8.0
UPPER DENTAL PLATE WIDTH(%)	7.7	6	7.1	0.6	6.1- 7.9
LOWER DENTAL PLATE WIDTH (%)	6.9	6	6.9	0.5	6.0- 7.7
PRECAUDAL VERTEBRAE	23	6	25.6		23- 28
CAUDAL VERTEBRAE	91	5	92.8		89- 95
CAUDAL VERTEBRAE TO BASE OF STING	75	5	73.2		72- 75
TOTAL VERTEBRAE	114	4	118.7		114- 121
DIPLOSPONDYLOUS VERTEBRAE	0	4	8.3		0- 14
SYNARCUAL VERTEBRAE	0	6	2.0		0- 3

TABLE 5

(continued)

		HOLOTYPE	N	MEAN	S.D.	RANGE
PELVIC RADIALS	♂	24	5	23.1		22- 24
	♀	-	1	-		27- 28*
PROPTERYGIAL RADIALS		36	6	37.1		36- 39
MESOPTERYGIAL RADIALS		14	6	14.6		14- 17
METAPTERYGIAL RADIALS		28	6	28.1		28- 29
TOTAL PECTORAL RADIALS		78	6	80.1		78- 82
UPPER TOOTH ROWS		62	6	41.5		26- 62
LOWER TOOTH ROWS		66	6	42.8		27- 66

*Left and right side counts of one female specimen.

FIG. 5

Plesiotrygon iwamae, dorsal view, male, 601 mm DL, MZUSP 10153 (holotype).

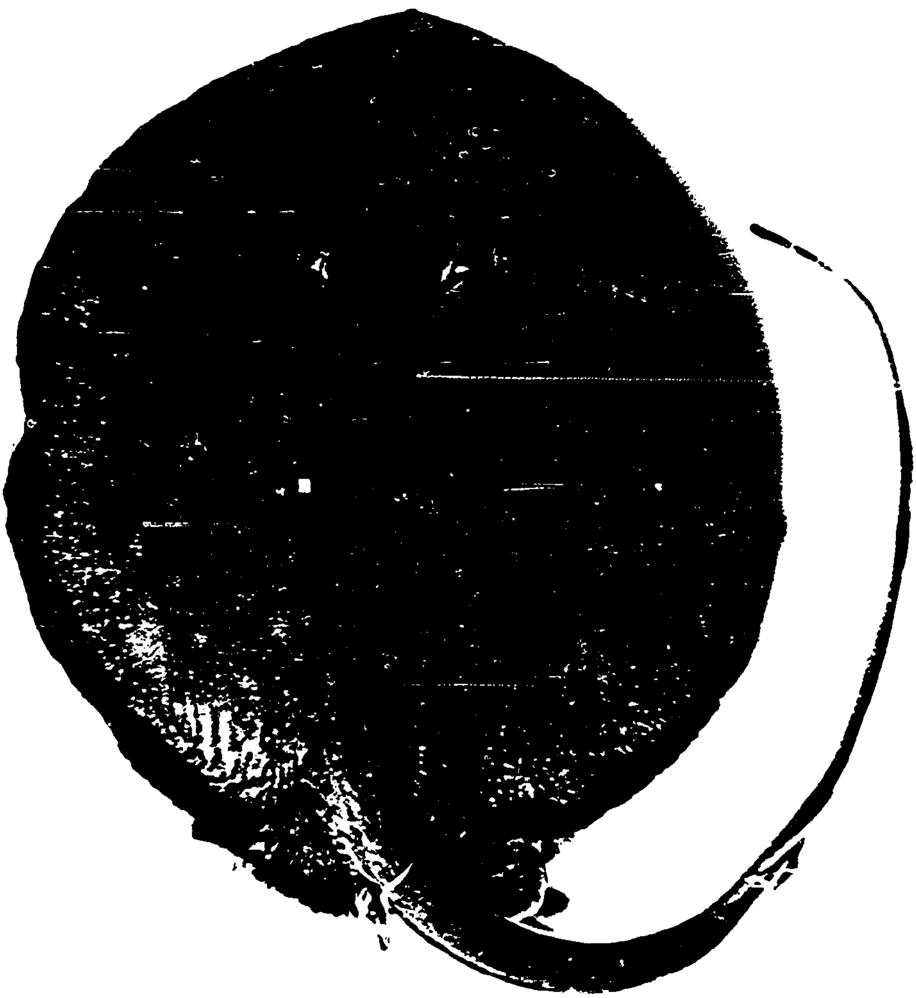


FIG. 6

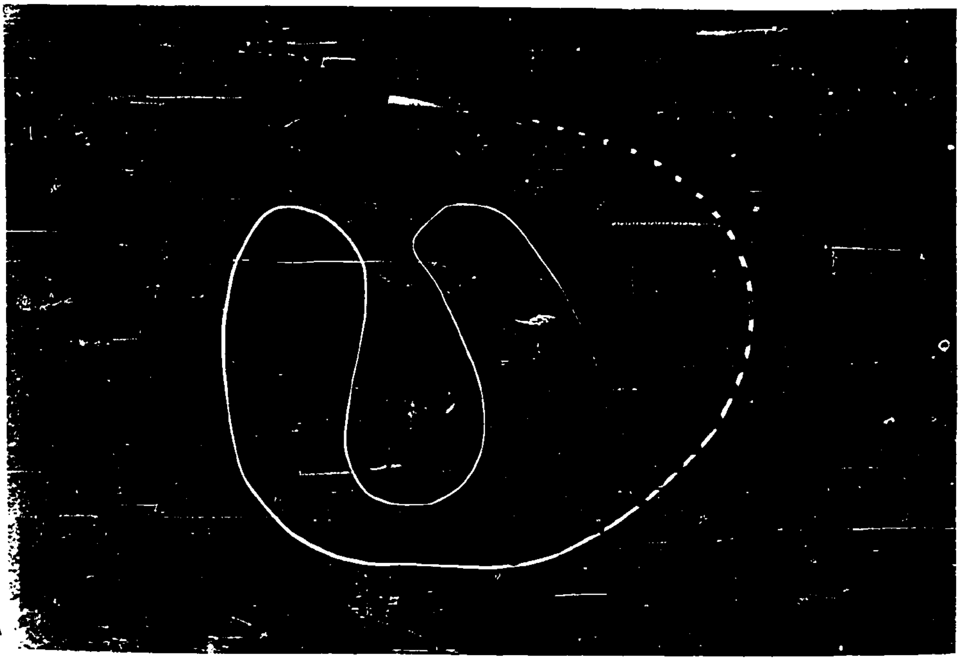
Plesiotrygon iwamae, dorsal view, female, 567 mm DL, FMNH 94500 (paratype).

FIG. 7

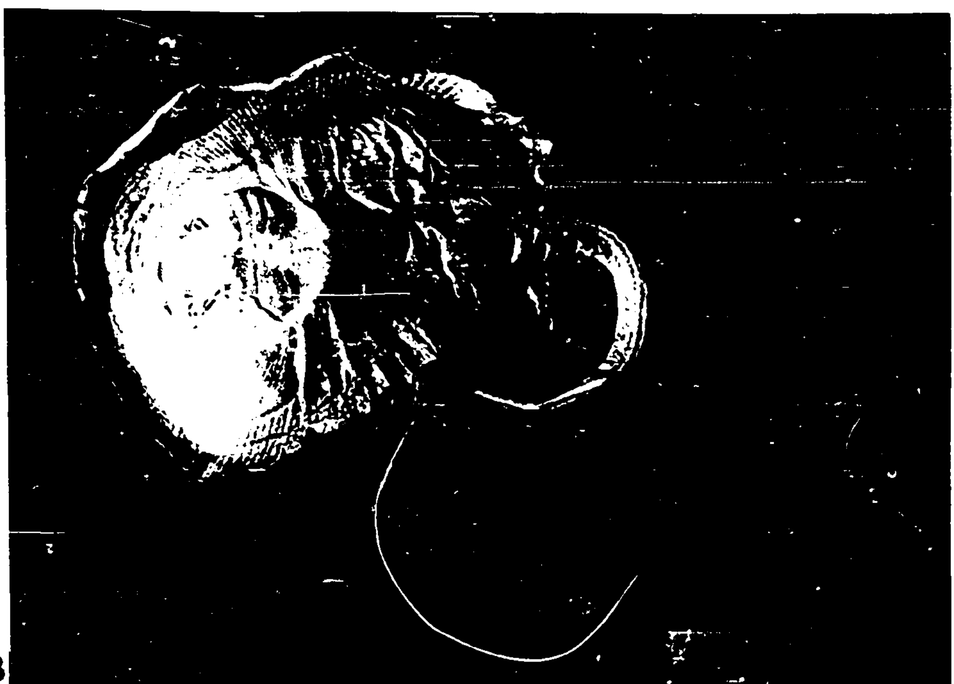
Plesiotrygon iwamae, dorsal view, juvenile male specimen of unknown present location, not seen by the author. Photographed during the 1976 Alpha Helix Expedition in the Amazon by Dr. K. Johansen (University of Aarhus, Denmark), courtesy of C. P. Mangun (College of William and Mary).

FIG. 8

Plesiotrygon iwamae, A.- Tail of juvenile male specimen, 226 mm DL, MZUSP 14789 (paratype). B.- Dorsal view of juvenile male specimen, 286 mm DL, ZMH 10343 (paratype).



A



B

FIG. 9

Plesiotrygon iwamae, A.- Dermal denticles from disc near midline, apical view, male, 226 mm DL, MZUSP 14789 (paratype). B - C. - Middorsal tail spine posterior to caudal sting, apical and lateral views, MZUSP 14789. D.- Intermediate and distal portions of caudal sting, dorsal view, MZUSP 14789.

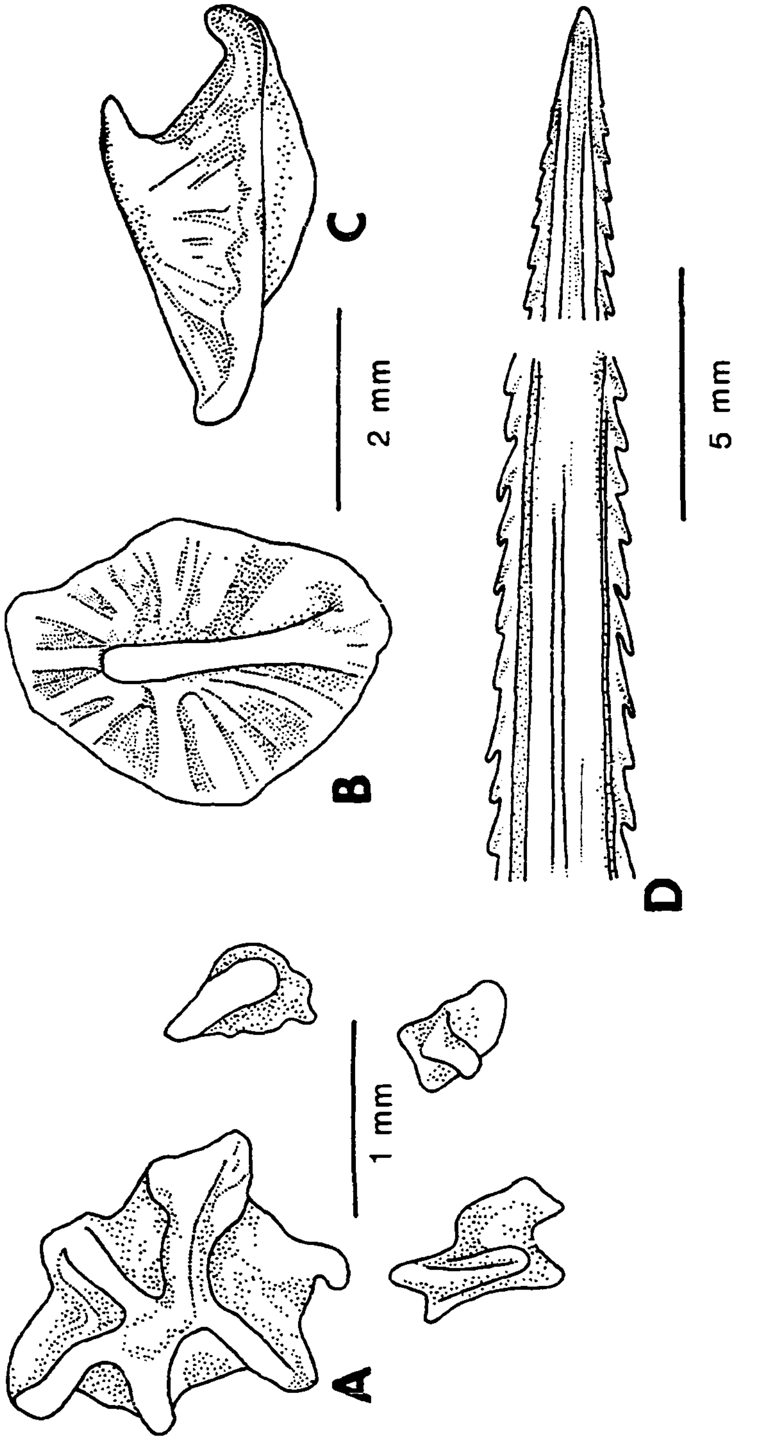

A
1 mm
B
C
2 mm
D
5 mm

FIG. 10

Plesiotrygon iwamae, A.- Exposed portions of upper and lower dental plates, male, 601 mm DL, MZUSP 10153 (holotype). B.- Idem, female, 567 mm DL, FMNH 94500 (paratype).

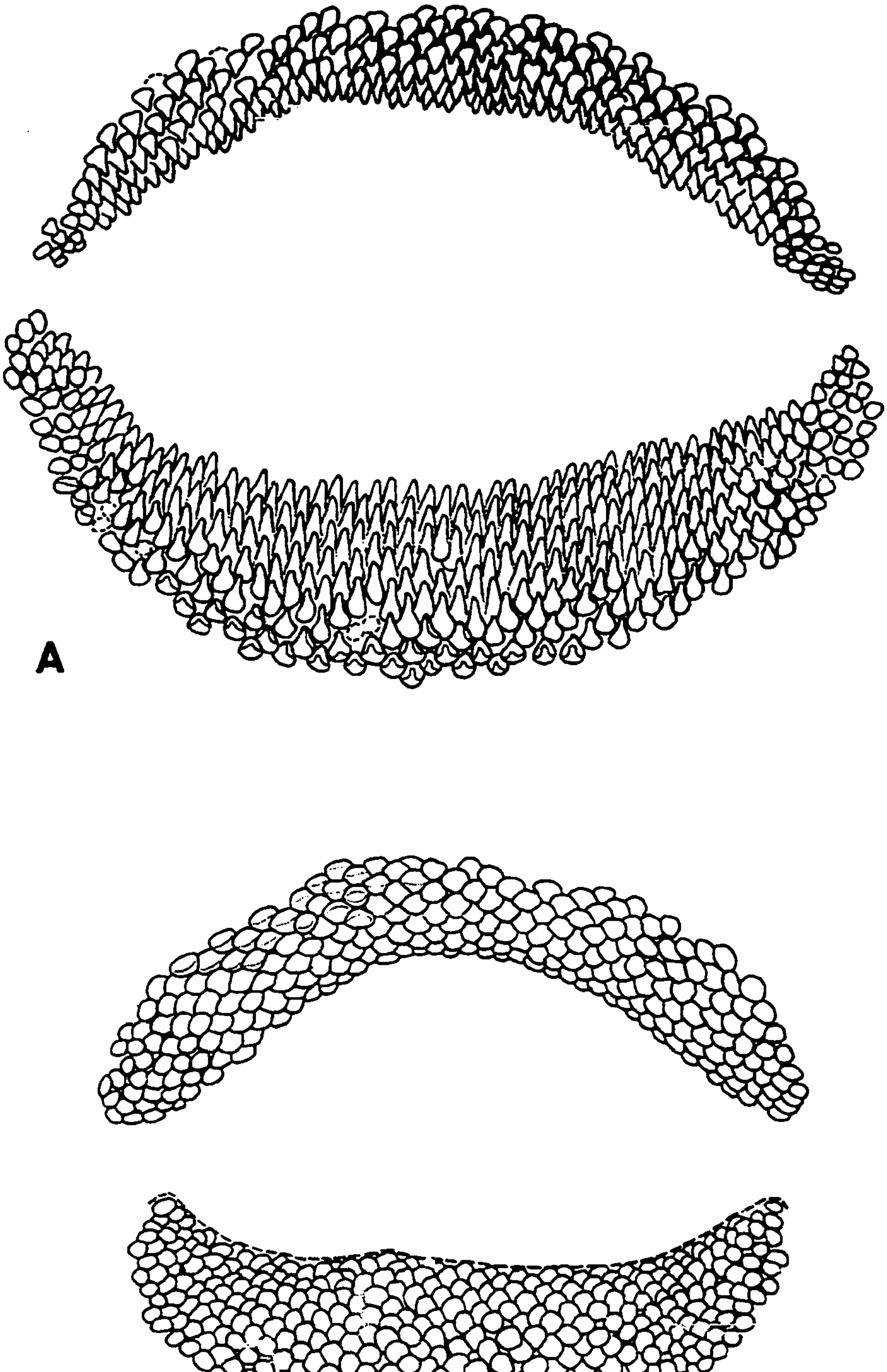
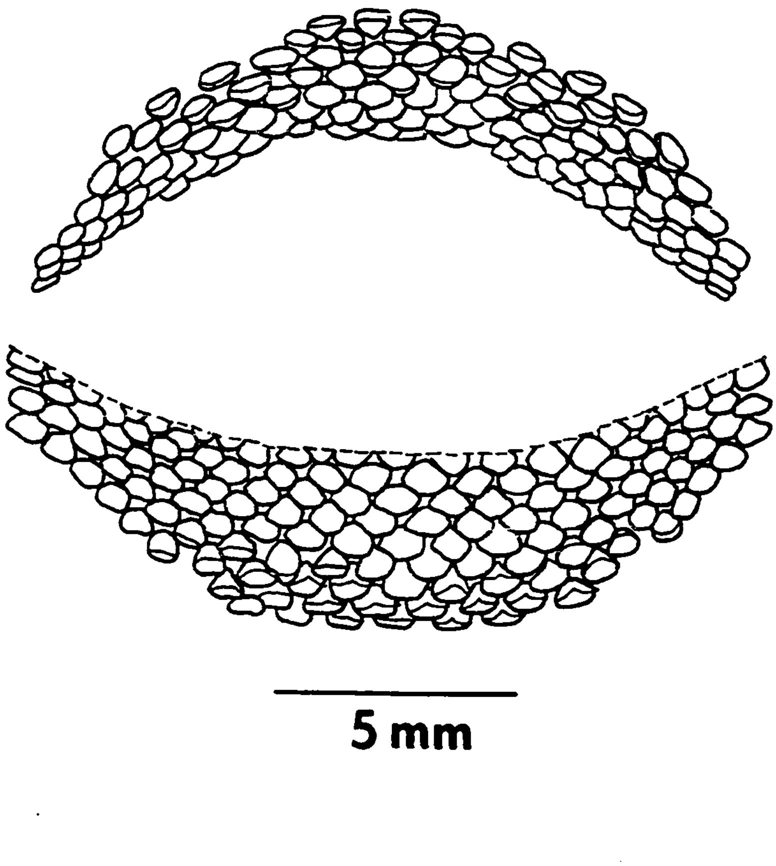

A
B
10 mm

FIG. 11

Plesiotrygon iwamae, exposed portions of upper and lower dental plates, juvenile male, 226 mm DL, MZUSP 14789 (paratype).



5 mm

FIG. 12

Plesiotrygon iwamae, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, male, 601 mm DL, MZUSP 10153 (holotype). F.- Tooth from lower jaw near symphysis, apical view, MZUSP 10153. G - K.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, female, 567 mm DL, FMNH 94500 (paratype). L.- Tooth from lower jaw near mouth corner, apical view, FMNH 94500.

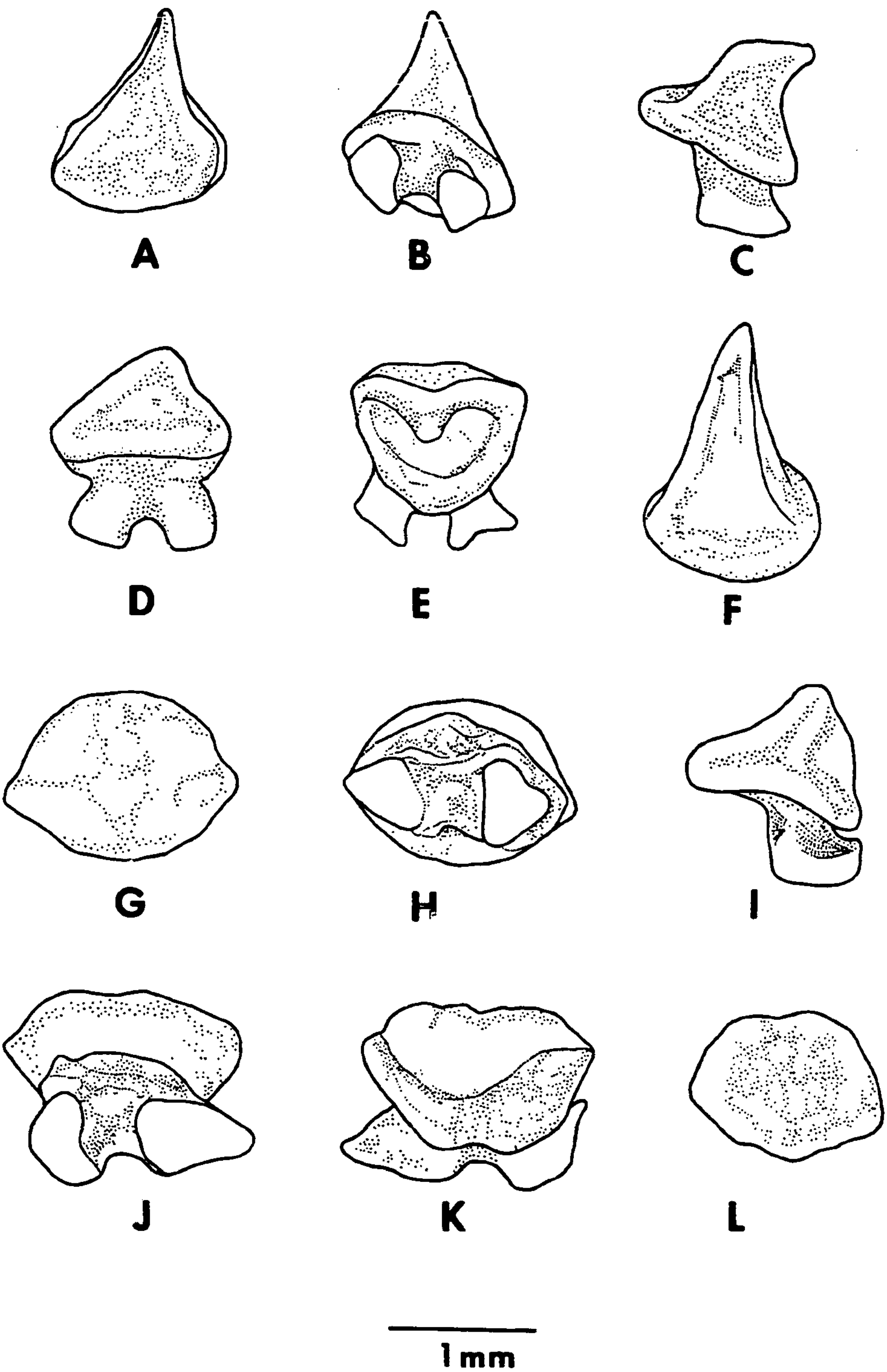
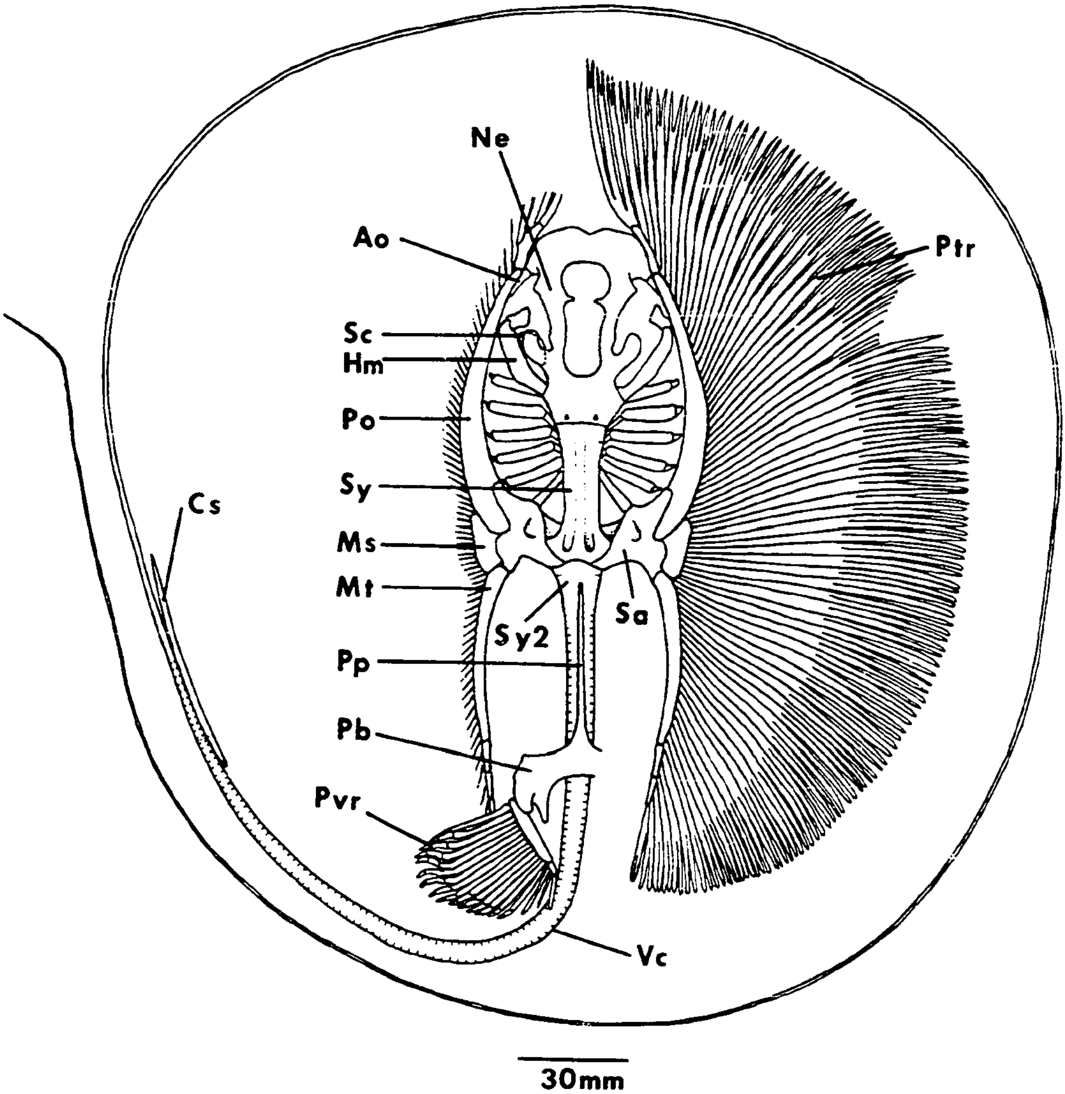

A
B
C
D
E
F
G
H
I
J
K
L
1mm

FIG. 13

Plesiotrygon iwamae, dorsal view of skeleton from radiograph, male, 226 mm DL, MZUSP 14789 (paratype). Pelvic girdle shown by transparency under vertebral column.



Ne
Ao
Sc
Hm
Po
Sy
Cs
Ms
Mt
Sy2
Sa
Pp
Pb
Pvr
Ptr
Vc
30mm

FIG. 14

Plesiotrygon iwamae, A - B.- Dorsal and ventral views of cranium from radiograph, male, 601 mm DL, MZUSP 10153 (holotype).

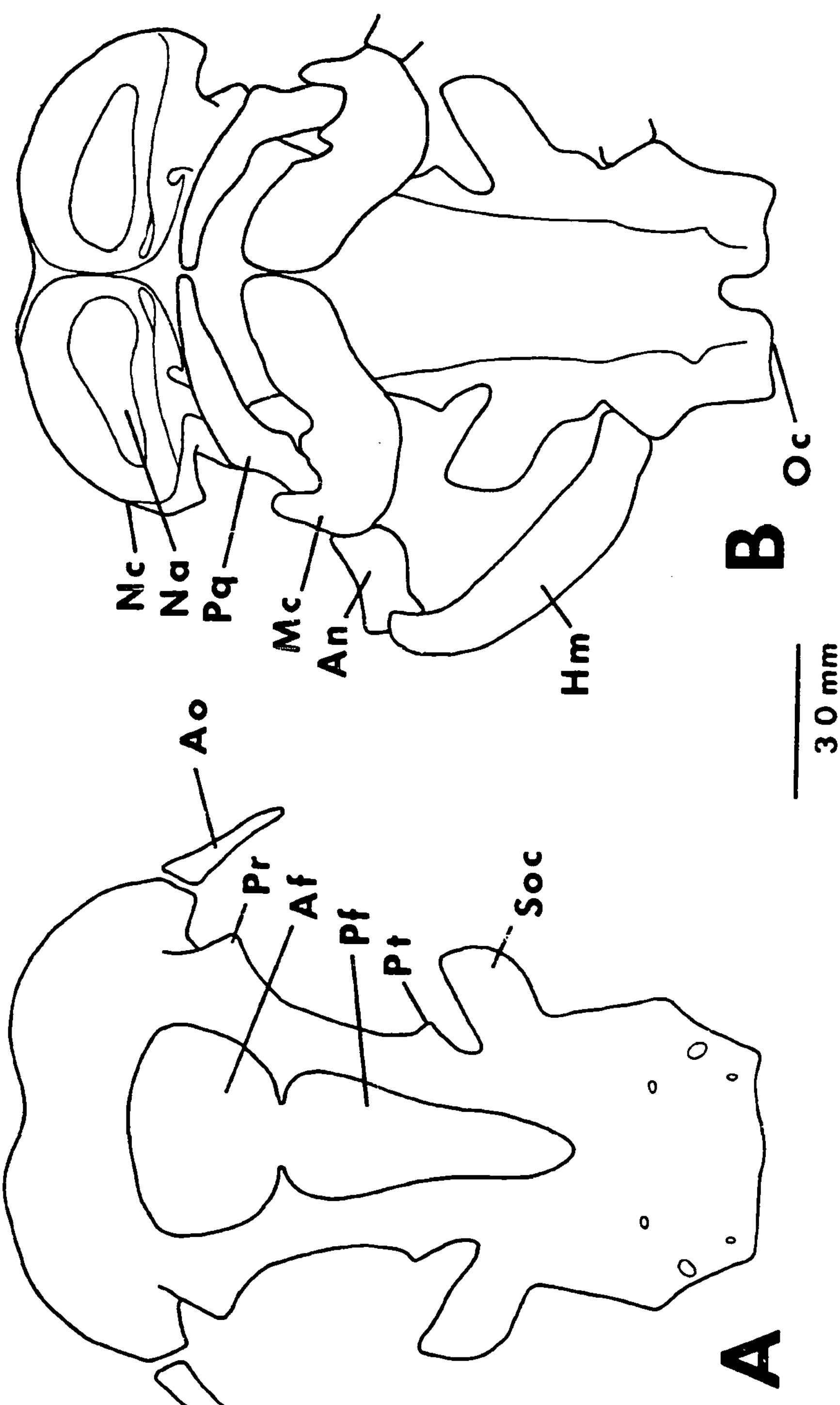

A
Ao
Pr
Af
Pf
Pt
Soc
B
Nc
Na
Pq
Mc
An
Hm
Oc
30 mm

FIG. 15

Plesiotrygon iwamae, A.- Dorsal view of ischiopubic bar, male, 215 mm DL, MNRJ 573 (paratype). B.- Ventral view of ventral portion of branchial skeleton (basibranchial plate and fourth ceratobranchial damaged), MNRJ 573.

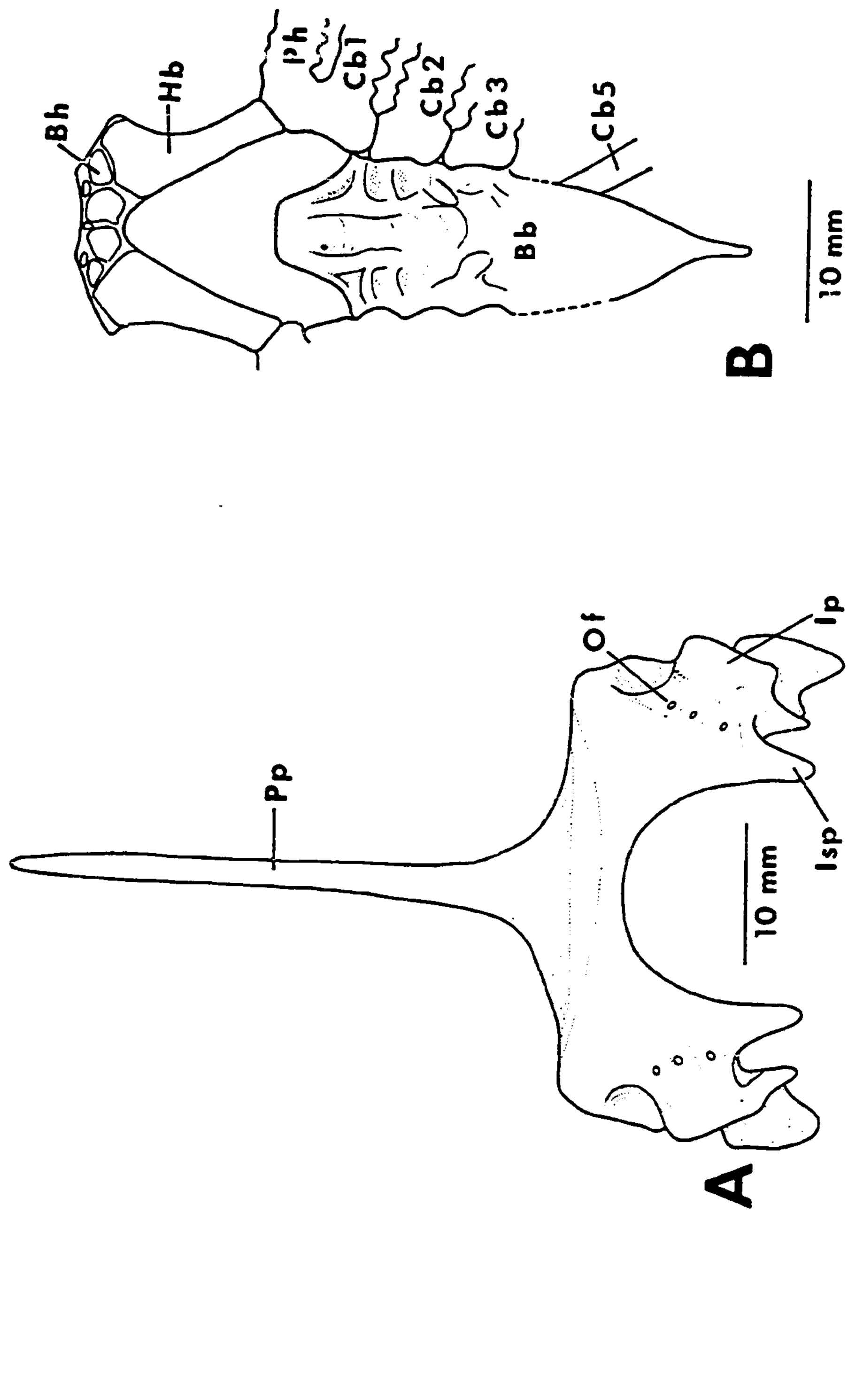

A
Pp
Of
Ip
Isp
10 mm
B
Bh
Hb
Ph
Cb1
Cb2
Cb3
Cb5
Bb
10 mm

FIG. 16

Plesiotrygon iwamae, A - C.- Lateral, ventral, and dorsal views of intact right clasper, adult male, 576 mm DL, USNM 258298 (paratype).

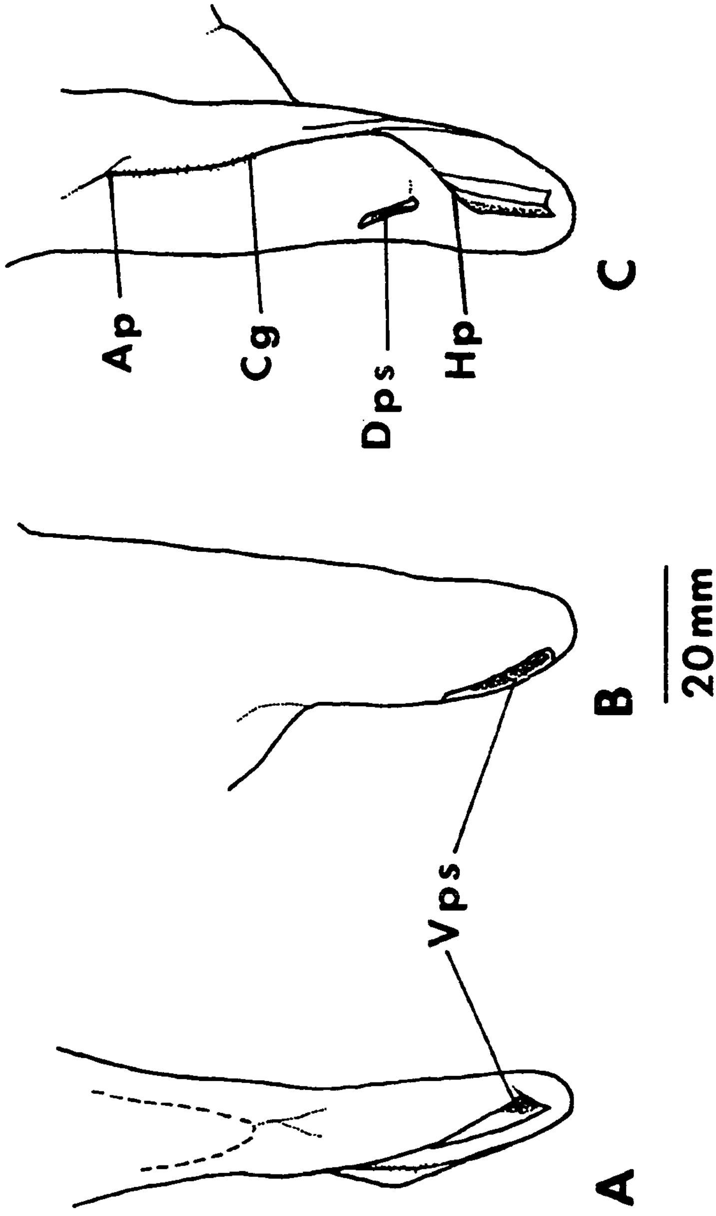
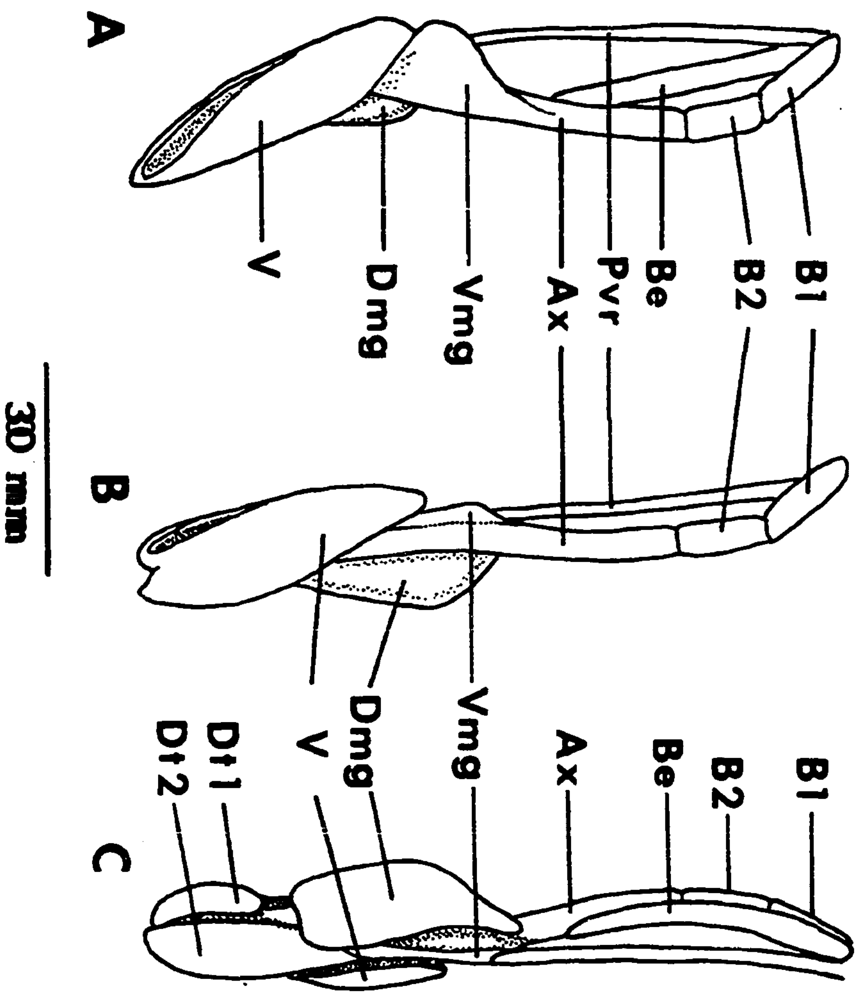

Ap
Cg
Dps
Hp
C
Vps
B
20mm
A

FIG. 17

Plesiotrygon iwamae, A - C.- Lateral, ventral, and dorsal views of dissected right clasper, adult male, 576 mm DL, USNM 258298 (paratype).


A
B
C
B1
B2
Be
Pvr
Ax
Vmg
Dmg
V
Dt1
Dt2
30 mm

Potamotrygon Garman, 1877

Trygon [in part]. Müller and Henle, 1841: 167, 197; Castelnau, 1855: 100-103; Duméril, 1865: 582; Günther, 1870: 472-483.

Taeniura [in part]. Müller and Henle, 1841: 197; Duméril, 1865: 619-625.

Taenura [sic]. Castelnau, 1855: 101-102.

Toenura [sic]. Castelnau, 1855, pl. 49.

Potamotrygon Garman, 1877: 210.

Ellipesurus [in part]. Ribeiro, 1907: 140, 183-187.

Potamotrigon [sic]. Miles, 1947: 41.

Potomotrygon [sic]. Castex, 1964b: 23, corrected in addendum.

Potamotrygan [sic]. Castex, 1964b: 29.

Potamotriygon [sic]. Achenbach, 1971: 7.

Type species: Potamotrygon histrix (Müller and Henle, in Orbigny, 1834) by subsequent selection of Jordan, 1919: 389.

Etymology: Potamotrygon, from Greek = freshwater ray.

Remarks.- Müller and Henle (1841) recognized the correct gender of Trygon (feminine) by citing adjective specific names in the feminine. Günther (1870) changed T. strogylopterus to T. strogyloptera to agree in gender with Trygon, but subsequently (Günther, 1880) described two new species (T. reticulatus and T. brachyurus) with masculine suffixes. More recently, Bailey (1969) commented on the correct gender of Potamotrygon (feminine). Ringuelet et al. (1967) mistakenly selected Pastinaca humboldtii as the type species of Potamotrygon.

Diagnosis.- A polytypic genus of Potamotrygonidae diagnosed by the following combination of characters: tail relatively short, less than two times DW in length, distally compressed with dorsal and ventral finfolds, lacking enlarged spines posterior to caudal sting; disc oval to circular with anteromedian prominence; eyes relatively large and pedunculate; ceratobranchials one to four fused to each other; 82 to 112 pectoral fin radials.

Description.- Disc oval to circular, anterior margin of disc convex with median fleshy prominence; posterior margins of disc convex, fused at their inner origins with dorsal surface of pelvic fins and base of tail. Pelvic fins partially or completely covered dorsally by disc, their anterior margins straight or concave, oblique to midline, posterior margins straight or convex.

Tail relatively short, less than two times DW, usually broken distally in adults; anterior portion of tail depressed, usually with lateral ridges, tapering from base to sting region. Distal portion of tail moderately compressed, with dorsal and ventral membranous finfolds, not supported by cartilaginous elements in adults. Middorsal spines in one or several parallel rows, gradually increasing in size from posterior disc to insertion of caudal sting, their number and relative size increasing with age. Lateral spines present or absent from tail base to sting region, usually more developed in adults. Tail dorsally with one to three serrated stings (Fig. 18), inserted nearly halfway from tail base to tip of tail. Dorsal surface of disc covered with dermal denticles, larger towards midline, more developed in adults. Enlarged tubercles occasionally present submarginally on disc or paramedially on scapular region.

Eyes relatively large, oval in shape, and prominent on dorsal surface of disc. Spiracles immediately behind orbits, oblique to midline, without external projections, with papillose projection on floor of spiracular cavity. Nostrils relatively large, their length usually less than two times in mouth width, and oblique to midline. Mouth transverse with arched upper jaw, lower jaw moderately waved or flat; roof of buccal cavity with fringed oral valve, one medial and two paramedial tegumentary ridges; floor of buccal cavity with three to eight (usually five) slender papillae, posteriorly with one medial and two paramedial tegumentary ridges. Teeth closely or loosely set in quincunx, in 14/13 to 54/59 longitudinal rows. Tooth crowns blunt or tricuspidate; tooth roots bilobed and pedicellate, with central nutrient foramen.

Anterior subpleural portion of lateral line system non-reticulate; suborbital canal with anterior loop pointing forward (see Garman, 1888 for detailed description of lateral line system).

Neurocranium (Figs. 19-22) elongated, depressed in front of orbital region; nasal capsules transversely elliptic, bulging ventrally, their anterior margins convex with median indentation between them. Vestigial, dagger-shaped, rostral appendix cartilage (Fig. 20) usually present in embryos, absent in adults. Preorbital processes usually well-developed and arched backwards. Preorbital width of cranium greater than width at nasal capsules. Postorbital processes more or less developed, always smaller than preorbital processes. Supraotic crests well-developed and expanded laterally, reaching anterior margins of spiracles. Cranial fontanelle keyhole-shaped, with more or less developed transverse constriction between anterior and supracranial portions, partially or completely covered by fibrous connective tissue.

Anterior portion of vertebral column with coalescent vertebrae forming two synarcual plates. First synarcual anteriorly broad, distally tapering, with articular facets for pharyngobranchials. Second synarcual posterior to pectoral girdle, with all vertebral centra radiographically distinct. Distal portion of vertebral column with five to fifteen diplospondylous vertebrae.

Branchial skeleton (Fig. 23) with segmented basihyal, formed by triangular median piece and one lateral bar on each side. Hypobranchial cartilage entire and long, with more or less developed projection on outer margin. Ventral pseudohyoid with five to eight gill rays, fused at inner margin with first ceratobranchial. Ceratobranchials one to four fused at their inner margins, each with four to seven gill bars. Basibranchial relatively long and narrow, its maximum width contained more than three times in length, with pointed anterior and posterior ends, laterally indented at articulations with ceratobranchials.

Scapulocoracoid relatively narrow, its maximum width less than distance from mouth to anterior margin of coracoid bar. Lateral face of scapulocoracoid with large anteroventral fenestra and small postventral fenestra. Coracoid bar relatively thin, its maximum diameter in median cross section contained nearly two times in maximum distance between mesocondyle and metacondyle.

Pelvic girdle (ischiopubic bar) with elongated prepubic process (Fig. 23, see also Garman, 1913, plate 54), and moderately developed prepelvic processes. Anterior margins of pelvic girdle concave, posterior margin nearly semicircular. Iliac processes long and angled outwards, dorsally covering lateral articular faces for the pelvic fin basal elements. Three obturator foramina on each side of pelvic girdle.

Pectoral fin plesodic, with 82 to 112 segmented radials (mode 95). Propterygium arched, its basal piece anteriorly reaching level of nasal capsules. Antorbital cartilage moderately elongate, triangular in dorsal view. Mesopterygium cuneiform in dorsal view, with 10 to 18 radials. Metapterygium distally segmented, with 31 to 41 radials. Pelvic fin with 21 to 29 radials in females, and 18 to 22 radials in males.

Claspers relatively long and stout (Figs. 24 and 25), their length 20.4-34.9 percent of DW in mature males. Claspers straight or slightly arched in lateral view, elliptic in cross section. Clasper groove anteriorly oblique and distally parallel to midline. Dorsal pseudosiphon oblique to midline, its length nearly equal to clasper width at level of terminal cartilages. Clasper axial cartilage straight or slightly arched in dorsal view, anteriorly depressed, distally cylindrical tapering towards tip, and articulated with pelvic basipterygium by two basal elements. Beta cartilage proximally cylindrical and articulated with first basal element, distally depressed, not reaching dorsal marginal cartilage. Dorsal marginal cartilage trapezoidal in dorsal view, arched in cross section forming roof of clasper groove. Ventral marginal cartilage fusiform in dorsal view, laterally fused to axial cartilage forming floor of clasper groove. Dorsal terminal 1 cartilage fusiform in lateral view, proximally articulated with dorsal marginal cartilage, ventrally attached to axial cartilage. Dorsal terminal 2 cartilage elongate, fusiform in dorsal view, proximally attached to ventral marginal cartilage, laterally expanded forming roof of ventral pseudosiphon. Ventral covering piece elongate, trapezoidal in lateral view, distally attached to dorsal terminal 1 and axial cartilages.

KEY TO THE SPECIES OF *Potamotrygon*

Remarks.- This artificial key is intended for the identification of adult and subadult specimens (larger than 150 mm in disc length). Illustrations and distributional data should always complement key characters. This key does not include two unidentified or undescribed species which are discussed later in the text.

1A. Dorsal surface of disc with yellow to orange ocelli, larger than eye in diameter, encircle by dark rings.....2

1B. Dorsal surface of disc without large ocelli; small circular spots or ocelli occasionally present above orbits or submarginally on disc..................................5

2A. Ocelli nearly circular, usually forming regular concentric series...3

2B. Ocelli irregular in shape and distribution.............4

3A. Teeth relatively large, in 18 to 39 rows in upper jaw; tooth crowns tetragonal, without prominent cusps except in mature males; ocelli not extending distally on tail... ....*P. motoro*

3B. Teeth very large, pavement like, in 14 to 26 rows in upper jaw; tooth crowns tetragonal or hexagonal; ocelli continue distally on tail; ocelli on disc occasionally with dark center or lunate in shape............*P. henlei*

4A. Ocelli white to yellow, lunate or irregular in shape, occasionally forming broken circles with dark center; dorsal tail spines in three parallel rows........*P. leopoldi*

4B. Ocelli deep orange to rusty red, entire, in various irregular shapes; dorsal tail spines in a single row..*P. ocellata*

5A. Dorsal disc with regular reticulate pattern of dark lines delimiting polygonal figures...........................6

5B. Dorsal disc without a regular reticulate pattern........8

6A. Reticulate shapes relatively large, their maximum diameter nearly equal to interocular distance; disc circular; distance from cloaca to insertion of caudal sting contained more than 2.7 times in disc width.....*P. brachyura*

6B. Reticulate shapes relatively small, their maximum diameter less than interocular distance; disc subcircular; distance from cloaca to insertion of caudal sting contained less than 2.7 times in disc width...............7

7A. Disc and tail relatively rough, with sharp denticles and spines; reticulate shapes of interorbital region like in Fig. 26A..................................*P. humerosa*

7B. Disc and tail relatively smooth, without sharp denticles or spines; reticulate shapes of interorbital region like in Fig. 26B.................................*P. orbignyi*

8A. Dorsal surface of disc entirely spotted with white or yellow...9

8B. Dorsal color pattern not as in 8A......................13

9A. Dorsal spots smaller than eye in diameter.............10

9B. Dorsal spots larger than eye in diameter, oval to reniform in shape; from Paraguay and lower Paraná river drainages..................................._P. falkneri_

10A. Dorsal tail spines in two or three parallel rows.......11

10B. Dorsal tail spines in a single row; dorsal yellow spots irregular in shape, occasionally forming vermiculations or fading in darker specimens; northern Colombian distribution in Magdalena and Atrato rivers......._P. magdalenae_

11A. Dorsal spots yellow, oval or reniform in shape, occasionally forming vermiculations or rosettes...............12

11B. Dorsal spots white to light yellow, circular in shape, isolated from each other, not forming vermiculations or rosettes; mid to lower Amazonian distribution.._P. scobina_

12A. Dorsal spots usually isolated from each other, occasionally forming vermiculations; from Parnaíba river drainage in Brazil...................................._P. signata_

12B. Dorsal spots usually grouped forming vermiculations or rosettes; from Paraguay, lower Paraná, and upper Amazon river drainages.............................._P. castexi_

13A. Dorsal disc with broken dark lines, not forming polygonal figures..14

13B. Dorsal disc uniformly colored or variously spotted, usually without broken dark lines........................15

14A. Dorsal disc light brown with dark lines delimiting triangular yellow figures, arranged in broken reticulate pattern; disc and tail relatively smooth....._P. dumerilii_

14B. Dorsal disc dark brown with dark vermiform lines; disc and tail relatively rough, with sharp denticles and spines..*P. histrix*

15A. Dorsal disc uniformly colored in light brown to dark grayish-brown, occasionally spotted with white, yellow, or black dots..16

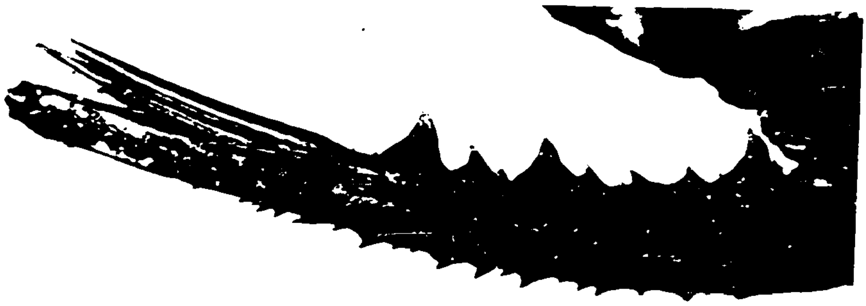
15B. Dorsal disc dark grayish-brown with groups of yellow to orange spots forming rosettes or brain-shaped figures; from Orinoco and Negro rivers.............*P. schroederi*

16A. Dorsal disc light brown to dark grayish-brown, usually with black dots, and occasionally with irregular yellow spots, more evident on lighter specimens; from Lake Maracaibo drainage............................*P. yepezi*

16B. Dorsal disc brown to dark grayish-brown, marginally with irregular white spots, occasionally with broken reticulate pattern of dark pigment, more evident on lighter specimens; a submarginal series of enlarged tubercles usually present on disc; from mid Amazon drainage....... ....*P. constellata*

FIG. 18

Caudal stings of Potamotrygon, A.- Double stings in P. humerosa, lateral view, female, 294 mm DL, MCZ 299-S (holotype). B.- Triple stings in P. magdalenae, lateral view, female, 235 mm DL, TBT 76-84. C.- Bifid sting in P. brachyura, dorsal view, male, 404 mm DL, MFA (uncatalogued specimen).



A

B

C

FIG. 19

Potamotrygon yepezi, dorsal view of skeleton, from radiograph and partial dissection, male, 181 mm DL, VIMS 06064. Pelvic girdle shown by transparency under vertebral column.

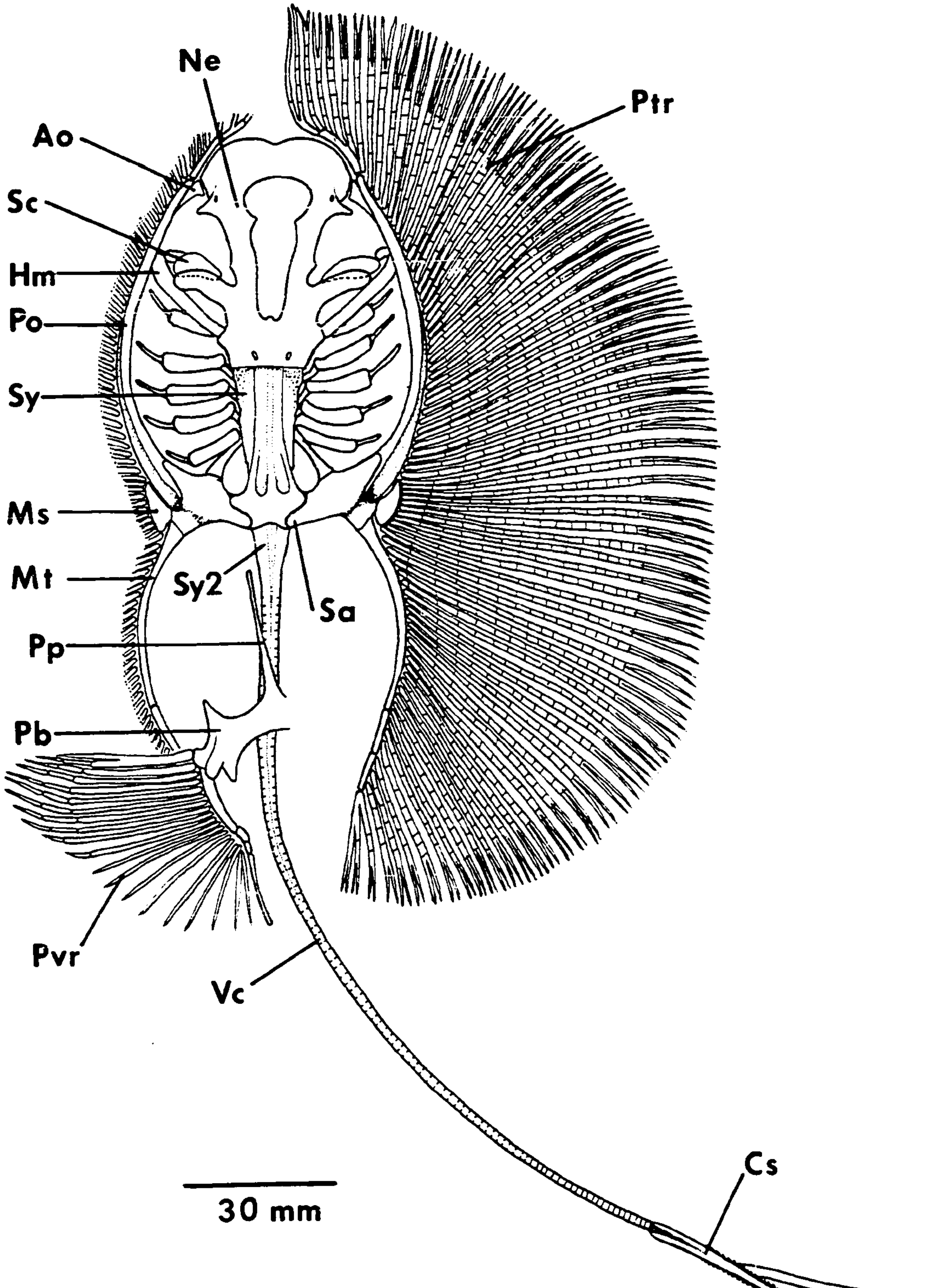

Ne
Ao
Sc
Hm
Po
Sy
Ms
Mt
Sy2
Sa
Pp
Pb
Pvr
Vc
Ptr
Cs
30 mm

FIG. 20

A - B.- Potamotrygon motoro, dorsal and ventral views of neurocranium, from dissection, male, 337 mm DL, MACN (uncatalogued specimen, formerly ILAFIR 11.

C.- Potamotrygon yepezi, dorsal view of rostral appendix cartilage from embryo, 48.5 mm DL, UFPB (uncatalogued specimen).

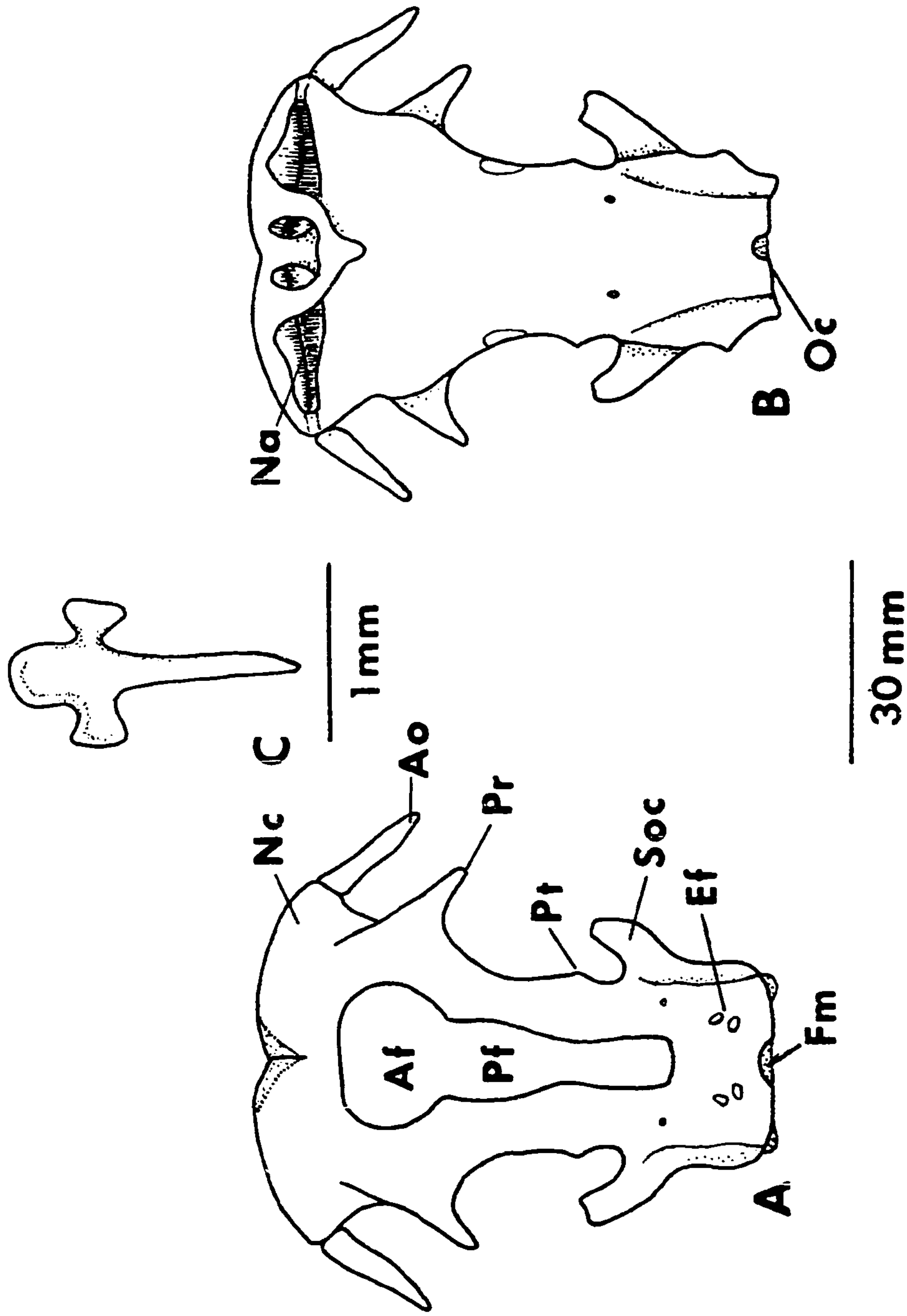

A
B
C
Na
Oc
Nc
Ao
Pr
Pt
Soc
Ef
Fm
Af
Pf
1mm
30mm

FIG. 21

Dorsal outlines of neurocrania of Potamotrygon, traced from radiographs, A.- P. histrix, MNHN 2449 (holotype); B.- Idem, MFA 317; C.- P. dumerilii, MFA 268; D.- P. constellata, MNHN A.1010 (lectotype); E.- Idem, MCZ 291-S (syntype of P. circularis); F.- P. humerosa, MCZ 299-S (holotype); G.- P. schuemacheri, MFA 293 (holotype); H.- Potamotrygon sp. A, MCZ 601-S; I.- P. schroederi, MZUSP 10290.

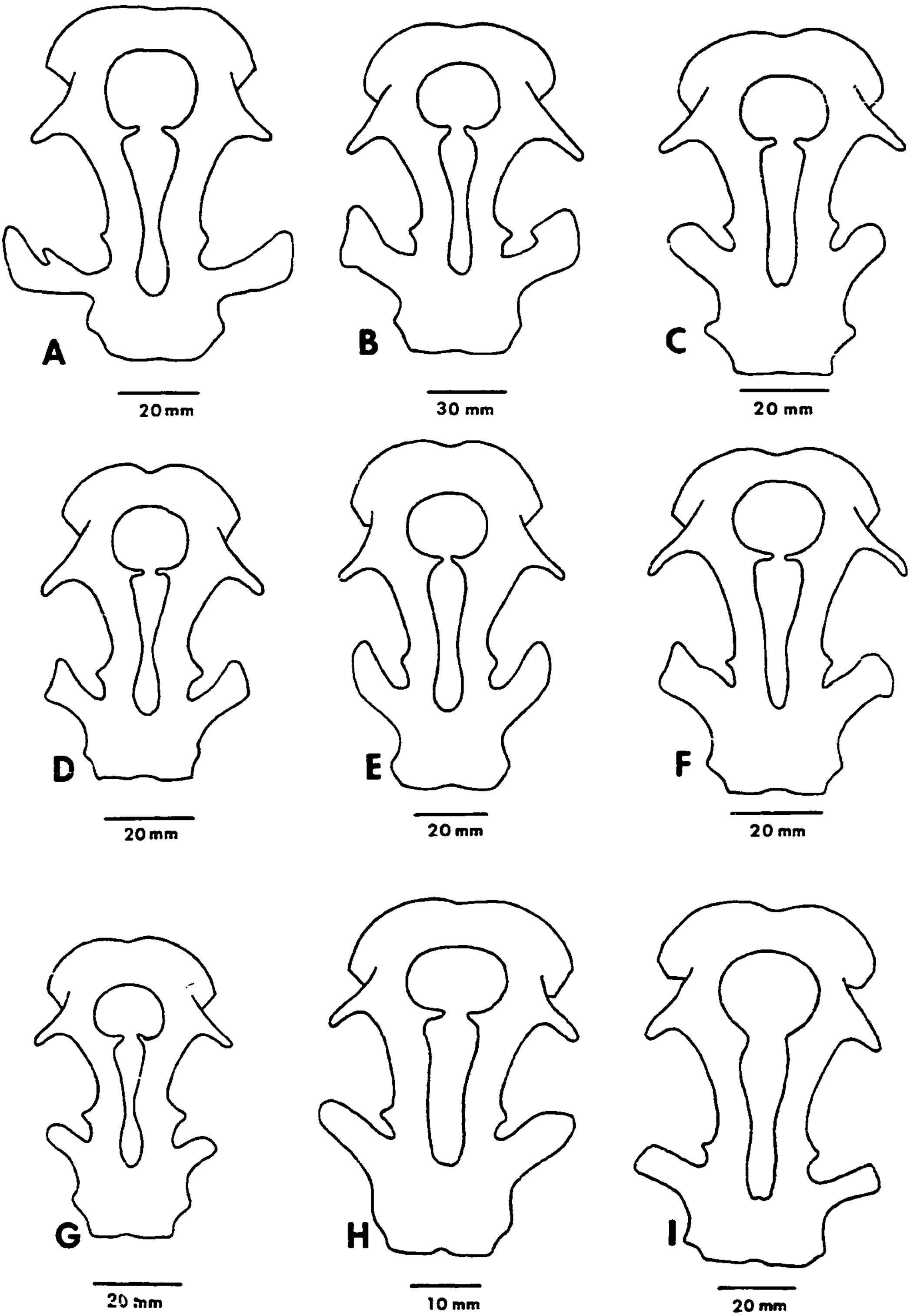

A
20 mm
B
30 mm
C
20 mm
D
20 mm
E
20 mm
F
20 mm
G
20 mm
H
10 mm
I
20 mm

FIG. 22

Dorsal outlines of neurocrania of _Potamotrygon_, traced from radiographs, A.- _P._ _castexi_, LACM 39934-1; B.- _P._ _signata_, MZUSP 19234; C.- _P._ _falkneri_, MFA 235 (paratype); D.- _P._ _scobina_, MCZ 602-S (holotype); E.- _P._ _yepezi_, VIMS 06064; F.- _P._ _magdalenae_, TBT 76-83; G.- _P._ _orbignyi_, BMNH 1870.3.10.1 (type of _Trygon_ _reticulatus_); H.- _P._ _brachyura_, BMNH 1879.2.12.4 (neotype); I.- _Potamotrygon_ sp. B, USNM 225575.

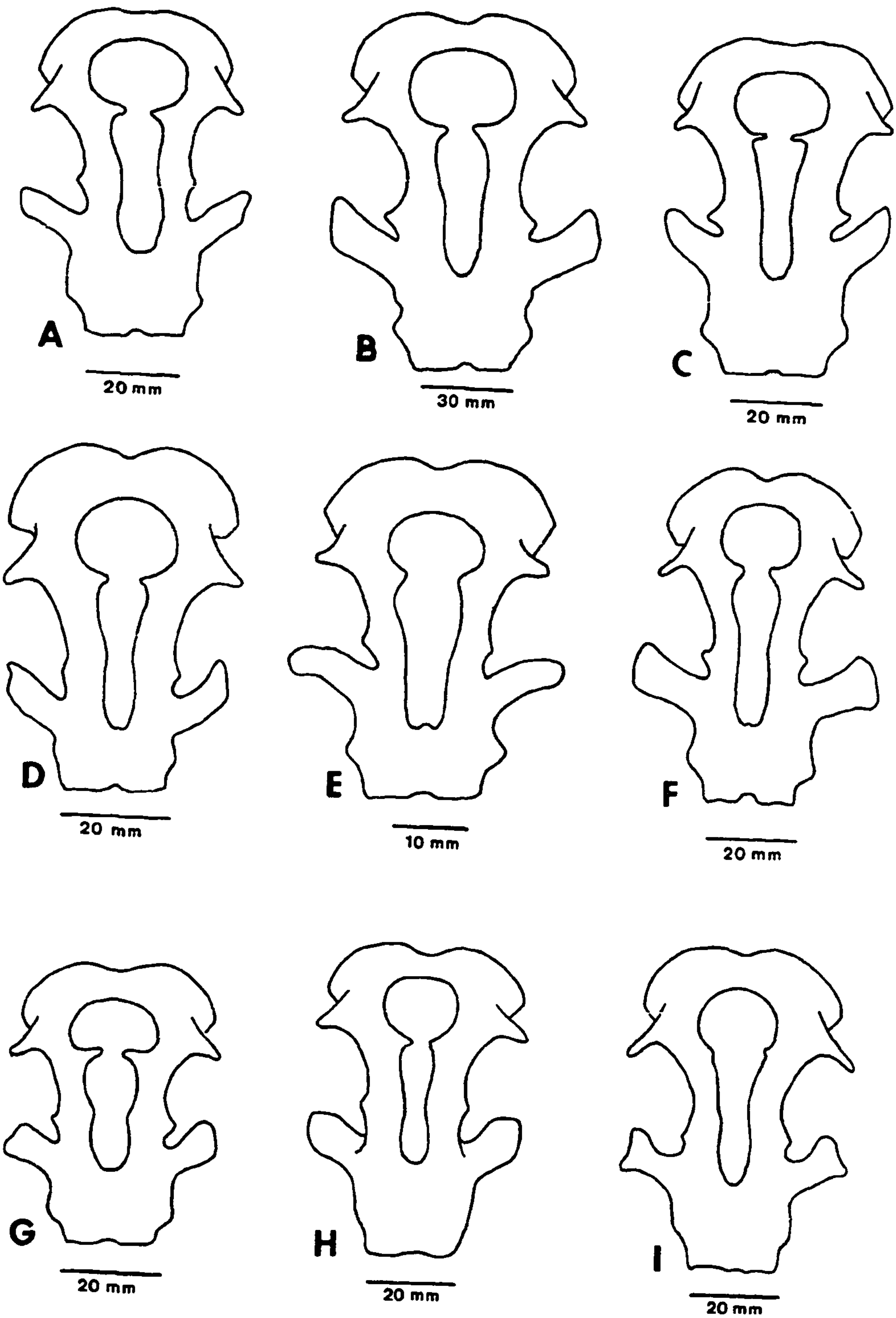

A
20 mm
B
30 mm
C
20 mm
D
20 mm
E
10 mm
F
20 mm
G
20 mm
H
20 mm
I
20 mm

FIG. 23

A.- Potamotrygon yepezi, dorsal view of ischiopubic bar, from dissection, male, 181 mm DL, VIMS 06064. B.- Potamotrygon magdalenae, ventral view of ventral portion of branchial skeleton, from dissection, embryonic female, 71.3 mm DL, SU 11553.

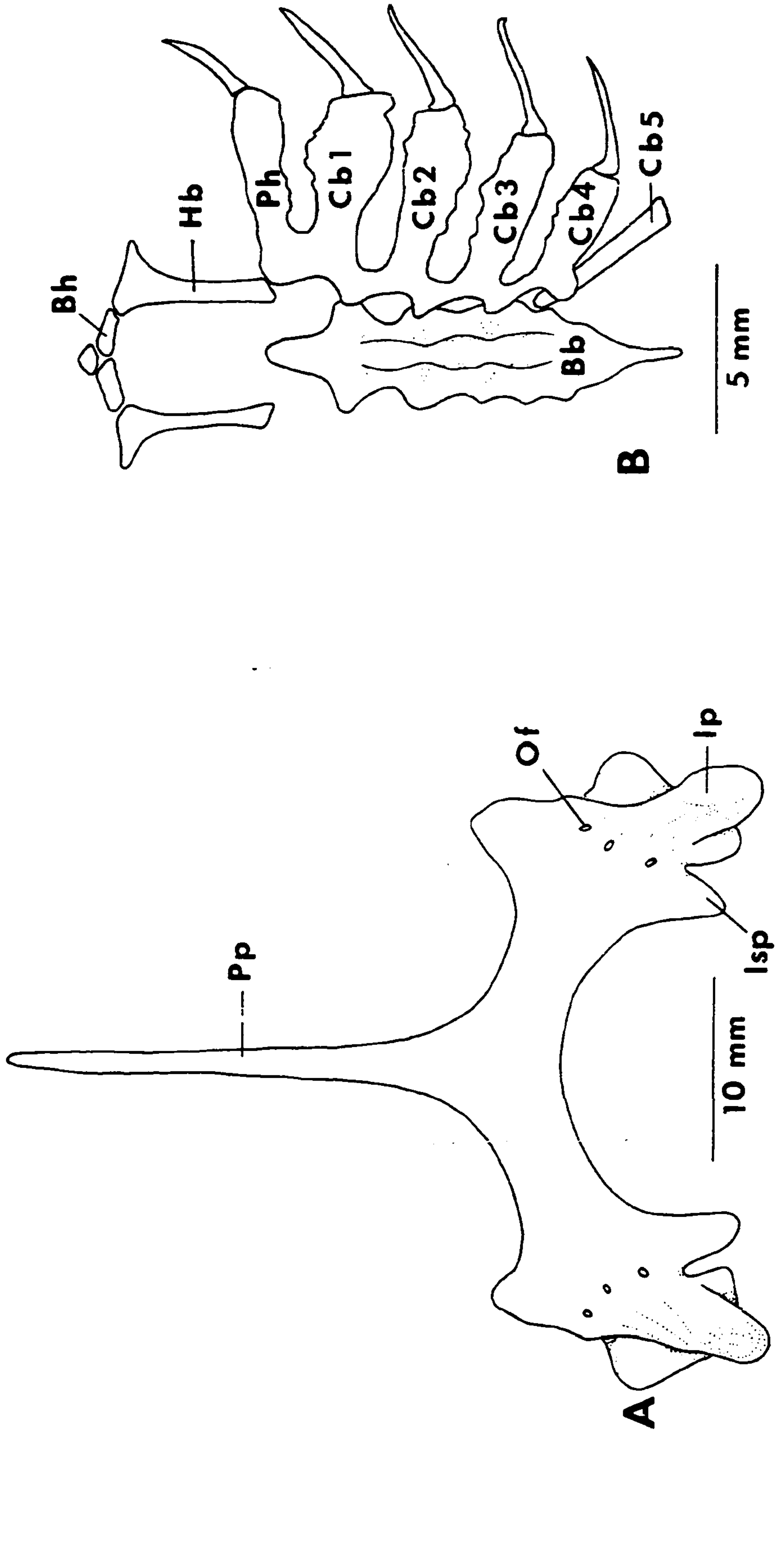

B
Bh
Hb
Ph
Cb1
Cb2
Cb3
Cb4
Cb5
Bb
5 mm
A
Pp
Of
Ip
Isp
10 mm

FIG. 24

Potamotrygon motoro, A - C.- Lateral, ventral, and dorsal views of intact right clasper, adult male, 337 mm DL, MACN (uncatalogued specimen), formerly ILAFIR 11.

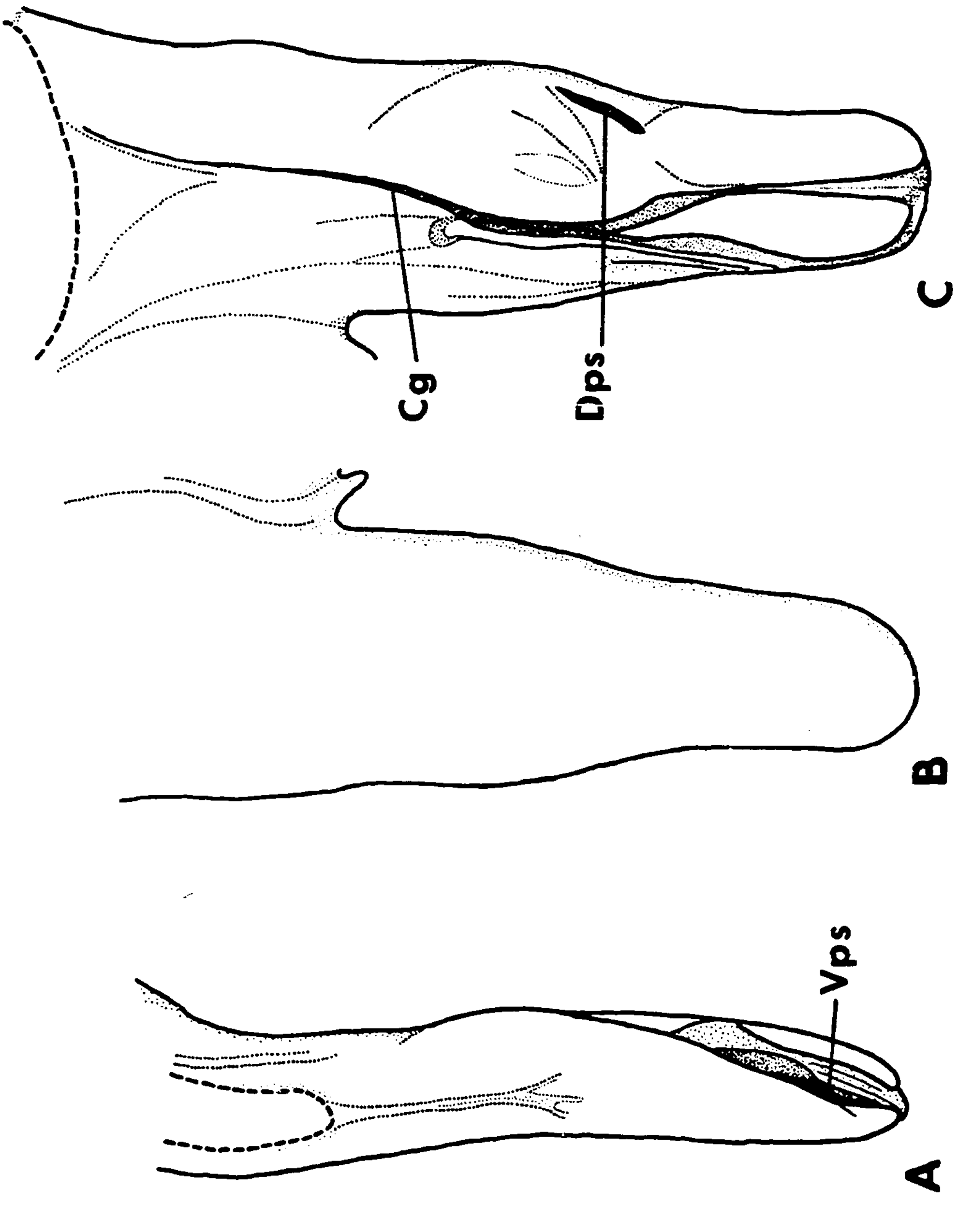

A
Vps
B
20 mm
C
Cg
Dps

FIG. 25

Potamotrygon motoro, A - C.- Lateral, ventral, and dorsal views of dissected right clasper, adult male, 337 mm DL, MACN (uncatalogued specimen), formerly ILAFIR 11.

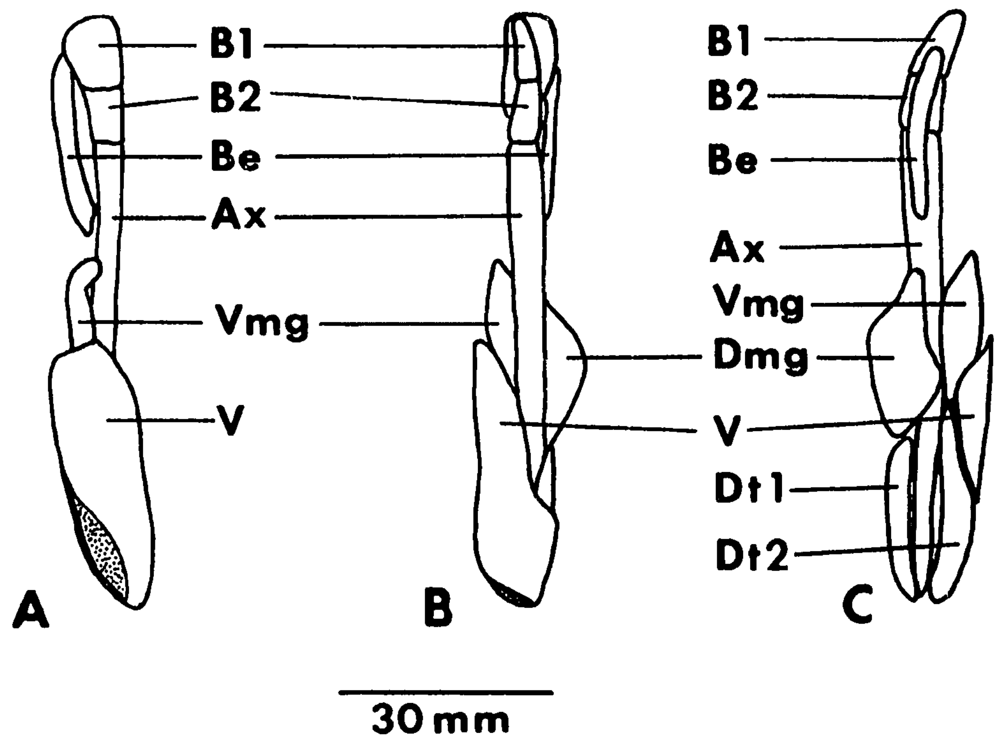
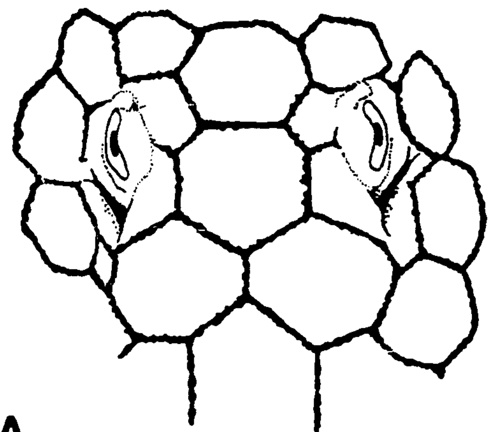
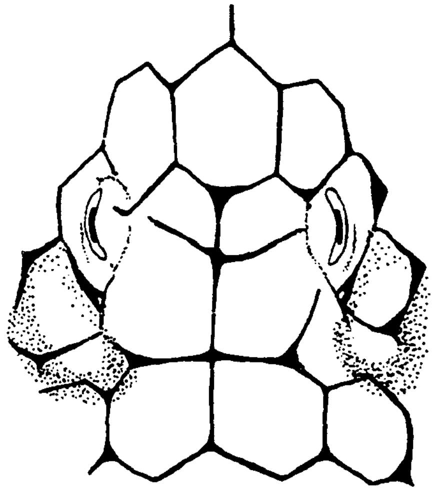

B1
B2
Be
Ax
Vmg
Dmg
V
Dt1
Dt2
A
B
C
30 mm

FIG. 26

Reticulate patterns of the interorbital region, actual size, A.- *Potamotrygon humerosa*. B.- *Potamotrygon orbignyi*.



A



B

Potamotrygon brachyura (Günther, 1880)

(Figs. 27-30)

Trygon brachyurus Günther, 1880: 8 (original description, Buenos Aires, not illustrated).

Potamotrygon brachyurus. Eigenmann and Eigenmann, 1891: 25.

Potamotrygon brachyura. Berg, 1897: 263.

Ellipesurus brachyurus. Bertoni, 1939: 51.

Potamotrygon brumi Devicenzi and Teague, 1942: 99, plate 6 (original description, Isla Queguay Grande, Río Uruguay).

Paratrygon brachyurus. Fowler, 1948: 5.

Paratrygon brumi. Fowler, 1970: 46.

Potamotrygon bruni [sic]. Taniuchi, 1982: 28.

Neotype: BMNH 1879.2.12.4 (herein selected), male, Buenos Aires, coll. E. White.

Type locality: Buenos Aires, Argentina.

Vernacular names: chucho de río (Uruguay); yavevih, yabebi, raya boba (Argentina and Paraguay).

Remarks.- No holotype designation was given in the original description. The female specimen mentioned by Günther was not found at the BMNH. The neotype selection is based on label and catalogue information, which cite the specimen as type. It is possible that this specimen was part of the original material examined by Günther, although it was not included in the publication.

Garman (1880) suggested the placement of Trygon brachyurus in the genus Potamotrygon. Berg (1897) correctly emended the specific name to P. brachyura to agree in gender with Potamotrygon. Engelhardt (1912) mistakenly treated P. brachyura as a variety of Potamotrygon histrix. Devicenzi and Teague (1942) described Potamotrygon brumi from Uruguay. This species was considered valid by subsequent authors (Buen, 1950; Ringuelet and Aramburu, 1961; Castex, 1963e, 1964b; Castex and Maciel, 1965). Castex (1966) placed P. brumi in the synonymy of P. brachyura, but the former species was still treated as valid by Ringuelet et al. (1967). The synonymy proposed by Castex (1966) is correct because all characters, proportions, and illustration in the original description of P. brumi agree with P. brachyura. The type of P. brumi was reported lost from the MNM in Montevideo (Luengo, 1966; Olazarri et al., 1970).

Diagnosis.- A species of Potamotrygon from the Paraguay and lower Paraná river drainages diagnosed by the following combination of characters: disc circular, tail usually shorter than disc, with caudal sting inserted on its basal portion, close to disc; distance from posterior margin of cloaca to insertion of caudal sting 28.0-36.0 percent of DW; disc with reticulate pattern of dark pigment on brown background.

Description.- Measurements and counts are given in Table 6. Disc circular, disc length 1.00-1.03 times DW. Posterior margin of disc convex, broadly fused with dorsal surface of pelvic fins at its inner origin. Pelvic fins usually covered dorsally by disc. Tail short, strongly tapering behind sting, with low dorsal and ventral finfolds. Caudal sting (Fig. 30) short, 1.0-1.6 times tail width, inserted on basal portion of tail, close to disc. The original description and redescriptions (Lahille, 1921; Devicenzi and Teague, 1942; Castex, 1964b) mentioned tail as shorter than disc. This true in specimens cited in present study, but none had intact tail. Longest examined tail contained 1.4 times in disc length. Castex (1966) mentioned exceptional specimens with tail equal to or longer than disc.

Eyes small, their length 2.5-5.3 in interorbital distance, 4.8-8.0 in interocular distance. Preocular distance 3.6-4.2 in DW, 1.7-2.0 times interocular distance. Spiracles wide, their length 1.8-4.0 times eye length, 2.7-3.8 in interspiracular distance. Mouth relatively small, 7.6-9.7 percent of DW, 0.9-1.2 times internarial distance; five to eight papillae on floor of buccal cavity. Preoral distance 20.5-22.8 percent of DW. Teeth large (Fig. 29) with tetragonal crowns, closely crowded in quincunx, white to brown in color, in 29/29 to 37/36 longitudinal rows, and five to eleven exposed teeth in median row of lower dental plate. Teeth sexually dimorphic, subadult and adult males with pointed teeth in one or both jaws, females with blunt teeth. Adult males show strong heterodonty in one or both jaws, with pointed teeth in median rows and blunt lateral teeth. Nostrils oblique to midline, their length 1.3-2.0 in internarial distance. Branchial basket relatively short and narrow, its greatest width 4.4-5.0 in DW, distance between first and fifth gill slits 7.2-8.5 in DW.

Median and anterior dorsal surface of disc covered with pointed denticles (Fig. 30) in adults, disc margins smooth. Denticles limited to midline in juveniles. Tail with five to eighteen relatively small middorsal spines (Fig. 30) in single row. Latero-caudal spines well-developed in adults, absent in juveniles.

Dorsal surface of disc light brown, with reticulate pattern of dark brown lines delimiting pentagonal or hexagonal spaces. Reticulated shapes decrease in size towards disc margins. Diameter of largest reticulum approximately equal to interocular distance. Reticulations more or less sharp, according to concentration of pigment in dark lines; when pigment scattered, reticulation fades and polygons tend to circular form. Dorsal color pattern described for _P. brachyura_ by Berg (1897) probably based on specimen of _P. motoro_. Tail light brown with irregular dark brown reticulations. Ventral surface white with dark pigmented disc margins and tail. Central dark spot present or absent ventrally on disc.

Geographic distribution.- Northeastern Argentina, western Brazil (Mato Grosso), central Paraguay, and western Uruguay (see Fig. 100). Found in lower Río Paraná down to Río de la Plata, in Río Uruguay below Monte Caseros, and in Río Paraguay below Cáceres. Ihering (1897) remarked that *P. brachyura* was the only species of *Potamotrygon* from Río de la Plata not represented in Amazonian waters. *Potamotrygon brachyura* is probably endemic to the Paraguay and lower Paraná river drainages. Citations of this species for the Orinoco and Amazon drainages (Castex, 1966, 1967b, 1968a) possibly represent misidentifications.

TABLE 6

MEASUREMENTS AND COUNTS ON SPECIMENS OF Potamotrygon brachyura

	NEOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	309	-	-	-	297- 858
DISC LENGTH (mm)	315	-			299- 874
DISC LENGTH (%)	101.9	11	101.7	1.0	100.2-103.4
TOTAL LENGTH (%)	157.2	1	160.3	-	-
INTERNAL DL (%)	90.6	10	91.9	1.3	90.2- 93.2
MOUTH TO SCAPULOCORACOID(%)	26.3	8	26.7	0.7	25.4- 28.0
MOUTH TO CLOACA (%)	58.7	6	62.6	2.2	58.7- 64.2
CLOACA TO STING (%)	31.6	8	30.9	2.3	28.0- 36.0
TAIL LENGTH (%)	69.2	7	55.0	11.4	48.1- 71.5
TAIL WIDTH (%)	6.8	8	7.4	0.5	6.8- 8.1
TAIL WIDTH AT STING BASE(%)	3.6	9	3.7	0.3	3.2- 4.4
TAIL HEIGHT (%)	3.9	8	4.2	0.3	3.7- 4.7
PELVIC FIN WIDTH (%)	22.5	9	22.1	1.8	19.3- 24.2
PELVIC FIN LENGTH (%)	19.2	9	19.6	1.6	17.1- 22.9
CLASPER LENGTH (%)	9.1	6	11.7	5.2	7.8- 21.7
STING LENGTH (%)	-	6	10.4	1.7	7.9- 11.9
PRECLOACAL LENGTH (%)	82.8	8	84.4	1.6	81.8- 87.3
PREORAL LENGTH (%)	23.0	8	21.9	0.8	20.5- 23.0
PRENARIAL LENGTH (%)	17.1	10	17.1	0.4	16.2- 17.9
BRANCHIAL BASKET LENGTH (%)	13.3	8	12.9	0.7	11.6- 13.8
BRANCHIAL BASKET WIDTH (%)	20.5	10	21.2	0.8	19.8- 22.3
MOUTH WIDTH (%)	9.1	8	8.6	0.6	7.6- 9.7
NOSTRIL LENGTH (%)	4.3	10	4.3	0.5	3.7- 9.3
INTERNARIAL WIDTH (%)	7.8	10	7.7	0.4	7.0- 8.5

TABLE 6

(continued)

	NEOTYPE	N	MEAN	S.D.	RANGE
EYE LENGTH (%)	2.3	11	1.9	0.4	1.1- 3.0
SPIRACLE LENGTH (%)	5.3	11	5.1	0.4	4.4- 5.5
INTEROCULAR WIDTH (%)	13.3	7	13.9	0.4	13.3-14.4
INTERSPIRACULAR WIDTH (%)	16.1	11	16.1	0.5	15.1-17.0
PREOCULAR LENGTH (%)	25.0	10	25.1	1.0	24.2-27.4
CRANIUM LENGTH (%)	21.3	6	20.9	1.0	19.1-22.2
CRANIUM WIDTH (%)	13.8	5	13.8	0.7	12.9-15.0
PREORBITAL WIDTH (%)	15.1	3	15.1	0.1	15.0-15.2
POSTORBITAL WIDTH (%)	8.0	2	7.8	-	7.6- 8.0
INTERORBITAL WIDTH (%)	7.6	10	8.1	0.5	7.5- 9.1
FONTANELLE LENGTH (%)	12.4	6	12.5	0.4	11.9-13.3
FONTANELLE WIDTH (%)	5.1	6	5.0	0.2	4.6- 5.3
UPPER DENTAL PLATE WIDTH(%)	8.1	8	7.6	0.4	6.9- 8.2
LOWER DENTAL PLATE WIDTH(%)	7.7	8	7.1	0.5	6.2- 7.7
PRECAUDAL VERTEBRAE	34	4	32	1.8	30- 34
CAUDAL VERTEBRAE	98	1	-	-	-
CAUDAL VERTEBRAE TO BASE OF STING	73	1	-	-	-
TOTAL VERTEBRAE	132	1	-	-	-
DIPLOSPONDYLOUS VERTEBRAE	21	1	-	-	-
SYNARCUAL VERTEBRAE	5	1	-	-	-
PELVIC RADIALS ♂	24	5	24.6	0.8	24- 26
PROPTERYGIAL RADIALS	49	8	49.8	0.8	49- 51
MESOPTERYGIAL RADIALS	18	8	17.8	0.8	17- 19

TABLE 6

(continued)

	NEOTYPE	N	MEAN	S.D.	RANGE
METAPTERYGIAL RADIALS	44	7	42.8	1.0	42- 44
TOTAL PECTORAL RADIALS	111	8	110.5	0.9	109-112
UPPER TOOTH ROWS	31	8	34.1	2.7	31- 37
LOWER TOOTH ROWS	29	8	32.2	2.4	29- 36
LOWER MEDIAN TEETH	-	7	8.0	2.8	5- 11
MIDDORSAL SPINES	11	5	15.0	6.5	7- 24

FIG. 27

Potamotrygon brachyura, dorsal view, male, 315 mm DL, BMNH 1879.2.12.4 (neotype).

FIG. 28

Potamotrygon brachyura, dorsal view, female, 381 mm DL, MFA (uncatalogued specimen). Photographed by G. M. Achenbach, from MFA files.

FIG. 29

Potamotrygon brachyura, A.- Exposed portions of upper and lower dental plates, female, 453 mm DL, MACN (uncatalogued specimen). B - F.- Tooth from upper jaw near symphysis, apical, basal, lateral, lingual, and labial views, female, MACN (same uncatalogued specimen). G.- Tooth from lower jaw near symphysis, apical view, female, MACN (same uncatalogued specimen).

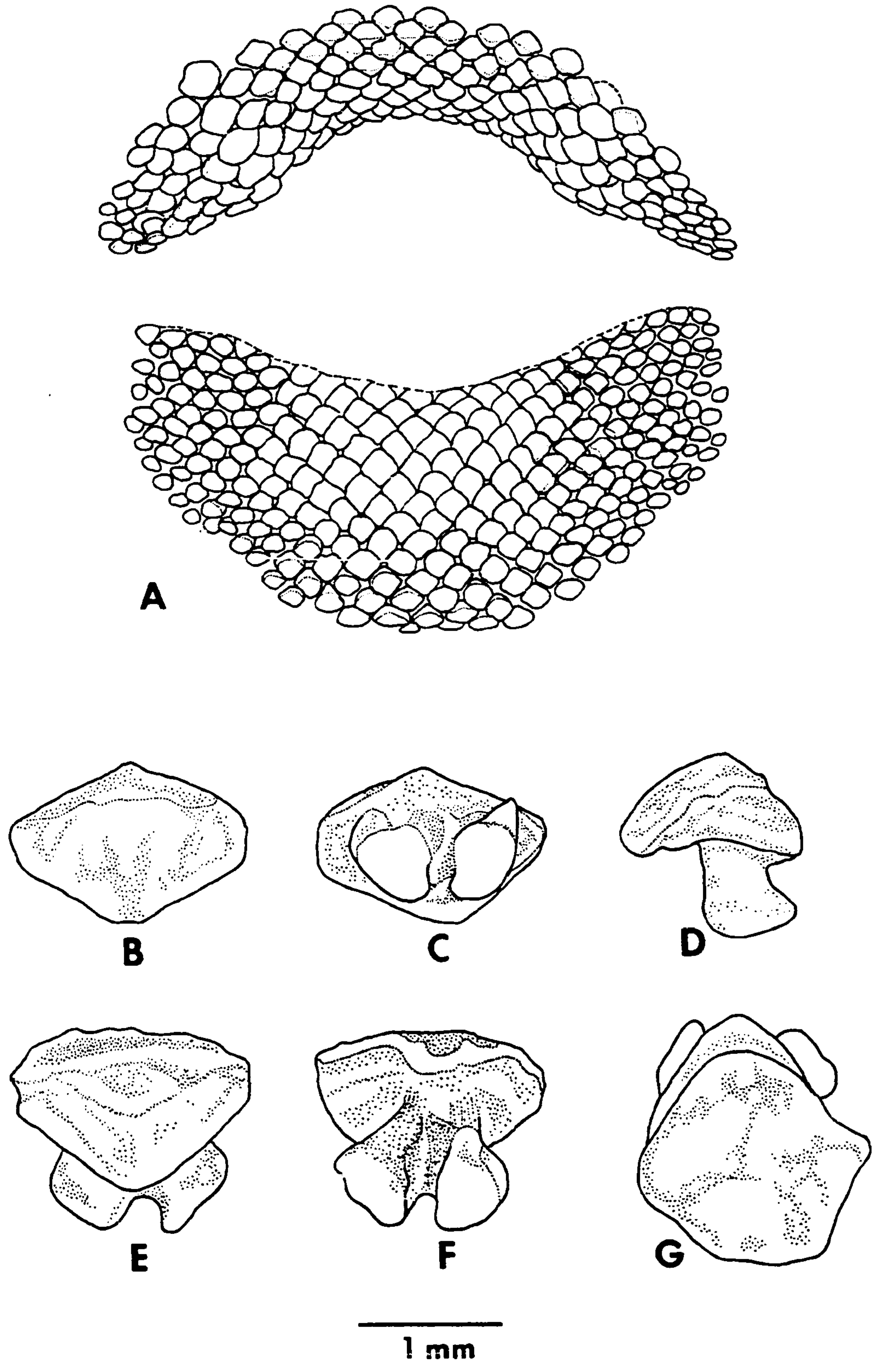
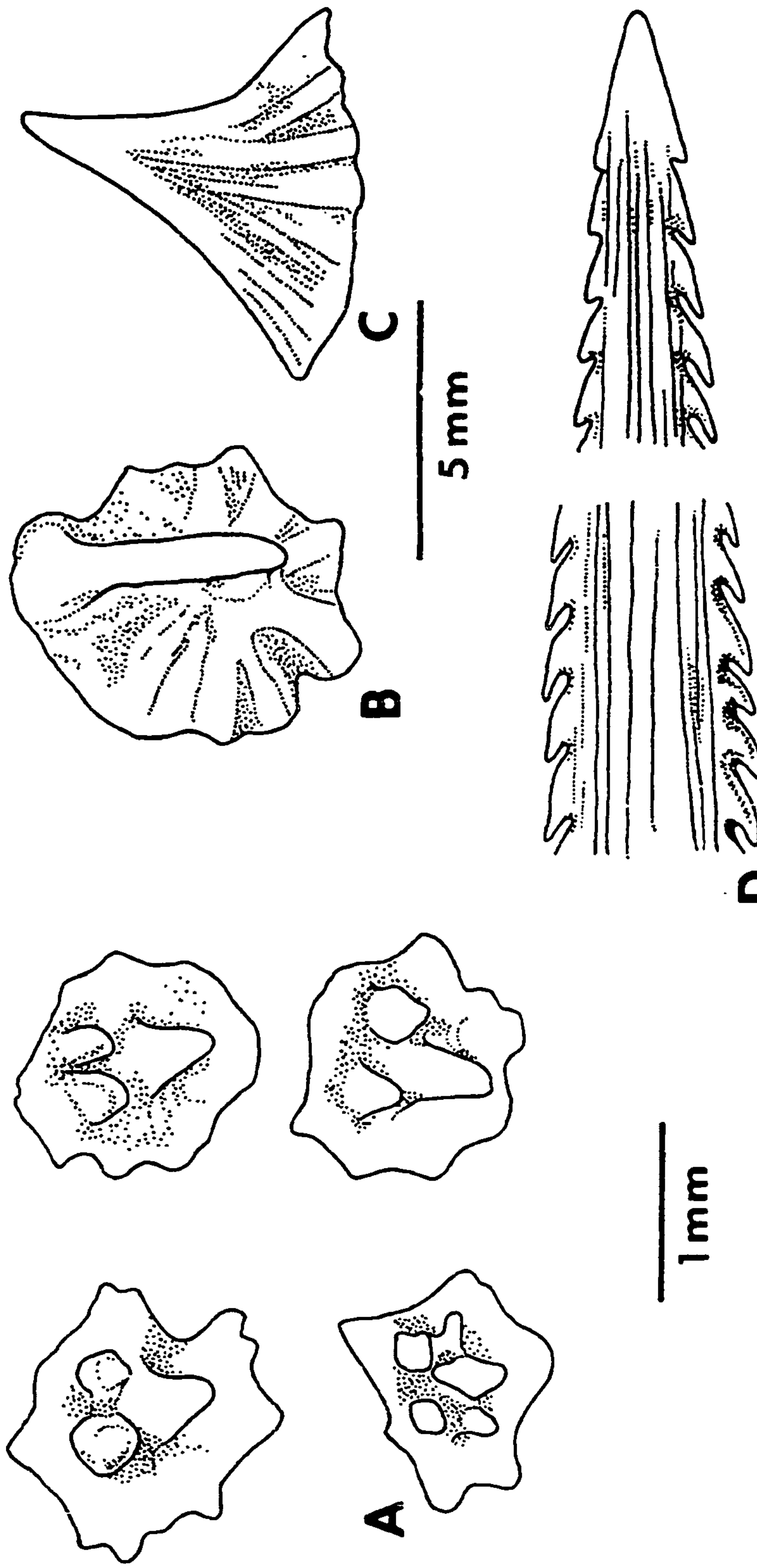

A
B
C
D
E
F
G
1 mm

FIG. 30

Potamotrygon brachyura, A.- Dermal denticles from disc near midline, apical view. B - C.- Middorsal tail spine anterior to caudal sting, apical and lateral views. D.- Intermediate and distal portions of caudal sting, dorsal views. All from female, 453 mm DL, MACN (uncatalogued specimen).


A
B
C
D
5 mm
1 mm

Potamotrygon castexi Castello & Yagolkowski, 1969

(Figs. 31-34)

Potamotrygon castexi Castello and Yagolkowski, 1969: 1-21 (original description, Rosario, Argentina).

Holotype: MACN 5777, by original designation, male, presently lost.

Type locality: Rosario, Río Paraná, Argentina.

Vernacular name: raya acordonada (Argentina).

Remarks.- The holotype dried in storage at MACN, and probably was thrown away. One paratype (ILAFIR 100), transfered to MACN was also lost (H. P. Castello, pers. comm.). The only available specimen from the type series is MFA 288. This paratype, a male from Río Colastiné Sur, Santa Fe, is in bad condition, with damaged disc margins and broken tail. The caudal sting and jaws are missing; the ventral surface was dissected, and two squares of skin removed from the dorsal surface. One additional specimen, collected by Dr. R. M. Bailey in Bolivia, was identified from a photograph and included in the original description, without type status. This specimen (UMMZ 204551) is available at the University of Michigan. The original description contained few diagnostic characters and poor photographs. Disc length, width, and total length were the only measurements given. The tooth counts given for the types are unintelligible, and could not be related to those obtained by the present method.

Diagnosis.- A species of Potamotrygon from the Paraguay, lower Paraná, and upper to mid Amazon drainages diagnosed by the following combination of characters: disc oval; dorsal surface of disc and tail brown, mottled with small yellow spots forming vermiculations or rosettes, and occasional ocelli; teeth with wider than long flat crowns, without prominent cusp except in mature males; middorsal tail spines low relative to basal diameter, in irregular parallel rows; yellow spots on disc usually less than eye in diameter, smaller than in P. falkneri, and larger than in P. magdalenae.

Description.- Measurements and counts are given in Table 7. Disc subcircular to oval, disc length 1.05-1.13 times DW. Posterior margins of pelvic fins dorsally exposed behind disc margin. Tail relatively short, its length in adults 0.9-1.1 times DW, with well-developed dorsal and ventral finfolds. Length of ventral finfold 31.4-53.0 ($\bar{x}$=43.3) percent of DW. One or two relatively long caudal stings, sting length 1.5-2.5 times tail width.

Eyes relatively large, their length 2.0-3.9 in interorbital distance, 3.7-7.2 in interocular distance. Spiracles relatively small, their length 1.0-2.6 times eye length, 2.2-4.6 in interspiracular distance. Mouth relatively large, 8.5-

10.8 percent of DW, 1.0-1.2 times internarial distance. Five (occasionally six) papillae on floor of buccal cavity. Teeth white (Fig. 32), with blunt rhombic crowns, wider than long, without prominent cusps except in mature males. Teeth crowded in quincunx, in 27/27 to 54/59 longitudinal rows, and five to twelve exposed teeth in median row of lower dental plate. Teeth sexually dimorphic (Fig. 33), mature males (larger than 270 mm DW) with pointed teeth in median rows of upper jaw, females with blunt teeth. Nostrils oblique to midline, their length 1.1-1.7 in internarial distance. Branchial basket relatively narrow, its greatest width 5.4-7.6 in DW, distance between first and fifth gill slits 3.6-4.2 in DW.

Dorsal surface of disc covered with denticles (Fig. 34), more devloped on midline, and on anterior disc margins of adult females. Tail with 16 to 57 relatively low middorsal spines (Fig. 34), with nearly circular base, in irregular parallel rows. Latero-caudal spines moderately developed in adults, near insertion of sting.

Dorsal surface of disc light brown to dark brown, with many circular to reniform yellow spots, usually smaller than eye in diameter, fused in labyrinthic patterns, or forming rosettes in large specimens. Some submarginal yellow spots brightly colored and encircled by dark pigment forming ocelli. Some scattered small black spots occasionally on disc. Dorsal surface of tail and pelvic fins with color pattern similar to disc. Ventral surface of disc white with gray margins, usually with dark central spot. Tail and posterior margin of pelvic fins grayish ventrally, with irregular white spots. Tentatively identified young specimen light brown dorsally, with dark reticulate pattern, lacking conspicuous yellow spots.

Geographic distribution.- Northeastern Argentina, central Paraguay, eastern Bolivia and Peru, and western Brazil (see Fig. 100). Found in lower Paraná, Paraguay and Guaporé rivers, and in the upper Amazon drainage, from Peru to Rio Solimões. Examination of a photograph taken by R. M. Correa de Castro (formerly at MZUSP) suggests the presence of _P. castexi_ in Rio Trombetas, Brazil, possibly extending its range to the lower Amazon drainage.

Biological remarks.- _Potamotrygon castexi_ is sympatric in the southern portion of its range (lower Paraná and Paraguay rivers) with _P. falkneri_. Some specimens from Río Paraná (MFA 236, MFA 279, and two uncatalogued specimens at MFA) have intermediate color patterns between species, suggesting their possible hybridization. Besides _P. falkneri_, the species _P. scobina_ and _P. signata_ show many morphological characters similar to _P. castexi_, including dentition, shape and distribution of tail spines, and coloration. Although they were not phylogenetically analyzed, these four species seem to form a species group.

TABLE 7

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Potamotrygon castexi*

	PARATYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	345	17	-	-	141.0-550
DISC LENGTH (mm)	390	17	-	-	150 -630
DISC LENGTH (%)	113.0	17	108.4	3.0	104.1-114.5
TOTAL LENGTH (%)	-	6	201.2	10.4	194.1-218.0
INTERNAL DL (%)	-	14	95.8	9.7	92.0-100.9
MOUTH TO SCAPULOCORACOID (%)	-	13	30.5	1.2	27.6- 33.2
MOUTH TO CLOACA (%)	-	15	65.7	3.0	60.6- 70.8
CLOACA TO STING (%)	-	11	56.4	3.9	50.1- 66.3
TAIL LENGTH (%)	-	7	101.6	7.5	91.4-111.7
TAIL WIDTH (%)	11.3	16	11.0	1.3	9.8- 15.0
TAIL WIDTH AT STING BASE(%)	5.8	14	5.3	0.7	4.3- 7.2
TAIL HEIGHT (%)	6.8	16	6.9	0.7	5.6- 8.1
PELVIC FIN WIDTH (%)	22.0	15	28.0	2.8	22.0- 32.1
PELVIC FIN LENGTH (%)	23.7	14	24.8	2.3	21.9- 28.4
CLASPER LENGTH (%)	29.6	13	22.6	5.4	10.7- 29.6
STING LENGTH (%)	-	14	23.3	3.6	19.1- 34.6
PRECLOACAL LENGTH (%)	93.3	16	89.9	2.5	85.9- 93.6
PREORAL LENGTH (%)	-	13	23.9	1.1	22.2- 25.4
PRENARIAL LENGTH (%)	13.9	14	17.9	1.5	13.9- 19.9
BRANCHIAL BASKET LENGTH(%)	18.5	16	14.9	1.2	13.1- 18.5
BRANCHIAL BASKET WIDTH (%)	26.7	15	25.3	1.0	23.8- 27.2
MOUTH WIDTH (%)	-	15	9.1	0.7	7.8- 10.8

TABLE 7

(continued)

	PARATYPE	N	MEAN	S.D.	RANGE
NOSTRIL LENGTH (%)	6.8	9	5.5	0.6	4.8- 6.8
INTERNARIAL WIDTH (%)	7.9	16	8.1	0.5	7.4- 9.5
EYE LENGTH (%)	3.3	17	3.2	0.7	2.4- 4.7
SPIRACLE LENGTH (%)	8.6	16	5.5	1.2	3.9- 8.6
INTEROCULAR WIDTH (%)	-	12	17.2	0.9	15.8-18.9
INTERSPIRACULAR WIDTH (%)	19.0	16	18.3	1.1	15.1-19.6
PREOCULAR LENGTH (%)	-	14	27.9	1.6	25.2-30.4
CRANIUM LENGTH (%)	-	3	26.6	-	24.8-28.2
CRANIUM WIDTH (%)	-	3	17.4	-	15.6-19.5
PREORBITAL WIDTH (%)	-	4	18.2	2.5	16.5-22.0
POSTORBITAL WIDTH (%)	-	1	9.7	-	-
INTERORBITAL WIDTH (%)	8.9	16	9.2	0.6	8.3-10.8
FONTANELLE LENGTH (%)	-	4	16.9	0.8	15.8-17.7
FONTANELLE WIDTH (%)	-	3	7.4	-	6.5- 8.2
UPPER DENTAL PLATE WIDTH(%)	-	13	7.8	0.6	6.9- 8.9
LOWER DENTAL PLATE WIDTH(%)	-	12	7.3	0.5	6.6- 8.3
PRECAUDAL VERTEBRAE	-	4	25.2	1.7	
CAUDAL VERTEBRAE	-	2	100.5	-	100- 101
CAUDAL VERTEBRAE TO BASE OF STING	-	3	79.0	-	76- 81
TOTAL VERTEBRAE	-	2	125.5	-	123- 128
DIPLOSPONDYLOUS VERTEBRAE	-	-	-	-	-
SYNARCUAL VERTEBRAE	-	1	2.0	-	-

TABLE 7

(continued)

		PARATYPE	N	MEAN	S.D.	RANGE
PELVIC RADIALS	♂	-	2	20.5	-	20- 21
	♀	-	2	24.5	-	24- 25
PROPTERYGIAL RADIALS		-	4	43.0	3.5	40- 48
MESOPTERYGIAL RADIALS		-	4	11.7	0.5	11- 12
METAPTERYGIAL RADIALS		-	4	32.7	3.5	31- 38
TOTAL PECTORAL RADIALS		-	4	87.5	5.3	82- 93
UPPER TOOTH ROWS		-	15	43.4	7.7	27- 54
LOWER TOOTH ROWS		-	15	42.6	8.7	27- 59
LOWER MEDIAN TEETH		-	13	6.8	1.7	5- 12
MIDDORSAL SPINES		-	13	33.3	15.4	16- 57

FIG. 31

Potamotrygon castexi, dorsal view, female, 300 mm DL, LACM 39934-1. Courtesy of Camm C. Swift (LACM).

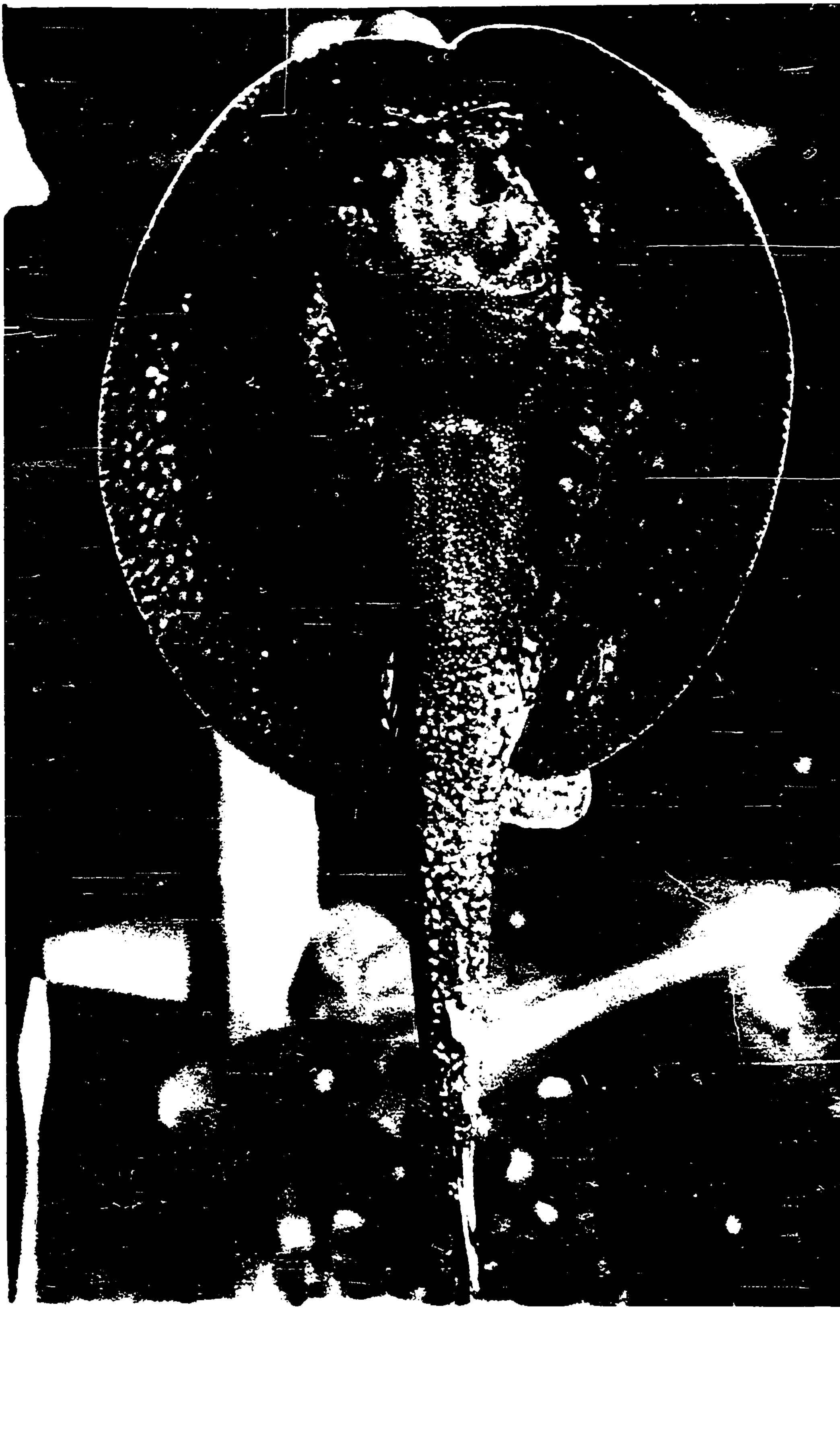


FIG. 32

Potamotrygon castexi, A.- Exposed portions of upper and lower dental plates, male, 396 mm DL, ANSP 142484. B.- Idem, female, 420 mm DL, ANSP 142487.

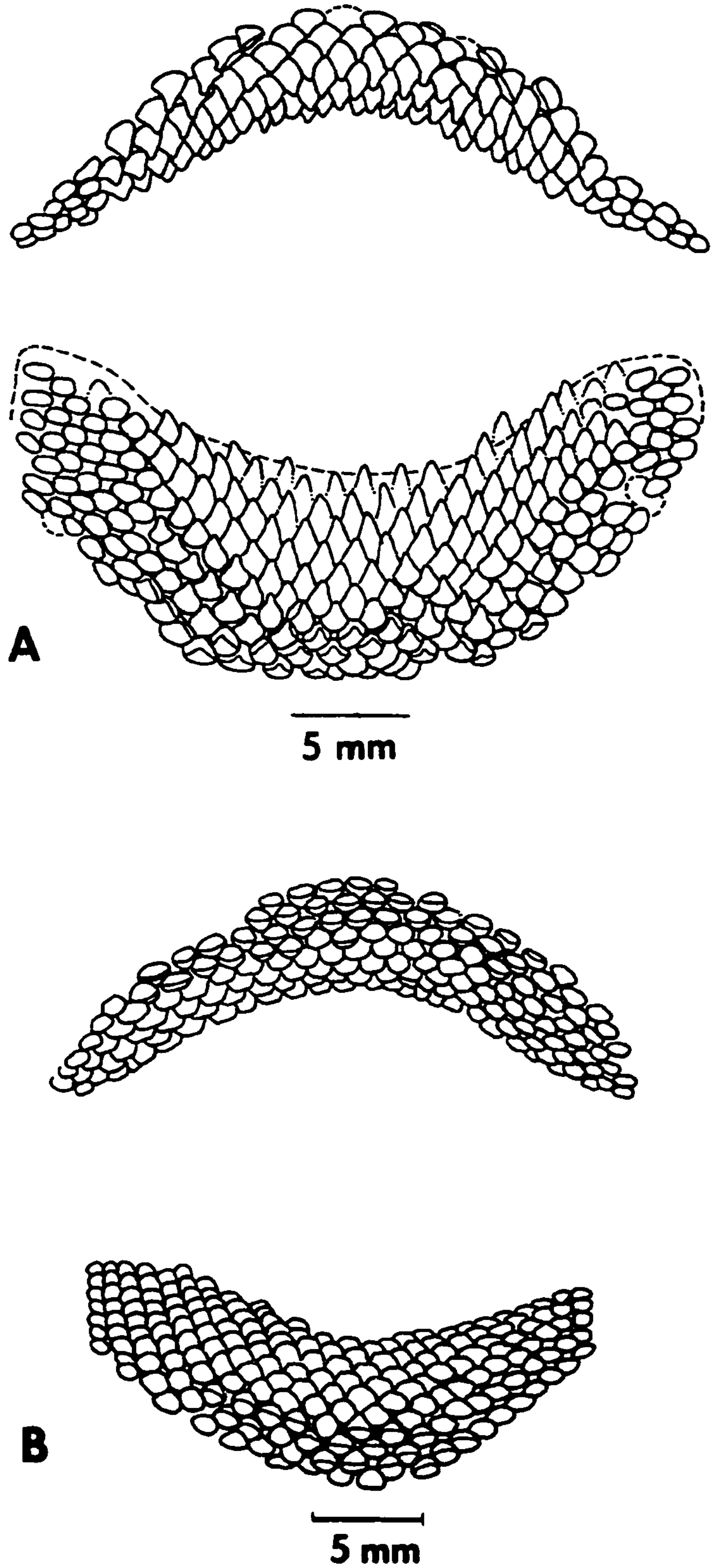

A
5 mm
B
5 mm

FIG. 33

Potamotrygon castexi, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, lingual, and labial views, male, 414 mm DL, ANSP 142486. F.- Tooth from upper jaw near mouth corner, apical view, ANSP 142486. G - K.- Tooth from upper jaw near symphysis, apical, basal, lateral, lingual, and labial views, female, 399 mm DL, UMMZ 204551. I.- Tooth from upper jaw near mouth corner, apical view, UMMZ 204551.

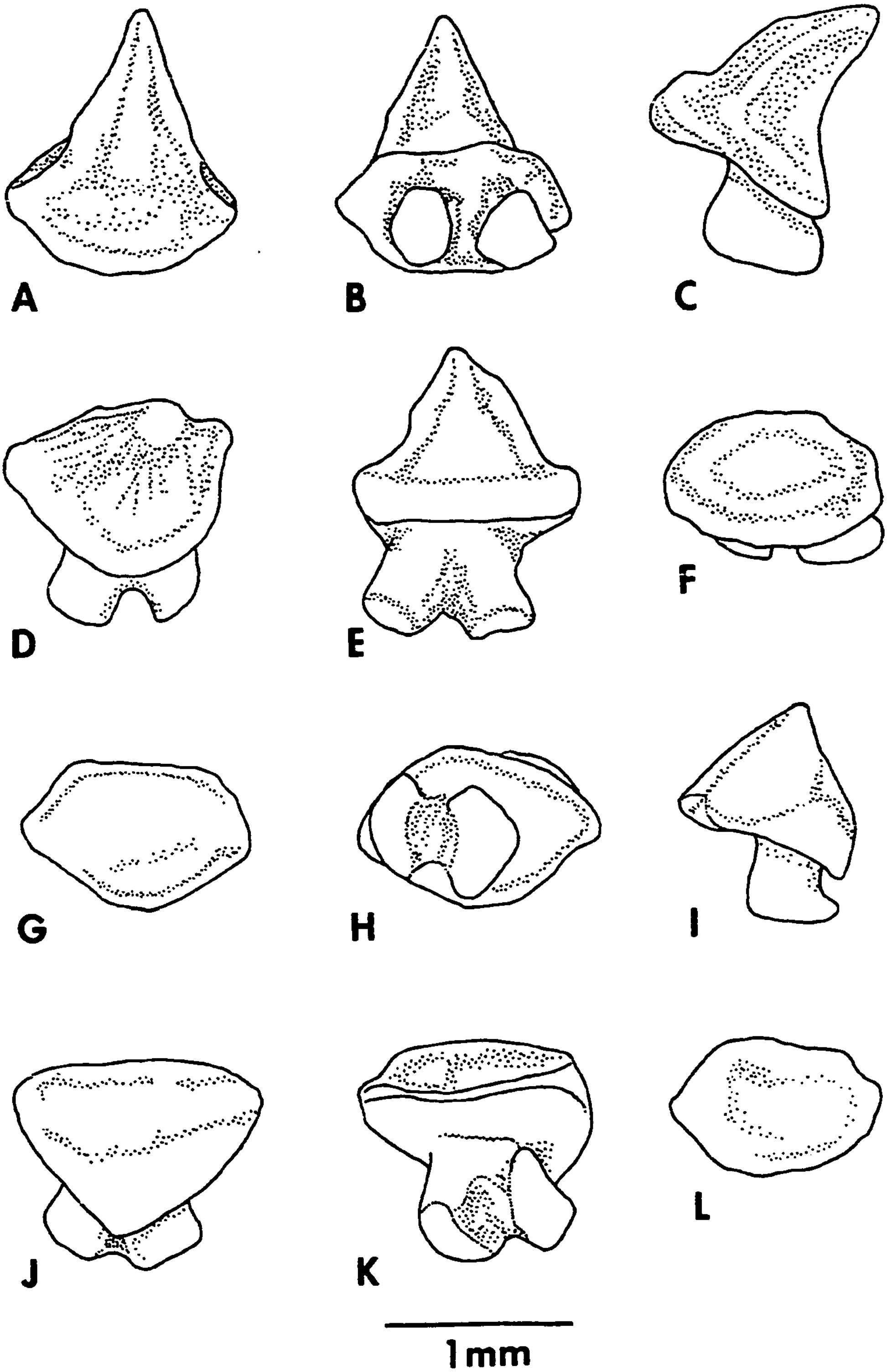
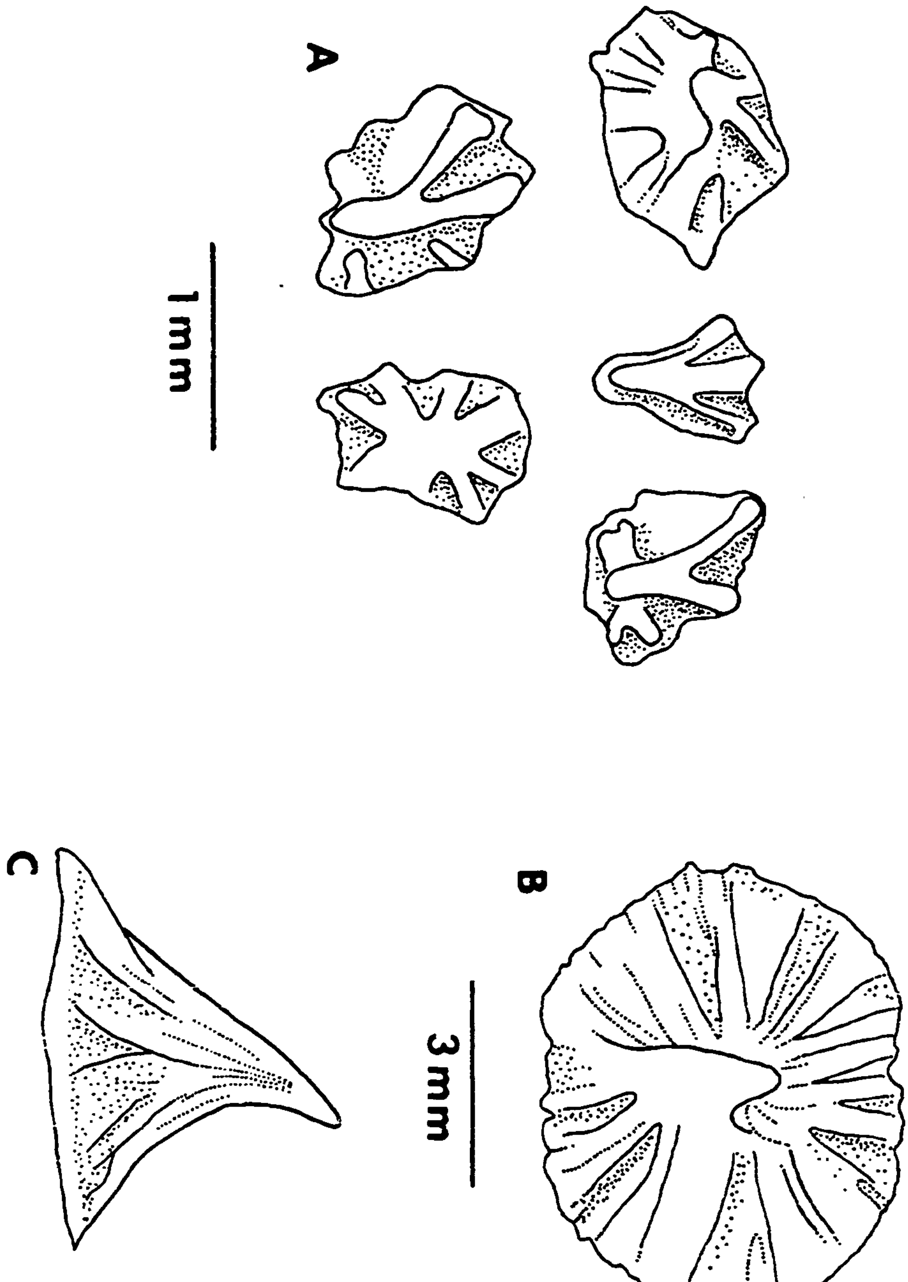

A
B
C
D
E
F
G
H
I
J
K
L
1mm

FIG. 34

Potamotrygon castexi, A.- Dermal denticles from disc near midline, apical view. B - C.- Middorsal tail spine anterior to caudal sting, apical and lateral views. All from female, 376 mm DL, UFPB 1473.


A
1 mm
B
C
3 mm

Potamotrygon constellata (Vaillant, 1880)

(Figs. 35-39)

Taeniura constellata Vaillant, 1880: 251 (original description, Calderón, not illustrated).

Potamotrygon circularis [in part] Garman, 1913: 419, plate 31, figs. 1-2 (original description, Teffé). NEW SYNONYMY.

Paratrygon circularis. Fowler, 1948: 5.

Lectotype: MNHN A.1010, by selection of Bertin (1939a), female, coll. Jobert.

Paralectotypes: MNHN A.1005, male; MNHN A.1006, male; MNHN A.1007, female.

Type locality: Calderão, Amazonas, Brazil.

Remarks.- The original description of T. constellata has been overlooked by all subsequent authors, including Garman, who described the junior synonym P. circularis. The type series of P. constellata, consisting of one lectotype and three paralectotypes, is in good condition, and can be identified with part of the type series of P. circularis. The lectotype has the tail and the caudal sting distally broken, and a bite scar on the right margin of the disc.

Garman's type series of P. circularis consisted of heterogenous material, from which one male (MCZ 291-S) can be identified with P. constellata, one male and one female (both MCZ 295-S) with P. motoro, and one dissected specimen (MCZ 296-S) cannot be identified to the specific level.

Diagnosis.- A species of Potamotrygon from the mid Amazon drainage diagnosed by the following combination of characters: disc oval, dorsal surface of disc brown to grayish-brown, irregularly spotted with white, occasionally with broken reticulate pattern of dark pigment; submarginal series of flattened tubercles usually present on disc; teeth relatively small and cuspidate, in 29 to 44 rows in upper jaw.

Description.- Measurements and counts are given in Table 8. Disc oval, disc length 1.04-1.14 times DW. Pelvic fins dorsally covered by disc. Tail broad and depressed at base, distally with low dorsal and ventral finfolds. No specimens with intact tails available for study; longest measured tail nearly equal to DW. Caudal sting (Figs. 37, 38) relatively long, its length 1.8-2.7 times tail width.

Eyes relatively large, eye length 2.2-3.1 in interorbital distance, 5.4-7.3 in interocular distance. Spiracles relatively large, their length 2.6-3.8 times eye length, 1.8-2.2 in interspiracular distance. Mouth relatively large and curved, with five papillae at bottom; mouth width 1.1-1.6 times internarial distance. Teeth relatively small (Fig. 38), loosely set in quincunx, in 29/28 to 44/43 longitudinal rows, and three to ten exposed in median row of lower dental plate. Tooth crowns slightly concave anteriorly, tricuspidate posteriorly. Teeth sexually dimorphic (Fig. 39), males with enlarged and pointed central cusp. No apparent monognathic heterodonty in males or females. Nostril length 1.1-1.5 in internarial distance. Branchial basket relatively wide, its greatest width 3.3-4.5 in DW, distance between first and fifth gill slits 4.8-6.0 in DW.

Dorsal surface of disc rough, covered with sharp denticles (Fig. 38), more developed on midline. Disc usually with submarginal series of enlarged and flat tubercles of various sizes (Fig. 38), larger than eye in diameter. Tubercles occasionally fused in pairs or larger groups. One paramedial pair of tubercles (or grouped tubercles) occasionally on scapular region. Tail with 12 to 37 enlarged middorsal spines (Fig. 38) in single row. Latero-caudal spines well-developed from tail base to distal portion.

Dorsal surface of disc brown to dark grayish-brown, marginally with irregular white spots. Lighter specimens occasionally with broken reticulate pattern of dark pigment. Ventral surface of disc usually dark brown, with white buccal and branchial regions. Tail dark brown, with alternate white and dark lateral bars.

Geographic distribution.- _Potamotrygon_ _constellata_ is known from the mid Amazon drainage, in Rio Solimões, Brazil, from the border with Colombia down to Manaus (see Fig. 100).

Thorson, Langhammer and Oetinger (1983) reported specimens (as *P. circularis*) from Río Arara in southern Colombia.

Additional references: Castex, 1964b (redescription, as *P. circularis*); Mayes et al., 1978 (intestinal parasites, as *P. circularis*); Thorson, Langhammer and Oetinger, 1983 (reproduction and development, as *P. circularis*).

TABLE 8

MEASUREMENTS AND COUNTS ON SPECIMENS OF Potamotrygon constellata

	HOLOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	281.	7	-	-	281- 432
DISC LENGTH (mm)	295	7	-	-	295- 479
DISC LENGTH (%)	104.9	7	110.1	3.3	104.9-114.3
TOTAL LENGTH (%)	186.1	2	180.1	-	174.1-186.1
INTERNAL DL (%)	92.5	7	94.7	3.1	92.5-101.3
MOUTH TO SCAPULOCORACOID(%)	31.1	7	33.2	2.8	29.7- 38.5
MOUTH TO CLOACA (%)	66.1	7	68.5	3.3	66.1- 72.9
CLOACA TO STING (%)	49.4	6	55.1	3.8	49.4- 59.7
TAIL LENGTH (%)	94.6*	1	-	-	-
TAIL WIDTH (%)	10.2	7	11.1	1.0	9.5- 12.4
TAIL WIDTH AT STING BASE(%)	4.5	6	5.0	0.3	4.5- 5.4
TAIL HEIGHT (%)	5.0	7	6.8	1.0	5.0- 7.9
PELVIC FIN WIDTH (%)	32.8	6	31.2	1.8	28.7- 33.7
PELVIC FIN LENGTH (%)	20.2	6	24.5	2.6	20.2- 27.3
CLASPER LENGTH (%)	-	5	24.9	3.8	19.3- 29.5
STING LENGTH (%)	27.7	4	24.5	2.7	21.0- 27.7
PRECLOACAL LENGTH (%)	85.7	5	87.8	1.7	85.7- 90.2
PREORAL LENGTH (%)	20.4	7	20.4	0.6	19.5- 21.4
PRENARIAL LENGTH (%)	13.5	7	15.1	1.0	13.5- 16.9
BRANCHIAL BASKET LENGTH(%)	16.4	7	17.8	1.5	16.4- 20.8
BRANCHIAL BASKET WIDTH(%)	22.5	7	26.3	3.4	22.0- 30.3

*Tail broken on holotype.

TABLE 8

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
MOUTH WIDTH (%)	8.3	7	9.3	1.0	8.3- 11.0
NOSTRIL LENGTH (%)	4.6	7	5.4	0.6	4.6- 6.3
INTERNARIAL WIDTH (%)	6.5	6	7.1	0.5	6.5- 7.9
EYE LENGTH (%)	3.0	6	2.6	0.3	2.2- 3.1
SPIRACLE LENGTH (%)	7.8	7	8.4	0.3	7.8- 8.9
INTEROCULAR WIDTH (%)	16.4	6	17.6	1.3	16.1- 19.4
INTERSPIRACULAR WIDTH (%)	15.1	7	17.1	1.6	15.1- 19.9
PREOCULAR LENGTH (%)	26.3	6	26.4	0.7	25.6- 27.5
CRANIUM LENGTH (%)	25.2	2	24.9	-	24.7- 25.2
CRANIUM WIDTH (%)	14.1	2	13.7	-	13.3- 14.1
PREORBITAL WIDTH (%)	17.5	2	16,8	-	16.1- 17.5
POSTORBITAL WIDTH (%)	8.1	2	7.6	-	7.2- 8.1
INTERORBITAL WIDTH (%)	6.8	7	7.5	0.7	6.7- 8.5
FONTANELLE LENGTH (%)	15.1	2	15.2	-	15.1- 15.4
FONTANELLE WIDTH (%)	5.8	2	5.6	-	5.4- 5.8
UPPER DENTAL PLATE WIDTH(%)	6.8	7	6.3	1.1	4.1- 7.3
LOWER DENTAL PLATE WIDTH(%)	5.2	7	5.5	1.0	3.7- 6.9
PRECAUDAL VERTEBRAE	30	2	28.5	-	27- 30
CAUDAL VERTEBRAE	99	2	98.5	-	98- 99
CAUDAL VERTEBRAE TO BASE OF STING	75	2	79.5	-	75- 84
TOTAL VERTEBRAE	129	2	127.0	-	125- 129
DIPLOSPONDYLOUS VERTEBRAE	10	1	-	-	-
SYNARCUAL VERTEBRAE	4	2	3.5	-	3- 4

TABLE 8

(continued)

		HOLOTYPE	N	MEAN	S.D.	RANGE
PELVIC RADIALS	♂	-	2	20.5	-	20- 21
	♀	27	1	-	-	-
PROPTERYGIAL RADIALS		42	3	44.3	-	42- 46
MESOPTERYGIAL RADIALS		15	3	15.0	-	-
METAPTERYGIAL RADIALS		38	3	36.3	-	35- 38
TOTAL PECTORAL RADIALS		95	3	95.6	-	95- 97
UPPER TOOTH ROWS		29	6	40.5	5.7	29- 44
LOWER TOOTH ROWS		28	6	36.5	5.3	28- 43
LOWER MEDIAN TEETH		6	5	6.4	2.5	3- 10
MIDDORSAL SPINES		12	7	23.7	10.8	12- 37

FIG. 35

Potamotrygon constellata, dorsal view, female, 295 mm DL, MNHN A.1010 (lectotype).

FIG. 36

Potamotrygon constellata, dorsal view, male, 438 mm DL, MCZ 291-S (syntype of *Potamotrygon circularis*).

FIG. 37

Potamotrygon constellata, A.- Tail spines, lateral view, female, 295 mm DL, MNHN A.1010 (lectotype). B.- Tail spines, dorsal view, male, 438 mm DL, MCZ 291-S (syntype of Potamotrygon circularis). C - D.- Triple caudal stings, lateral and dorsal views, TBT (uncatalogued specimen, not seen by the author).

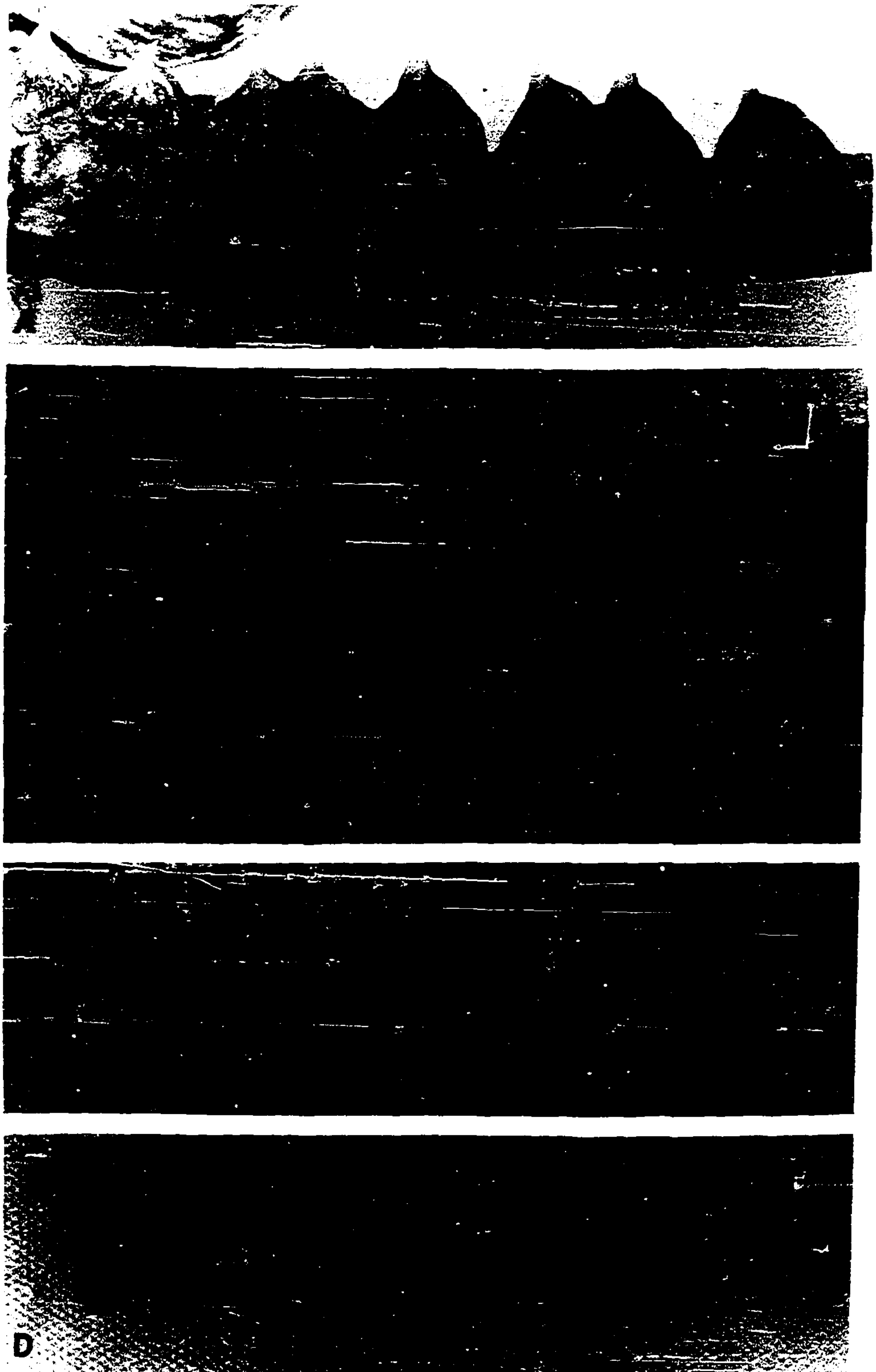

D

FIG. 38

Potamotrygon constellata, A - B.- Exposed portions of upper and lower dental plates, male, 438 mm DL, MCZ 291-S (syntype of Potamotrygon circularis). C.- Dermal denticles from disc near midline, MCZ 291-S. D.- Idem, male, 479 mm DL, MNHN A.1005 (paralectotype). E.- Submarginal tubercles from disc, apical view, MCZ 291-S. H - I.- Intermediate and distal portions of caudal sting, dorsal views, MCZ 291-S.

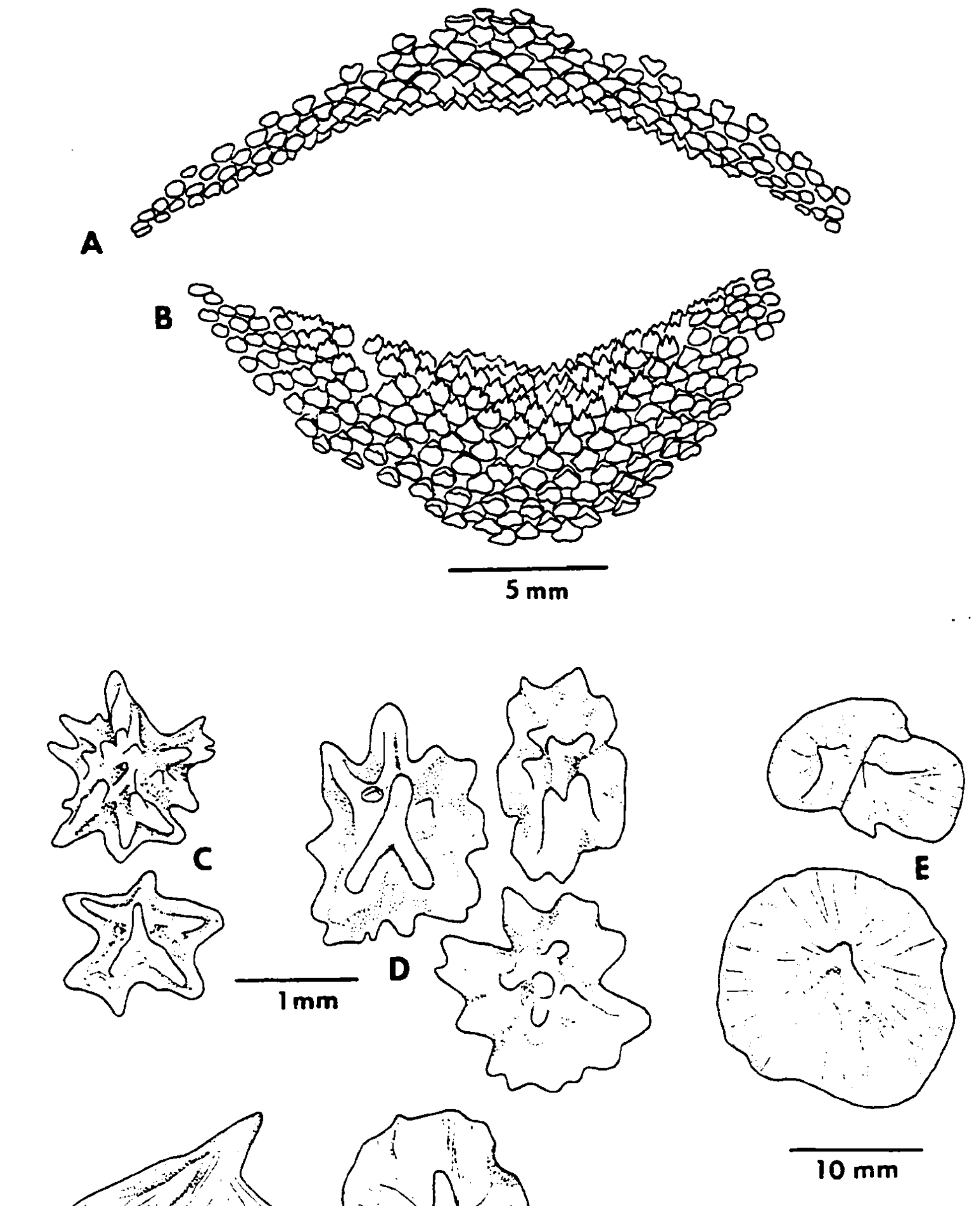
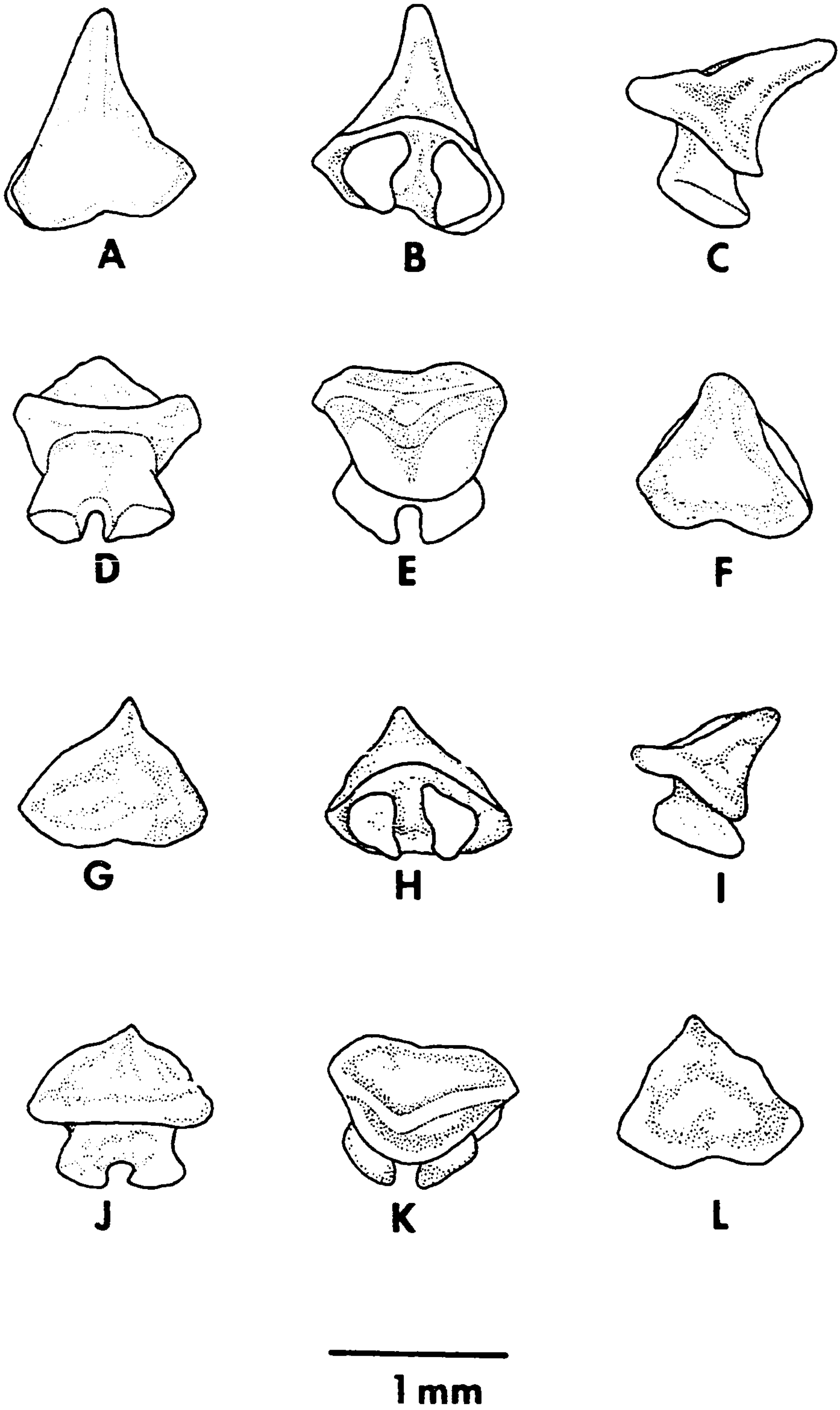

A
B
5 mm
C
D
1 mm
E
10 mm
H
I
F
10 mm
G

FIG. 39

Potamotrygon constellata, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, male, 400 mm DL, MNHN A.1006 (paralectotype). F.- Tooth from lower jaw near mouth corner, apical view, MNHN A.1006. G - K.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, male, 438 mm DL, MCZ 291-S (syntype of Potamotrygon circularis). L.- Tooth from lower jaw near symphysis, apical view, MCZ 291-S.


A
B
C
D
E
F
G
H
I
J
K
L
1 mm

Potamotrygon dumerilii (Castelnau, 1855)

(Figs. 40-44)

Trygon (Taenura) dumerilii Castelnau, 1855: 101 (original description, Rio Araguaia, Brazil).

Taenura dumerilii Castelnau, 1855, plate 48 (original illustration).

Taeniura dumerilii. Duméril, 1865: 622.

Potamotrygon dumerilii. Garman, 1877: 213.

Ellipesurus dumerilii. Ribeiro, 1907: 186.

Paratrygon dumerilii. Fowler, 1948: 8.

[non] Taeniura motoro. Günther, 1870: 484.

[non] Ellipesurus spinicauda. Garman, 1877: 213.

[non] Taeniura mülleri. Eigenmann and Eigenmann, 1891: 25.

[non] Taeniura henlei. Eigenmann and Eigenmann, 1891: 25.

[non] Potamotrygon motoro. Garman, 1913: 423.

[non] Paratrygon motoro. Fowler, 1948: 8.

Holotype: MNHN 2367, by original indication, female, coll. F. de Castelnau.

Type locality: Rio Araguaia, Brazil.

Remarks.- Holotype (Fig. 40) only partially preserved, retaining the dorsal skin, eyes, jaws, and tail, lacking the caudal sting; a square of skin has been removed from the dorsal surface. No accurate measurements could be taken on the holotype. Color pattern and dentition are diagnostic for the holotype. The original illustration misrepresented the dorsal color pattern, and exaggerated the size of the latero-caudal spines. Duméril (1865) mentioned that the actual color pattern of _P. dumerilii_ was clearly distinct from those of species with ocellated patterns.

Günther (1870) cited _P. dumerilii_ as a synonym of _P. motoro_ (an ocellated species), and was followed by several subsequent authors (Ribeiro, 1907; Garman, 1913; Bertin, 1939; Fowler, 1948, 1970; Buen, 1950). Ribeiro (1907, 1923) considered that _P. dumerilii_ possibly represented the adult color morph of _P. motoro_. Other authors (Eigenmann and Eigenmann, 1891; Bertoni, 1914; Castex, 1964b) recognized the independent status of _P. dumerilii_. Castex (1964b) remarked that, based on the original illustration of _P. dumerilii_, it was impossible to associate this species with _P. motoro_. Altough the original illustration was inaccurate, examination of the holotype confirmed that the two species are distinct in coloration. Other characters that differentiate _P. dumerilii_ from _P. motoro_ are the relatively smaller mouth and teeth of the former species.

Castex (1964b, 1965a) misidentified one specimen of _P. dumerilii_ [MFA 268, not MFA 218 (sic)] as _P. histrix_, and subsequently (Castex, 1969a) selected it as an allotype for the latter species. A second specimen of _P. dumerilii_ (MFA 328) was similarly misidentified by Castex (1969a).

Diagnosis.- A species of _Potamotrygon_ from Araguaia and lower Paraná river drainages diagnosed by the following combination of characters: disc light brown dorsally, with broken reticulate pattern of dark lines delimiting yellow triangular figures; teeth small, loosely set in quincunx, with prominent central cusp and small accessory cusps.

Description.- Measurements and counts are given in Table 9. Disc oval, disc length 1.06-1.13 times DW. Pelvic fins dorsally covered by disc. Tail broken in all available specimens, shorter than disc length. Caudal sting relatively large, its length 2.1-2.4 times tail width. Eyes relatively large, their length 2.4-2.9 in interorbital distance, 5.6-5.9 in interocular distance. Spiracles relatively small, their length 2.1-2.5 times eye length, 2.1-2.5 in interspiracular distance. Mouth relatively small, its width 7.6-8.3 percent of DW, and nearly equal to internarial distance. Five slender papillae at bottom of buccal cavity. Teeth relatively small (Fig. 42), white to caramel in color, loosely set in quincunx, in 36/28 to 37/37 longitudinal rows, and five to seven exposed teeth in median row of lower dental plate. Tooth crowns (Fig. 43) with concave anterior margin, a central cusp and two small accessory cusps on posterior margin. Central cusp triangular and pointed in males, less developed in females. Monognathic heterodonty in lower jaw of male, with pointed median teeth and blunt lateral teeth. Nostril length 1.3 in internarial distance. Branchial basket relatively broad, its greatest width 3.6-4.0 in DW, distance between first and fifth gill slits 5.7 in DW.

Disc dorsally covered with denticles (Fig. 44), more developed on midline. Tail with 29 to 33 middorsal spines in one irregular row (Fig. 44). Latero-caudal spines moderately developed from tail base to caudal sting.

Dorsal surface of disc light brown, with broken reticulate pattern of dark lines, delimiting nearly triangular yellow figures ("moñitos" of Castex, 1964b). Ventral surface white with brown margins, or entirely dark pigmented. Central dark spot usually present ventrally on disc. Tail light brown dorsally and ventrally, with irregular white and yellow spots.

Geographic distribution.- Potamotrygon dumerilii is known from the type locality (Rio Araguaia, Brazil), and from lower Paraná and Paraguay rivers (see Fig. 100).

Additional references: Bertoni, 1914 (citation for Paraguay); Boulenger, 1896 (citation for Paraguay, as Taeniura dumerilii); Eigenmann, 1907, 1910 (citations for Paraguay).

TABLE 9

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Potamotrygon dumerilii*

	HOLOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	307	-	-	-	285- 307
DISC LENGTH (mm)	347	3	-	-	306- 347
DISC LENGTH (%)	113.0	3	109.6	3.4	106.1-113.0
TOTAL LENGTH (%)	-	-	-	-	-
INTERNAL DL (%)	-	2	88.6	-	81.4- 95.8
MOUTH TO SCAPULOCORACOID(%)	-	2	33.0	-	32.7- 33.4
MOUTH TO CLOACA (%)	-	2	72.1	-	69.6- 74.7
CLOACA TO STING (%)	-	2	51.5	-	50.8- 52.2
TAIL LENGTH (%)	-	-	-	-	-
TAIL WIDTH (%)	13.2	3	11.8	1.2	10.9- 13.2
TAIL WIDTH AT STING BASE(%)	5.6	3	5.2	0.4	4.7- 5.6
TAIL HEIGHT (%)	-	2	6.1	-	5.9- 6.3
PELVIC FIN WIDTH (%)	-	2	28.4	-	25.7- 31.2
PELVIC FIN LENGTH (%)	-	2	22.5	-	21.8- 23.3
CLASPER LENGTH (%)	-	2	24.7	-	24.3- 25.2
STING LENGTH (%)	-	2	25.3	-	24.3- 26.4
PRECLOACAL LENGTH (%)	-	2	90.1	-	88.8- 91.5
PREORAL LENGTH (%)	-	2	19.8	-	19.5- 20.1
PRENARIAL LENGTH (%)	-	2	14.1	-	13.9- 14.3
BRANCHIAL BASKET LENGTH(%)	-	2	18.1	-	17.4- 18.8
BRANCHIAL BASKET WIDTH (%)	-	2	25.2	-	24.9- 25.6
MOUTH WIDTH (%)	7.6	3	8.0	0.4	7.6- 8.3

TABLE 9

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
NOSTRIL LENGTH (%)	-	2	6.1	-	6.0- 6.2
INTERNARIAL WIDTH (%)	-	2	7.6	-	7.4- 7.8
EYE LENGTH (%)	-	2	3.3	-	3.2- 3.5
SPIRACLE LENGTH (%)	-	2	7.9	-	6.8- 9.0
INTEROCULAR WIDTH (%)	-	2	19.5	-	19.1- 19.9
INTERSPIRACULAR WIDTH (%)	-	2	18.1	-	17.4- 18.9
PREOCULAR LENGTH (%)	-	2	26.2	-	25.8- 26.7
CRANIUM LENGTH (%)	-	1	24.8	-	-
CRANIUM WIDTH (%)	-	1	15.2	-	-
PREORBITAL WIDTH (%)	-	1	19.1	-	-
POSTORBITAL WIDTH (%)	-	1	9.0	-	-
INTERORBITAL WIDTH (%)	-	2	8.9	-	8.6- 9.3
FONTANELLE LENGTH (%)	-	1	15.9	-	-
FONTANELLE WIDTH (%)	-	1	6.9	-	-
UPPER DENTAL PLATE WIDTH(%)	-	2	6.4	-	6.1- 6.7
LOWER DENTAL PLATE WIDTH(%)	-	2	5.7	-	5.7- 5.7
PRECAUDAL VERTEBRAE	-	2	27.5	-	27- 28
CAUDAL VERTEBRAE	-	-	-	-	-
CAUDAL VERTEBRAE TO BASE OF STING	-	1	73	-	-
TOTAL VERTEBRAE	-	-	-	-	-
DIPLOSPONDYLOUS VERTEBRAE	-	-	-	-	-
SYNARCUAL VERTEBRAE	-	2	2.5	-	2- 3

TABLE 9

(continued)

		HOLOTYPE	N	MEAN	S.D.	RANGE
PELVIC RADIALS	♂	-	1	19	-	-
	♀	-	1	25	-	-
PROPTERYGIAL RADIALS		-	2	14.5	-	14- 15
METAPTERYGIAL RADIALS		-	2	35.5	-	34- 37
TOTAL PECTORAL RADIALS		-	2	94.0	-	93- 95
UPPER TOOTH ROWS		36	3	36,6	0.5	36- 37
LOWER TOOTH ROWS		37	3	32.3	4.5	28- 37
LOWER MEDIAN TEETH		7	3	5.6	1.1	5- 7
MIDDORSAL SPINES		-	2	31.0	-	29- 33

FIG. 40

Potamotrygon dumerilii, dorsal view, female, 347 mm DL, MNHN 2367 (holotype).

FIG. 41

Potamotrygon dumerilii, dorsal view, male, 313 mm DL, MFA 268. Courtesy of MFA files.

FIG. 42

Potamotrygon dumerilii, A.- Exposed portions of upper and lower dental plates, male, 313 mm DL, MFA 268. B.- Idem, female, MFA 267.

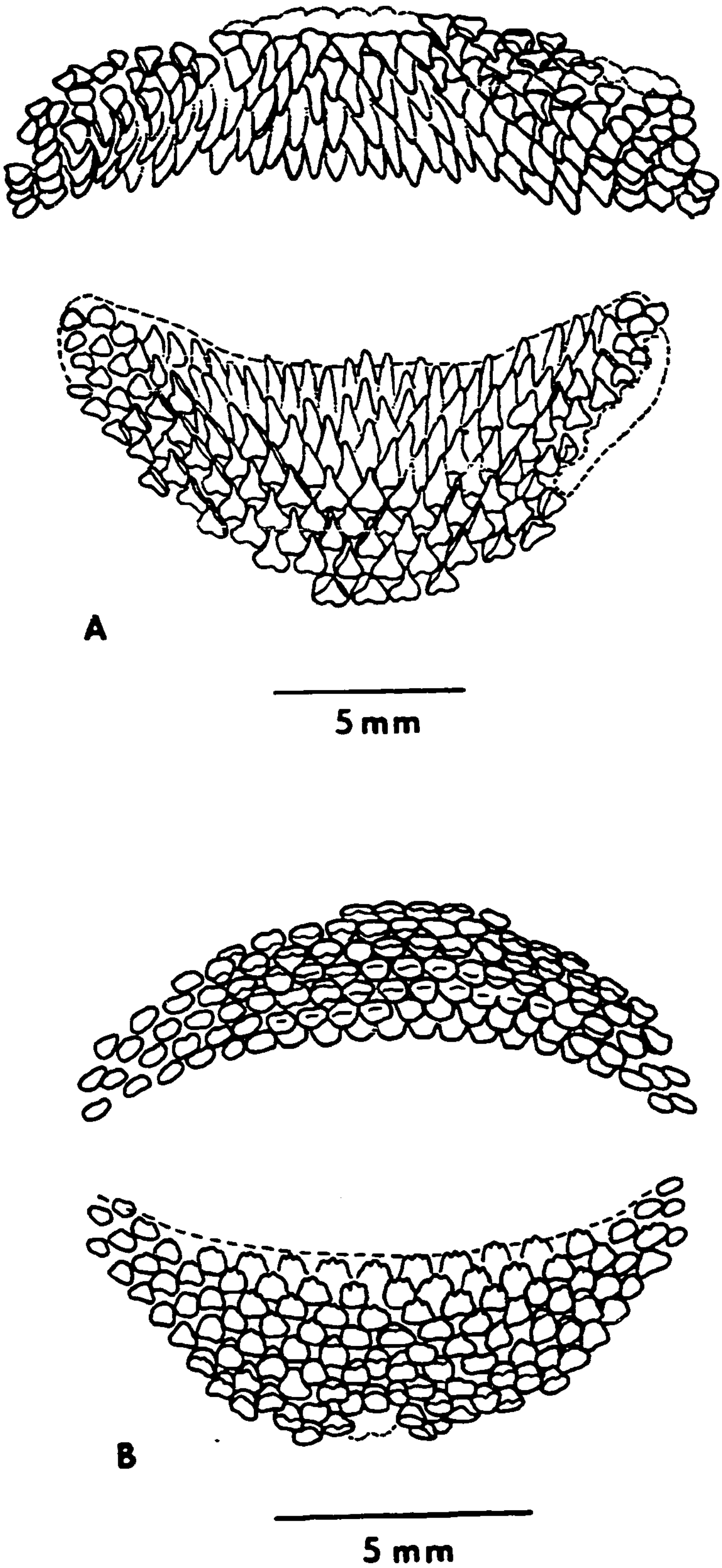

A
5 mm
B
5 mm

FIG. 43

Potamotrygon dumerilii, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, lingual, and labial views, male, 313 mm DL, MFA 268. F.- Tooth from upper jaw near mouth corner, MFA 268. G - K.- Tooth from upper jaw near symphysis, apical, basal, lateral, lingual, and labial views, female, 347 mm DL, MNHN 2367 (holotype). L.- Tooth from lower jaw near symphysis, apical view, MNHN 2367.

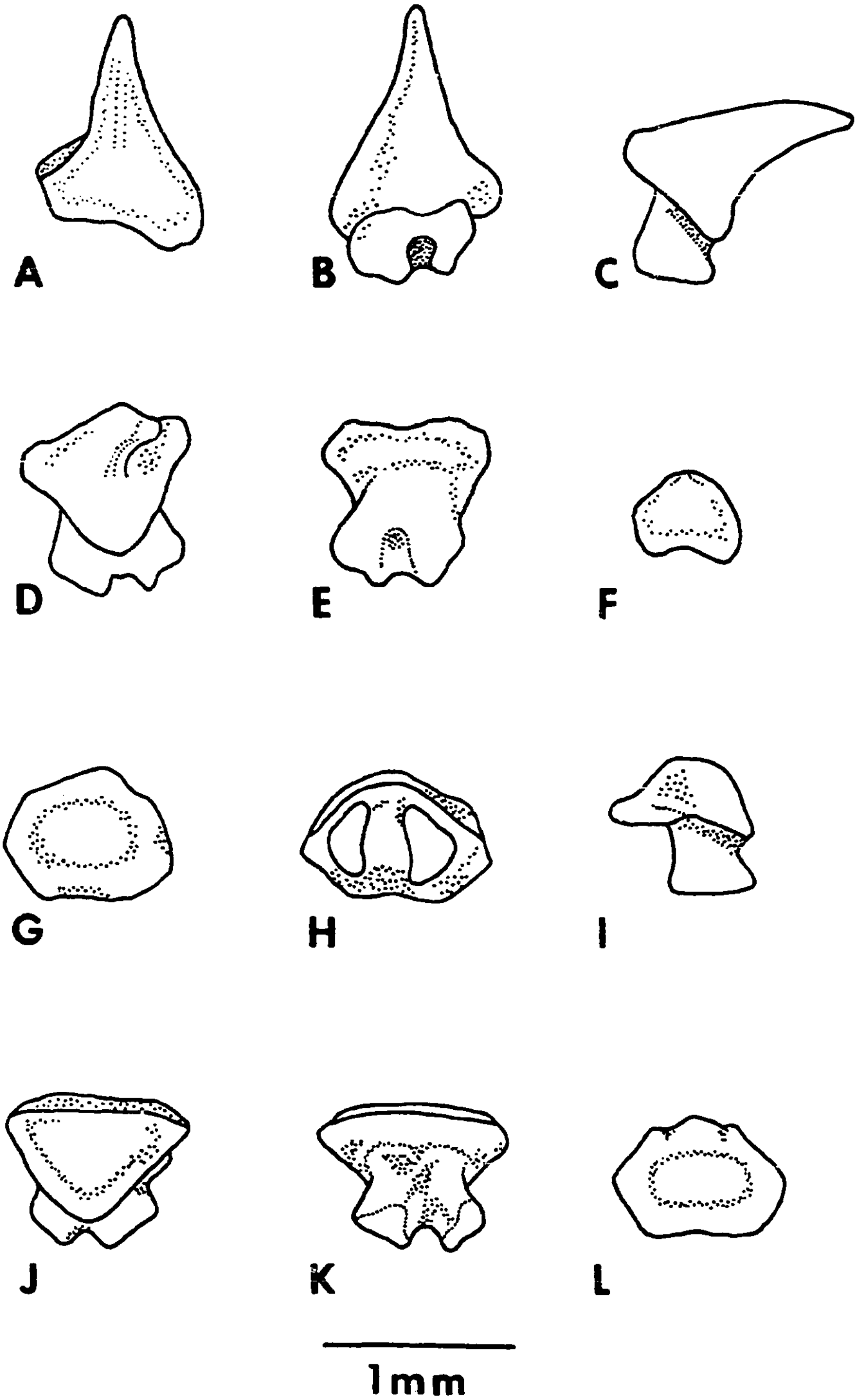
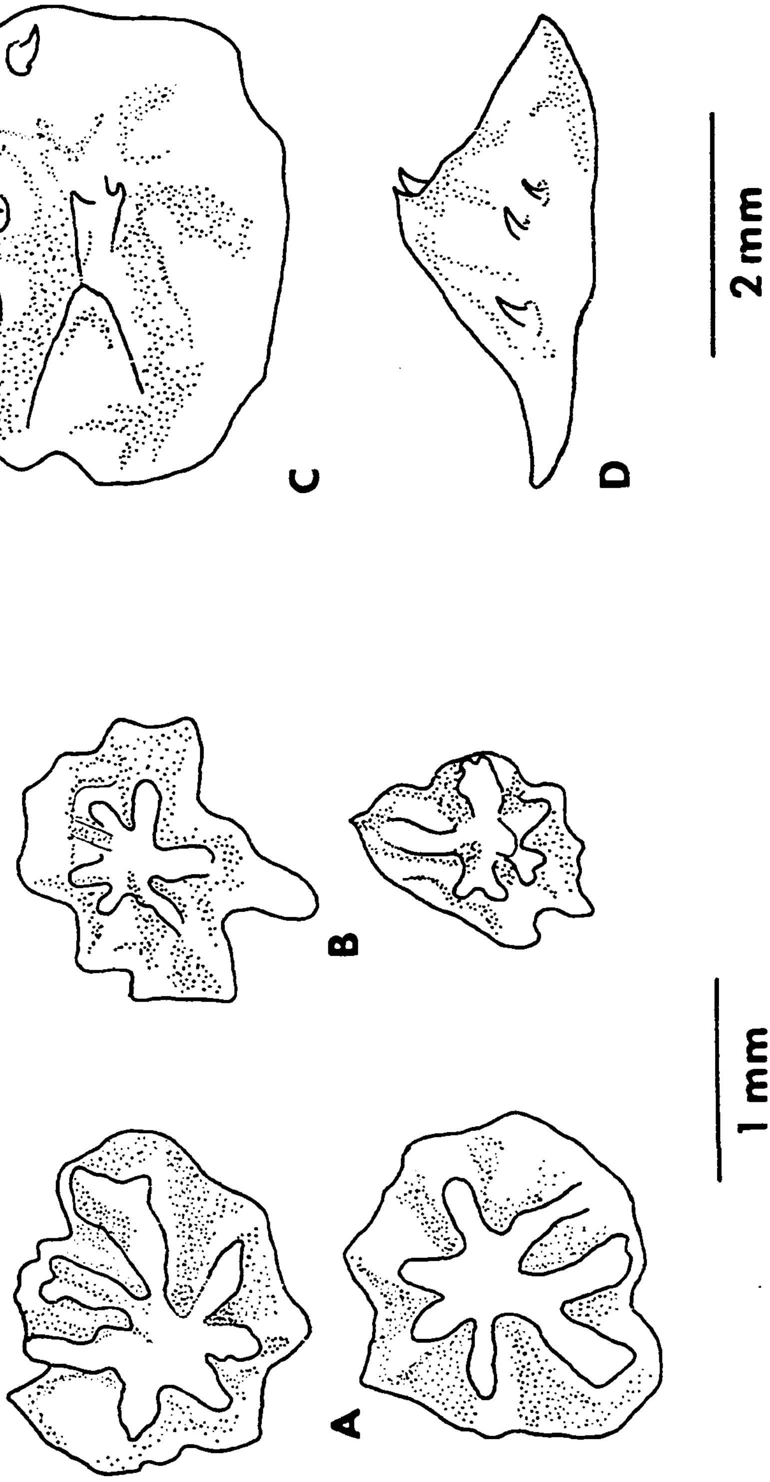

A
B
C
D
E
F
G
H
I
J
K
L
1mm

FIG. 44

Potamotrygon dumerilii, A.- Dermal denticles from disc near midline, apical view, female, 347 mm DL, MNHN 2367 (holotype). B.- Idem, male, 313 mm DL, MFA 268. C - D.- Middorsal tail spine anterior to caudal sting, apical and lateral views, MFA 268.


A
B
C
D
1 mm
2 mm

Potamotrygon falkneri Castex & Maciel, 1963

(Figs. 45-49)

Potamotrygon ·istrix [sic]. Castex, 1963b: 52.

Potamotrygon hystrix. Castex, 1963b: 54, 119.

Potamotrygon falkneri Castex and Maciel in Castex, 1963e: 56-61, figs. 16-17 (original description, Paraná, Río Paraná).

Potamotrygon menchacai Achenbach, 1967: 1-8 (original description, Río Colastiné, Santa Fe, Argentina). NEW SYNONYMY.

Holotype: MFA 236, by original indication, female.

Paratype: MFA 235, by original indication, female.

Type locality: Paraná, Rio Paraná, Entre Rios, Argentina.

Vernacular names: raya reticulada, raya fina, raya pitití (Argentina).

Remarks.- No collection numbers for the two type specimens were given in the original description. Castex (1964b) subsequently designated one holotype [sic], MFA 235, which does not correspond with the specimen figured as type in the original description. Castex (1964b, 1965a) designated one allotype of P. falkneri, MFA 279, but this specimen is deprived of type status because it does not belong to the original type series. There were no labels or other indications of possible type status on any specimens of P. falkneri in the MFA collection. A typescript list of stingray specimens in the museum indicated MFA 235 as "type", and MFA 347 as "holotype". The former specimen (MFA 235) probably belongs in the type series, as indicated in the typescript list and by Castex (1964b), although it does not correspond with the specimens figured in the original description. Measurements taken on this specimen closely correspond ($\pm$2.1%) with those given for the second specimen (=paratype) in the original description. The specimen MFA 347, an adult male, can be excluded from the type series, which contained only females. Identification of the holotype was based on the comparison of the measurements given for the type with those of specimen MFA 236 (the small observed deviations probably are due to differences in measuring methods, and subsequent damage of the specimen), and by matching details of the color pattern of MFA 236 with the photograph of the type in the original description. The holotype has a broken tail, the caudal sting and the lower tooth plate are missing, and the ventral surface is partially dissected. A square of skin was removed from the dorsal surface of the holotype, at the base of the tail. The paratype (MFA 235) has a broken tail, and its jaws were removed and kept in a separate jar.

The holotype of P. menchacai (MFA 289) agrees with P. falkneri in all examined characters (dentition, tail spines, morphometrics and meristics), excepting the yellow spots on the disc, which are relatively larger than in typical specimens of P. falkneri. This condition is interpreted as an intraspecific variation of the color pattern, and P. menchacai is regarded as a synonym of P. falkneri.

Diagnosis.- A species of Potamotrygon from the lower Rio Paraná and Rio Paraguay drainages, diagnosed by the following combination of characters: dorsal surface of disc dark brown, with irregular yellow spots, oval to reniform, usually larger than eye in diameter; teeth relatively small, wider than long, with flat crowns lacking prominent cusps except in mature males; 22 to 50 tooth rows in upper jaw; middorsal tail spines low relative to basal diameter, in irregular parallel rows.

Description.- Measurements and counts are given in Table 10. Disc subcircular to oval, disc length 1.02-1.09 times DW. Posterior margins of pelvic fins dorsally exposed behind disc margins. Tail relatively short, its length nearly equal to DW, with well-developed dorsal and ventral finfolds; height of ventral finfold 4.0-4.7 in tail width at insertion of caudal sting, length of ventral finfold 44.2-61.5 percent of DW. One or two relatively long caudal stings (Fig. 49), sting length 1.3-2.3 times tail width.

Eyes relatively large, their length 2.3-3.9 in interorbital distance, 4.1-7.2 in interocular distance. Spiracles relatively small, their length 1.2-2.4 times eye length, 2.9-

3.6 in interspiracular distance. Mouth relatively large, its width 7.8-9.9 percent of DW, 1.0-1.3 times internarial width. Five pointed papillae on floor of buccal cavity. Teeth crowded in quincunx, in 22/26 to 50/44 longitudinal rows, and five to ten exposed teeth in median row of lower dental plate. Teeth white, relatively small (Figs. 47, 48), wider than long, with blunt rhombic crowns, without prominent cusps except in mature males. Teeth sexually dimorphic, mature males (larger than 400 mm DW) with pointed teeth in median rows of upper jaw, and cuspless teeth in lateral rows. Male lower dental plate similar to females. No other apparent monognathic heterodonty in males and females. Nostril length 1.3-2.3 in internarial distance. Branchial basket relatively narrow, its greatest width 3.8-4.5 in DW, distance between first and fifth gill slits 6.4-7.7 in DW.

Middorsal surface of disc covered with denticles (Fig. 49), disc margins smooth. Adults with 18 to 56 middorsal spines on tail, in irregular parallel rows. Middorsal spines (Fig. 49) low relative to basal diameter. Latero-caudal spines moderately developed in adults, near insertion of sting. Juveniles with smooth disc and tail, lacking developed spines and denticles.

Dorsal surface of disc dark brown, with oval to reniform yellow spots, usually larger than eye in diameter. Dorsal surface of tail and pelvic fins with color pattern similar to disc. Ventral surface white, usually with central dark spot on disc, and brown disc margins. Ventral surface of tail gray, with irregular white spots.

Geographic distribution.- Northeastern Argentina, central Paraguay, and western Brazil, in Mato Grosso (see Fig. 100). Found in Rio Cuiabá, Rio Paraguay, and in Rio Paraná, from Guaíra to Entre Rios.

Biological remarks.- According to Castex (1965a), P. falkneri is found in deep waters with strong current, in the vicinity of Guaíra and Iguaçu in Rio Paraná.

Additional reference: Castex, 1967d (photograph of dental plates).

TABLE 10

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Potamotrygon falkneri*

	HOLOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	451	16	-	-	127.2-465
DISC LENGTH (mm)	488	16	-	-	137.8-498
DISC LENGTH (%)	108.2	16	106.8	1.6	102.2-109.3
TOTAL LENGTH (%)	-	1	221.6	-	-
INTERNAL DL (%)	-	16	96.3	2.2	94.1-101.8
MOUTH TO SCAPULOCORACOID (%)	-	13	30.0	0.9	28.4- 32.0
MOUTH TO CLOACA (%)	68.2	16	66.2	2.3	62.0- 69.0
CLOACA TO STING (%)	57.2	16	52.1	3.2	47.5- 60.0
TAIL LENGTH (%)	95.3*	1	123.4	-	-
TAIL WIDTH (%)	11.7	16	11.5	0.5	10.2- 13.2
TAIL WIDTH AT STING BASE(%)	4.5	16	4.8	0.6	3.5- 6.0
TAIL HEIGHT (%)	6.3	16	6.2	1.0	4.3- 10.0
PELVIC FIN WIDTH (%)	25.9	16	26.6	2.5	24.2- 30.0
PELVIC FIN LENGTH (%)	26.1	16	25.5	2.0	22.5- 28.7
CLASPER LENGTH (%)	-	10	21.7	6.8	11.6- 34.9
STING LENGTH (%)	-	14	20.5	2.4	16.6- 23.8
PRECLOACAL LENGTH (%)	91.3	16	88.8	2.5	88.0- 92.7
PREORAL LENGTH (%)	23.0	16	23.6	1.4	20.3- 26.9
PRENARIAL LENGTH (%)	17.1	16	18.4	0.7	16.6- 20.6
BRANCHIAL BASKET LENGTH (%)	13.1	15	14.5	0.6	13.1- 15.4
BRANCHIAL BASKET WIDTH(%)	24.6	15	24.1	0.9	22.2- 25.8

*Tail broken on holotype.

TABLE 10

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
MOUTH WIDTH (%)	8.7	15	8.8	0.7	7.8- 10.1
NOSTRIL LENGTH (%)	4.8	15	4.6	0.9	3.7- 6.2
INTERNARIAL WIDTH (%)	7.8	15	7.8	0.4	7.2- 9.2
EYE LENGTH (%)	2.9	16	3.2	0.7	2.3- 4.8
SPIRACLE LENGTH (%)	5.6	16	5.6	0.4	4.9- 6.5
INTEROCULAR WIDTH (%)	15.8	16	16.4	1.0	15.2- 18.5
INTERSPIRACULAR WIDTH (%)	19.0	16	18.4	1.1	16.2- 20.3
PREOCULAR LENGTH (%)	26.1	16	27.6	1.1	25.5- 30.2
CRANIUM LENGTH (%)	-	4	24.5	0.6	23.9- 25.3
CRANIUM WIDTH (%)	-	4	16.4	0.2	16.3- 16.7
PREORBITAL WIDTH (%)	-	4	17.3	1.1	16.3- 19.0
POSTORBITAL WIDTH (%)	-	4	10.4	0.6	9.7- 11.0
INTERORBITAL WIDTH (%)	9.5	16	9.4	0.7	8.5- 11.2
FONTANELLE LENGTH (%)	-	4	15.5	0.7	14.9- 16.6
FONTANELLE WIDTH (%)	-	4	7.5	1.5	5.9- 9.6
UPPER DENTAL PLATE WIDTH (%)	7.5	16	7.5	0.3	6.8- 8.3
LOWER DENTAL PLATE WIDTH(%)	-	16	7.3	0.4	6.4- 7.8
PRECAUDAL VERTEBRAE	-	6	28.0	1.2	26- 30
CAUDAL VERTEBRAE	-	4	96.7	1.2	95- 98
CAUDAL VERTEBRAE TO BASE OF STING	-	4	74.5	4.6	70- 81
TOTAL VERTEBRAE	-	4	125.2	0.5	125- 126
DIPLOSPONDYLOUS VERTEBRAE	-	4	10.5	2.3	9- 13
SYNARCUAL VERTEBRAE	-	6	2.1	0.7	1- 3

TABLE 10

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
PELVIC RADIALS	-	4	20.5	0.5	20-21
	-	2	26.0	-	25-27
PROPTERYGIAL RADIALS	-	6	46.6	1.2	46-48
MESOPTERYGIAL RADIALS	-	6	13.6	1.0	12-15
METAPTERYGIAL RADIALS	-	6	37.3	1.0	36-39
TOTAL PECTORAL RADIALS	-	6	97.3	1.6	95-99
UPPER TOOTH ROWS	47	16	36.1	7.7	22-50
LOWER TOOTH ROWS	-	16	36.1	6.2	26-44
LOWER MEDIAN TEETH	-	16	7.5	1.4	5-10
MIDDORSAL SPINES	47	10	34.7	12.5	18-56

FIG. 45

Potamotrygon falkneri, dorsal view, female, 315 mm DL, MFA 235 (paratype).

FIG. 46

Potamotrygon falkneri, dorsal view, male, 286 mm DL, MFA 289 (type of Potamotrygon menchacai).

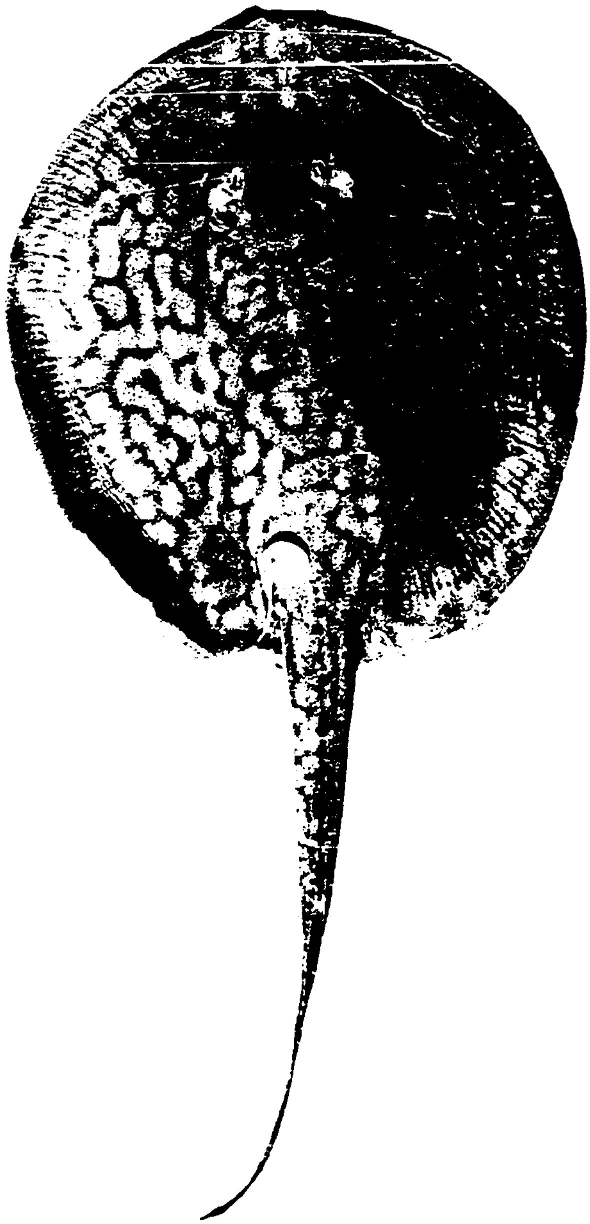
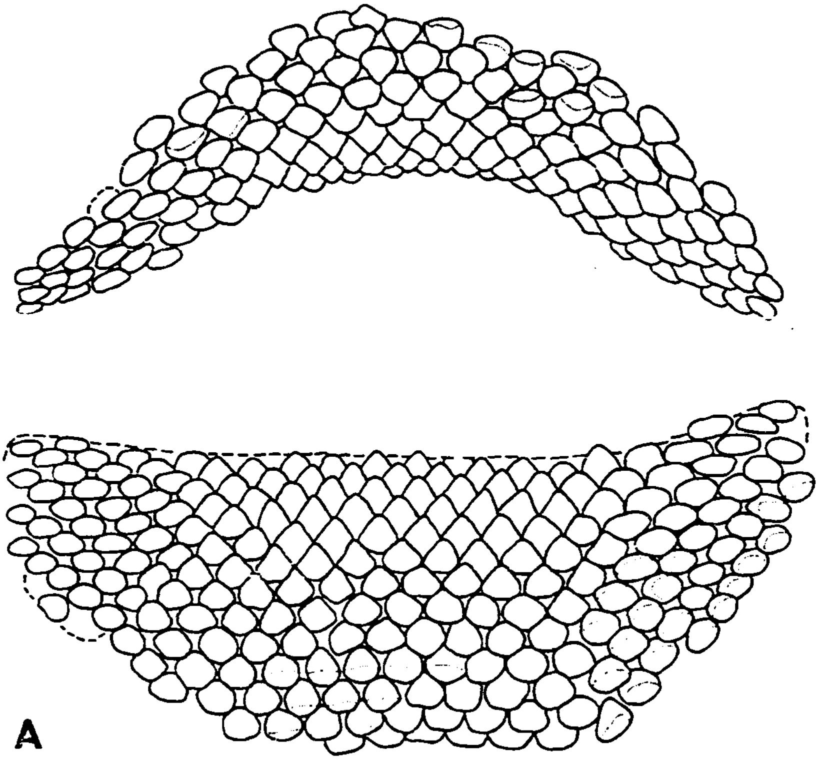


FIG. 47

Potamotrygon falkneri, A.- Exposed portions of upper and lower dental plates, male, 291 mm DL, ZMH 10339. B.- Idem, female, 315 mm DL, MFA 235 (paratype).


A

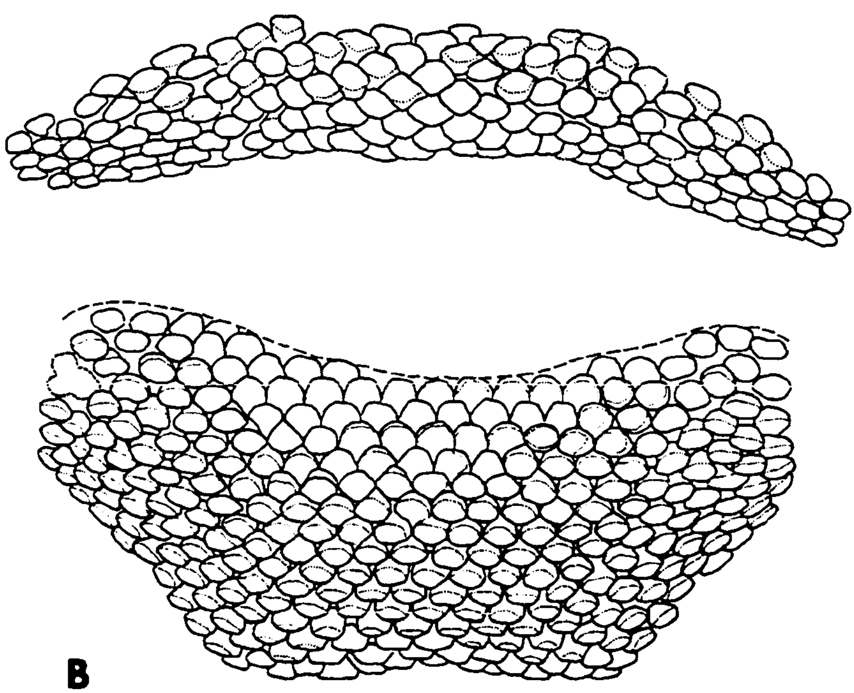

B

FIG. 48

Potamotrygon falkneri, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, female, 442 mm DL, BMNH 1895.5.11.276. F.- Tooth from lower jaw near mouth corner, apical view, BMNH 1895. 5.11.276.

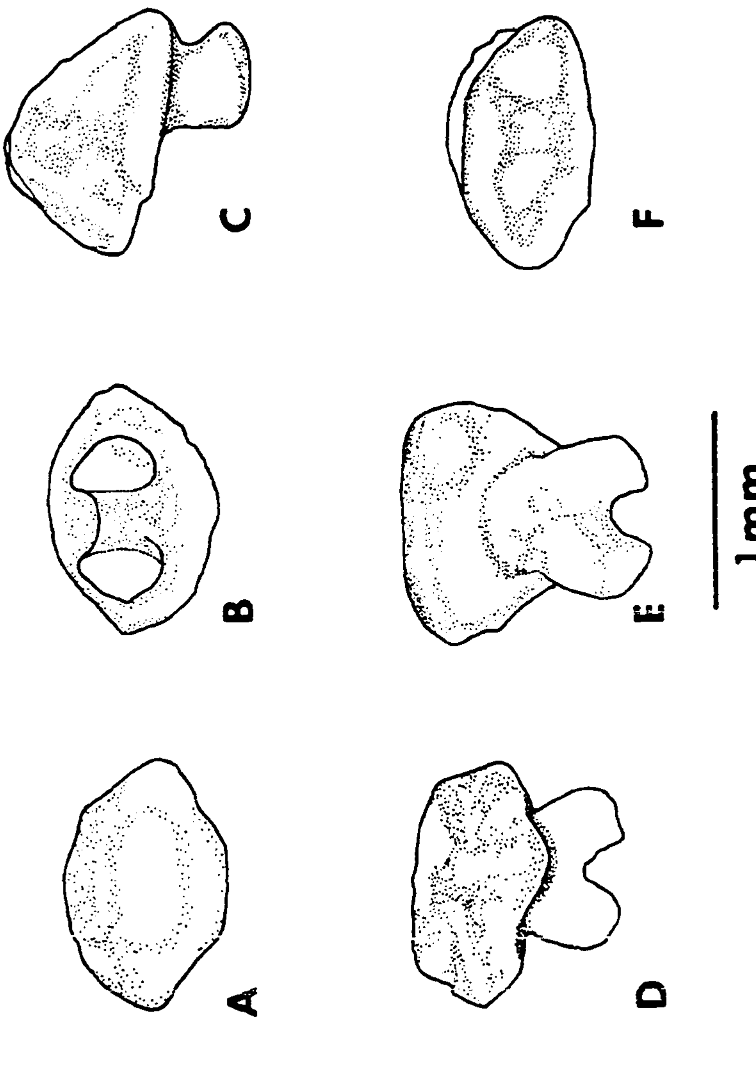
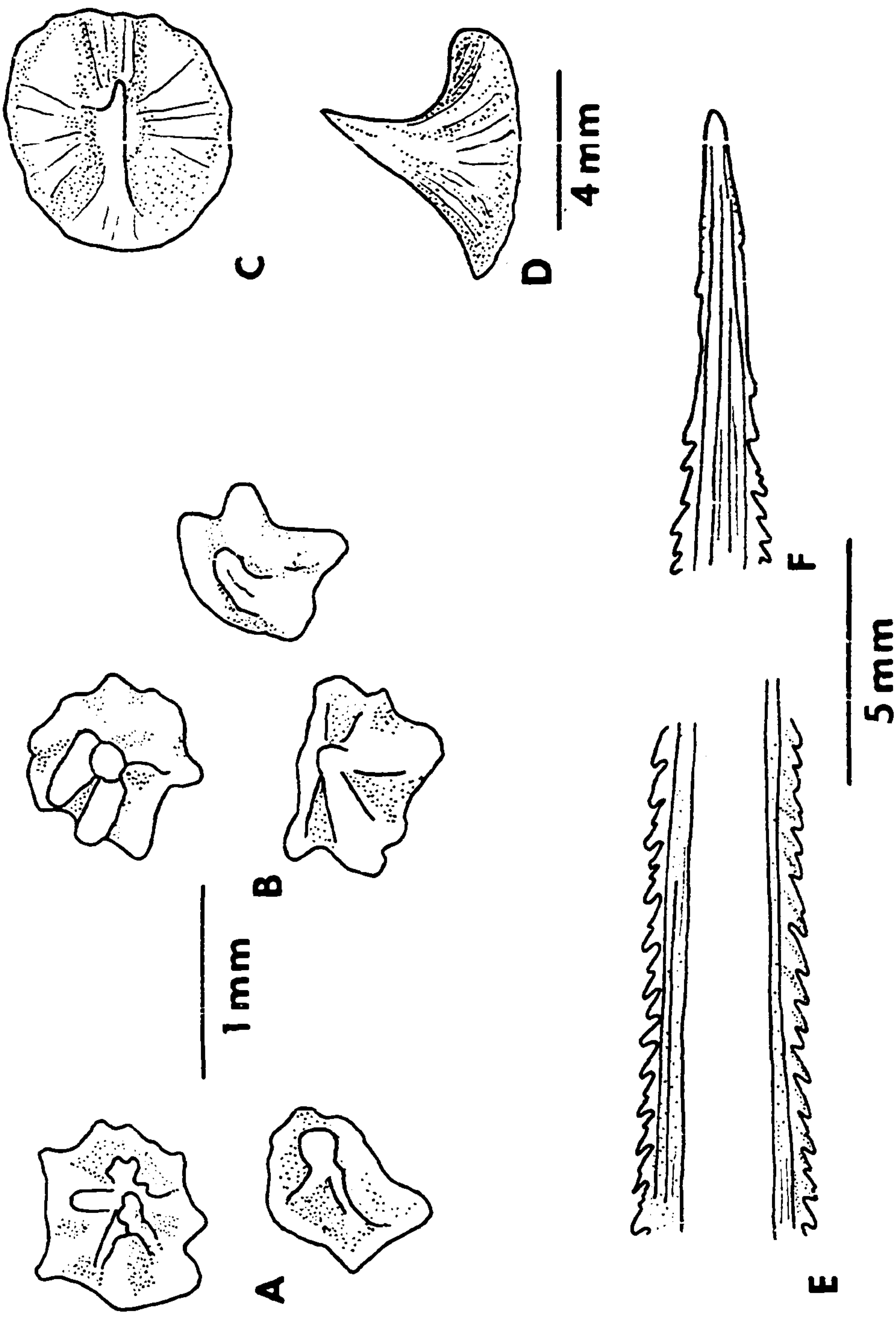

A
B
C
D
E
F
1mm

FIG. 49

Potamotrygon falkneri, A.- Dermal denticles from disc near midline, apical view, female, 315 mm DL, MFA 235 (paratype). B.- Idem, female, 422 mm DL, MZUSP 14578. C - D.- Mid-dorsal tail spine anterior to caudal sting, apical and lateral views, male, 291 mm DL, ZMH 10339. E - F.- Intermediate and distal portions of caudal sting, ZMH 10339.


A
B
1 mm
C
D
4 mm
E
F
5 mm

Potamotrygon henlei (Castelnau, 1855)

(Figs. 50-53)

Trygon (Taenura) henlei Castelnau, 1855: 102 (original description, Rio Tocantins).

Taenura henlei Castelnau, 1855, plate 48, fig. 3 (original illustration).

Taeniura henlei. Duméril, 1865: 623.

Holotype: MNHN 2353, by original indication, sex unknown, coll. F. Castelnau.

Type locality: Rio Tocantins, Brazil.

Vernacular name: arraia de fogo (Brazil).

Remarks.- The holotype is in poor condition, only dorsal skin, tail, and part of the vertebral column preserved. The jaws are missing, one eye, spiracular cartilage, and part of hyomandibular remain intact. No accurate measurements could be taken on the holotype. Color pattern, mid-dorsal spines, and denticles are diagnostic for the holotype.

Duméril (1865) considered Taeniura henlei as a valid species, and distinct from Potamotrygon motoro. All subsequent authors (Günther, 1870; Garman, 1877, 1913; Berg, 1895; Fowler, 1948; Castex, 1964b) mistakenly placed T. henlei in the synonymy of P. motoro, based only on the original descriptions. Examination of the holotype of T. henlei, and study of additional specimens from Rio Tocantins, showed that this species differs from P. motoro, by having double or triple rows of middorsal tail spines (P. motoro usually has a single row), and by having yellow ocelli distally on the tail (ocelli in P. motoro are limited to the disc and base of the tail). The dentition of these two species is also distinct, P. henlei having relatively larger and fewer teeth than P. motoro.

Potamotrygon henlei resembles Potamotrygon leopoldi, described from Rio Xingu and known only from two specimens. Both species have triple rows of middorsal spines on the tail, and ocelli occurring distally on the tail. Potamotrygon henlei differs from P. leopoldi in dentition, by having relatively larger teeth, in lower number of rows. Regression of number of tooth rows in upper jaw on DW for P. henlei: $y = 0.02x + 10.52$, correlation coefficient = 0.94. Same regression for P. leopoldi: $y = 0.07x + 6.64$. Computed Student's t value for the difference between the two regressions (according to Steel and Torrie, 1960) equals 2.747, indicating significant difference at 95 percent confidence level, with six degrees of freedom.

The original description of Trygon garrapa Schomburgk (1843) contains two possibly diagnostic characters for P. henlei. The yellow ocelli continue distally on the tail, as shown in the original illustration, and the teeth are flat, pavement-like (..."a series of rough flat teeth, in each jaw, like a file"...). A negative character for the synonymy is the presence of a single row of middorsal tail spines in T.

garrapa (..."a single row of weak spines runs along the upper ridge of the tail"...). Potamotrygon henlei is yet unkown from Rio Branco, the type locality of T. garrapa. No type specimen is known for T. garrapa, which preferably should be treated as a doubtful species (see further discussion under comments on doubtful species).

Diagnosis.- A species of Potamotrygon from Rio Tocantins and Araguaia drainages, diagnosed by the following combination of characters: color pattern with yellow to orange ocelli on dark gray background, forming irregular lunate figures in center of disc of adults; ocelli present distally on tail, behind caudal sting; teeth large, pavement-like, in 14 to 26 rows in upper jaw.

Description.- Measurements and counts are given in Table 11. Disc nearly circular, disc length 1.00-1.10 times DW. Pelvic fins usually covered dorsally by disc. Tail relatively short, its length 0.9-1.0 times DW, with low dorsal and ventral fin-folds. Caudal sting relatively long, its length 1.6-2.3 times tail width. Eyes large, their length 2.0-2.5 in interorbital distance, 3.5-4.6 in interocular distance. Preocular distance 3.2-3.6 in DW, 1.2-1.6 times interocular distance. Spiracles relatively small, their length 1.2-1.6 times eye length, 2.5-3.7 in interspiracular distance. Mouth relatively large, its width 7.9-10.5 percent of DW, and 0.9-1.4 times internarial distance. Five short buccal papillae, two extreme lateral papillae smaller than medial and paramedial. Preoral distance 18.8-23.8 percent of DW. Teeth white, very large (Fig. 53) with blunt hexagonal crowns, without prominent cusps; teeth closely crowded in pavement-like quincunx, in 14/13 to 26/30 longitudinal rows, and six to ten exposed teeth in median row of lower dental plate. Sexual dimorphism in dentition unknown because mature male specimens were not available in collections. Nostrils relatively small, their length 0.9-1.6 in internarial distance. Branchial basket relatively narrow, its greatest width 4.0-4.2 in DW, distance between first and fifth gill slits 6.4-7.2 in DW.

Middorsal surface of disc rough, covered with pointed denticles (Fig. 53), with stellate roots and triangular cusp. Denticles anteriorly on dorsal surface of females; disc margins smooth. Tail with 13 to 45 middorsal spines, in double or triple parallel rows; middorsal tail spines (Fig. 53) relatively high to basal diameter, with round base and recurved pointed cusp. Latero-caudal spines well-developed in adults, especially near insertion of caudal sting. Juveniles with smooth disc and tail, lacking developed denticles and spines.

Dorsal surface of disc dark olivaceous-brown or dark gray, with circular or irregular light yellow to orange ocelli, decreasing in size towards disc margins. Diameter of largest ocellus equal to spiracle length. Nine to twelve ocelli in row from base of tail to anterior disc. Each ocellus encircled by dark ring, occasionally with intermediate orange ring. Ocelli in adults irregular in shape forming lunate figures, sometimes encircling black spot in center, and sometimes fused in pairs forming figure eights. Ocelli continue posteriorly to caudal sting on dorsal and lateral surfaces of tail. Ventral surface white, with brown margins of disc and pelvic fins, or occasionally completely dark-pigmented. Dark central spot usually present ventrally on disc. Ventral surface of tail dark brown with irregular white spots.

Geographic distribution.- Northern Brazil, in Rio Tocantins and Rio Araguaia drainages in Pará (see Fig. 100). *Potamotrygon henlei* is possibly endemic to these drainages.

TABLE 11

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Potamotrygon henlei*

	HOLOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	-	3	186.8	10.4	178.7-198.6
DISC LENGTH (mm)	-	5	-	-	143.0-269
DISC LENGTH (%)	-	5	107.9	2.4	104.4-110.9
TOTAL LENGTH (%)	-	3	186.8	10.4	178.7-198.6
INTERNAL DL (%)	-	5	92.8	2.7	89.2- 96.1
MOUTH TO SCAPULOCORACOID(%)	-	5	33.0	1.6	31.6- 35.6
MOUTH TO CLOACA (%)	-	5	65.0	2.8	62.4- 70.1
CLOACA TO STING (%)	-	5	44.6	3.0	41.4- 49.6
TAIL LENGTH (%)	-	3	93.8	6.1	89.3-100.8
TAIL WIDTH (%)	-	5	10.5	0.8	9.3- 11.6
TAIL WIDTH AT STING BASE(%)	-	5	5.0	0.6	4.4- 6.1
TAIL HEIGTH (%)	-	5	7.0	0.4	6.6- 7.7
PELVIC FIN WIDTH (%)	-	5	29.1	1.5	26.6- 30.4
PELVIC FIN LENGTH (%)	-	5	23.3	1.8	20.2- 24.6
CLASPER LENGTH (%)	-	3	11.1	1.0	10.5- 12.3
STING LENGTH (%)	-	4	21.2	2.0	19.4- 23.3
PRECLOACAL LENGTH (%)	-	5	86.5	2.2	83.8- 89.9
PREORAL LENGTH (%)	-	5	21.6	1.8	18.8- 23.8
PRENARIAL LENGTH (%)	-	5	15.3	1.2	13.7- 16.4
VRANCHIAL BASKET LENGTH (%)	-	5	14.5	0.6	13.8- 15.6
BRANCHIAL BASKET WIDTH (%)	-	5	24.6	0.9	24.0- 25.7
MOUTH WIDTH (%)	-	5	9.4	1.0	7.9- 10.5
NOSTRIL LENGTH (%)	-	5	6.0	1.0	5.2- 7.8

TABLE 11

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
INTERNARIAL WIDTH (%)	-	5	7.9	0.5	7.3- 8.7
EYE LENGTH (%)	-	5	4.8	0.4	4.2- 5.2
SPIRACLE LENGTH (%)	-	5	6.6	1.3	5.7- 8.6
INTEROCULAR WIDTH (%)	-	5	20.5	1.5	18.3- 21.8
INTERSPIRACULAR WIDTH (%)	-	5	20.8	0.8	19.8- 22.1
PREOCULAR LENGTH (%)	-	5	28.3	1.1	27.5- 30.4
CRANIUM LENGTH (%)	-	1	28.7	-	-
CRANIUM WIDTH (%)	-	1	18.6	-	-
PREORBITAL WIDTH (%)	-	1	20.9	-	-
POSTORBITAL WIDTH (%)	-	-	-	-	-
INTERORBITAL WIDTH (%)	-	5	10.8	0.9	9.9- 12.5
FONTANELLE LENGTH (%)	-	1	19.1	-	-
FONTANELLE WIDTH (%)	-	1	9.3	-	-
UPPER DENTAL PLATE WIDTH(%)	-	5	8.0	1.0	6.9- 9.8
LOWER DENTAL PLATE WIDTH (%)	-	5	8.0	0.5	7.5- 8.8
PRECAUDAL VERTEBRAE	-	1	27	-	-
CAUDAL VERTEBRAE	-	1	101	-	-
CAUDAL VERTEBRAE TO BASE OF STING	-	1	78	-	-
TOTAL VERTEBRAE	-	1	128	-	-
DIPLOSPONDYLOUS VERTEBRAE	-	1	9	-	-
SYNARCUAL VERTEBRAE	-	1	1	-	-
PELVIC RADIALS ♀	-	1	23	-	-
PROPTERYGIAL RADIALS	-	1	50	-	-

TABLE 11
(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
MESOPTERYGIAL RADIALS	-	1	14	-	-
METAPTERYGIAL RADIALS	-	1	37	-	-
TOTAL PECTORAL RADIALS	-	1	101	-	-
UPPER TOOTH ROWS	-	8*	16.1	4.0	14- 26
LOWER TOOTH ROWS	-	6**	17.6	6.1	13- 30
LOWER MEDIAN TEETH	-	5	8.4	1.5	6- 10
MIDDORSAL SPINES	40	5	33.6	12.4	13- 45

*Includes two counts made by G. M. Santos at INPA and one count from a photograph.

**Includes one count from a photograph.

FIG. 50

Potamotrygon henlei, dorsal view, female, 188 mm DL, MZUSP 14768.

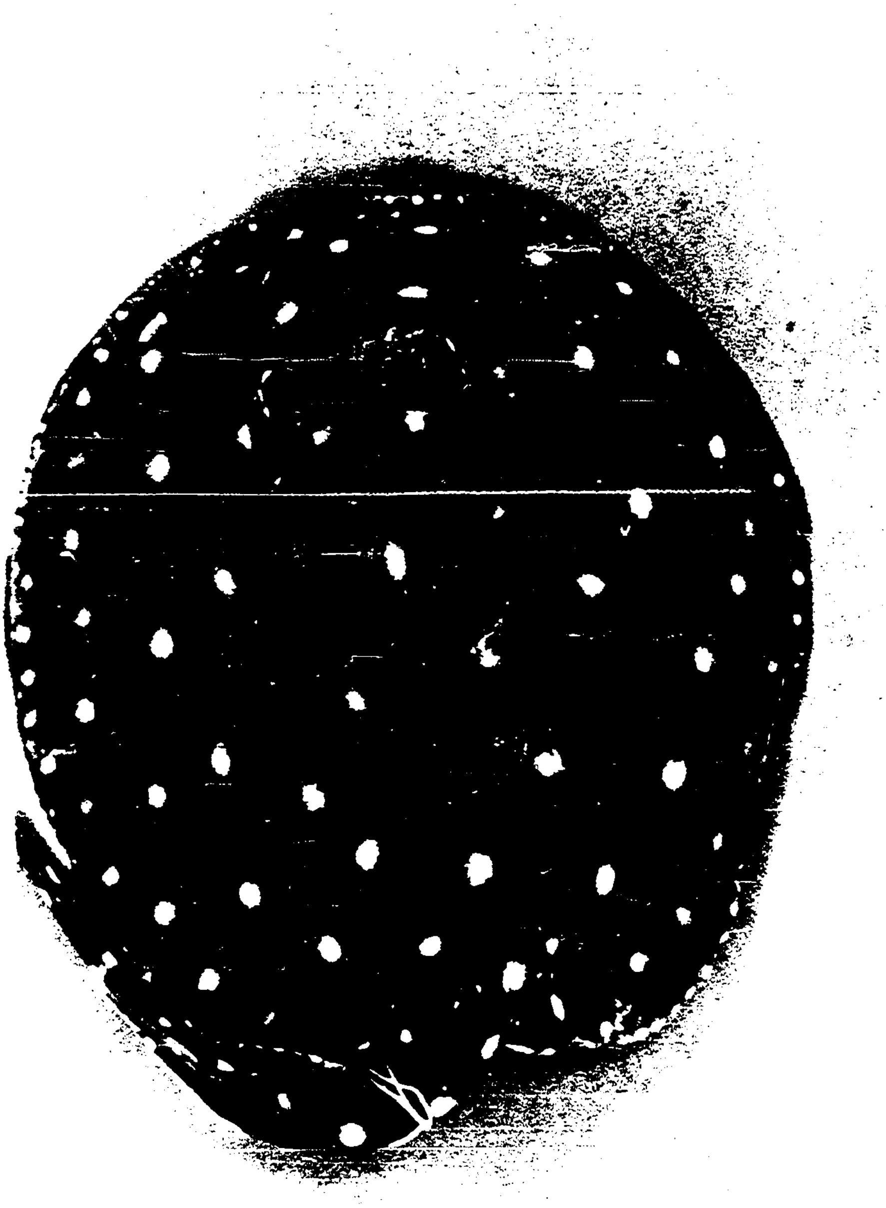


FIG. 51

Potamotrygon henlei, dorsal view, female, approximately 15 kg of weight (not measured, not seen by the author, specimen discarded in the field); aborted embryo, 125 mm DW (not seen by the author), preserved at INPA (uncatalogued specimen). From Pau D'Arco, Rio Araguaia below Conceição do Araguaia, PA, Brasil. Photograph and data courtesy of Geraldo M. Santos (INPA).

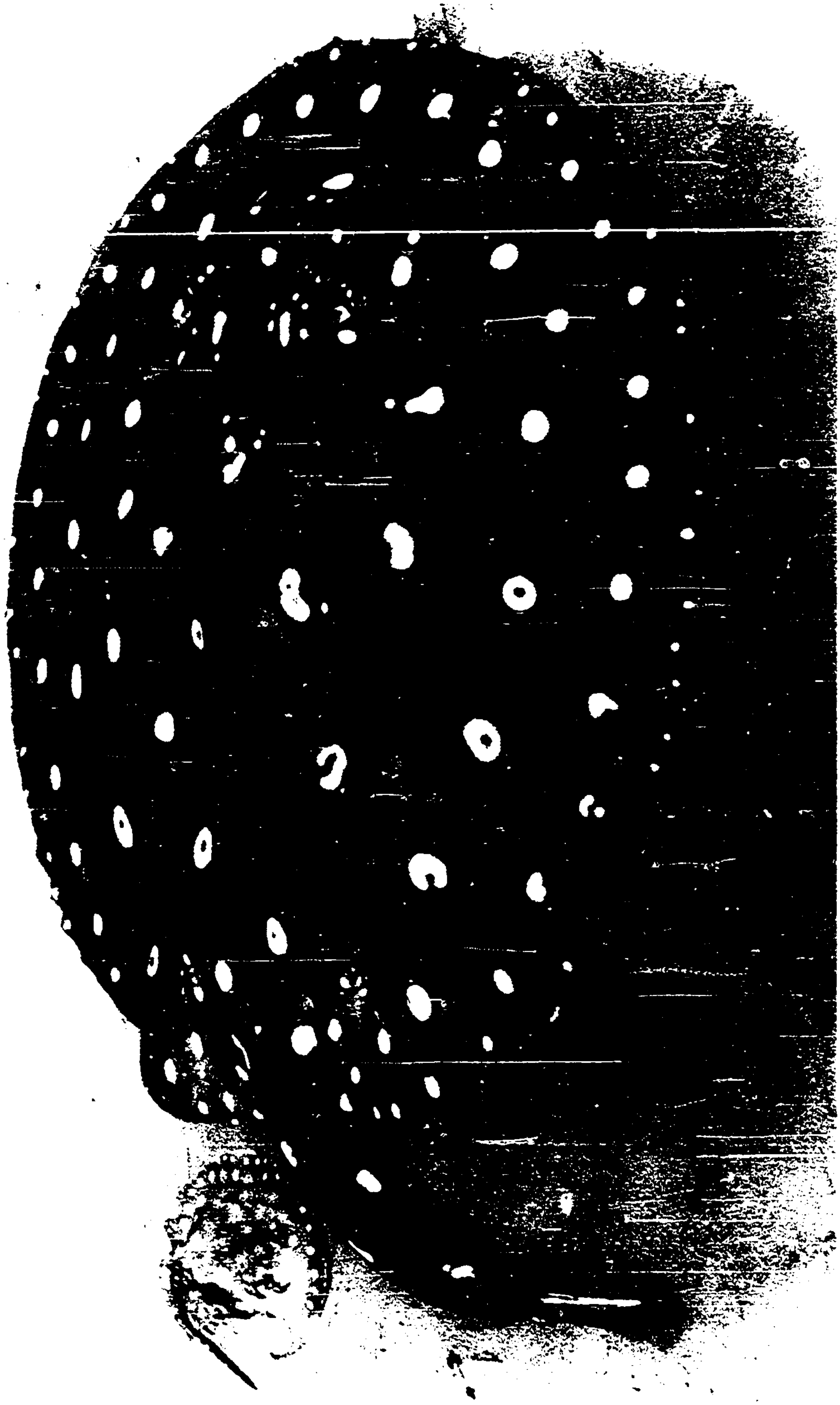


FIG. 52

Potamotrygon henlei, exposed portions of upper and lower dental plates, female, 188 mm DL, MZUSP 14768.

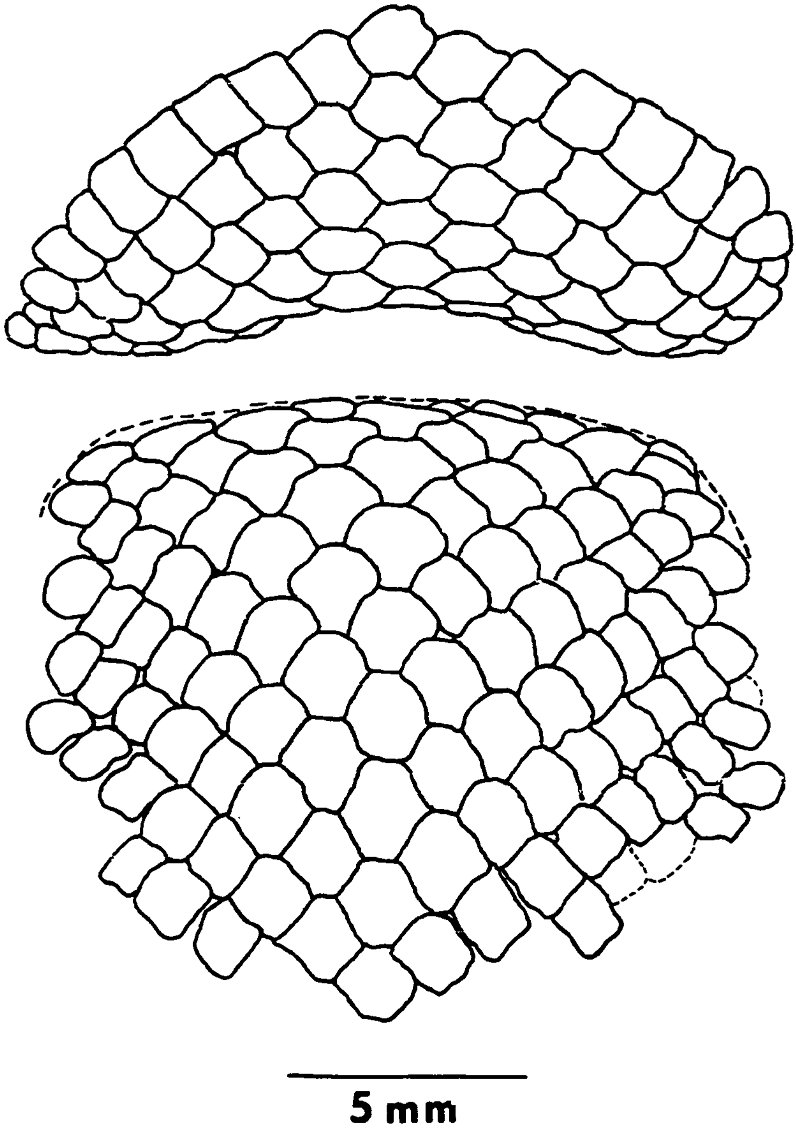
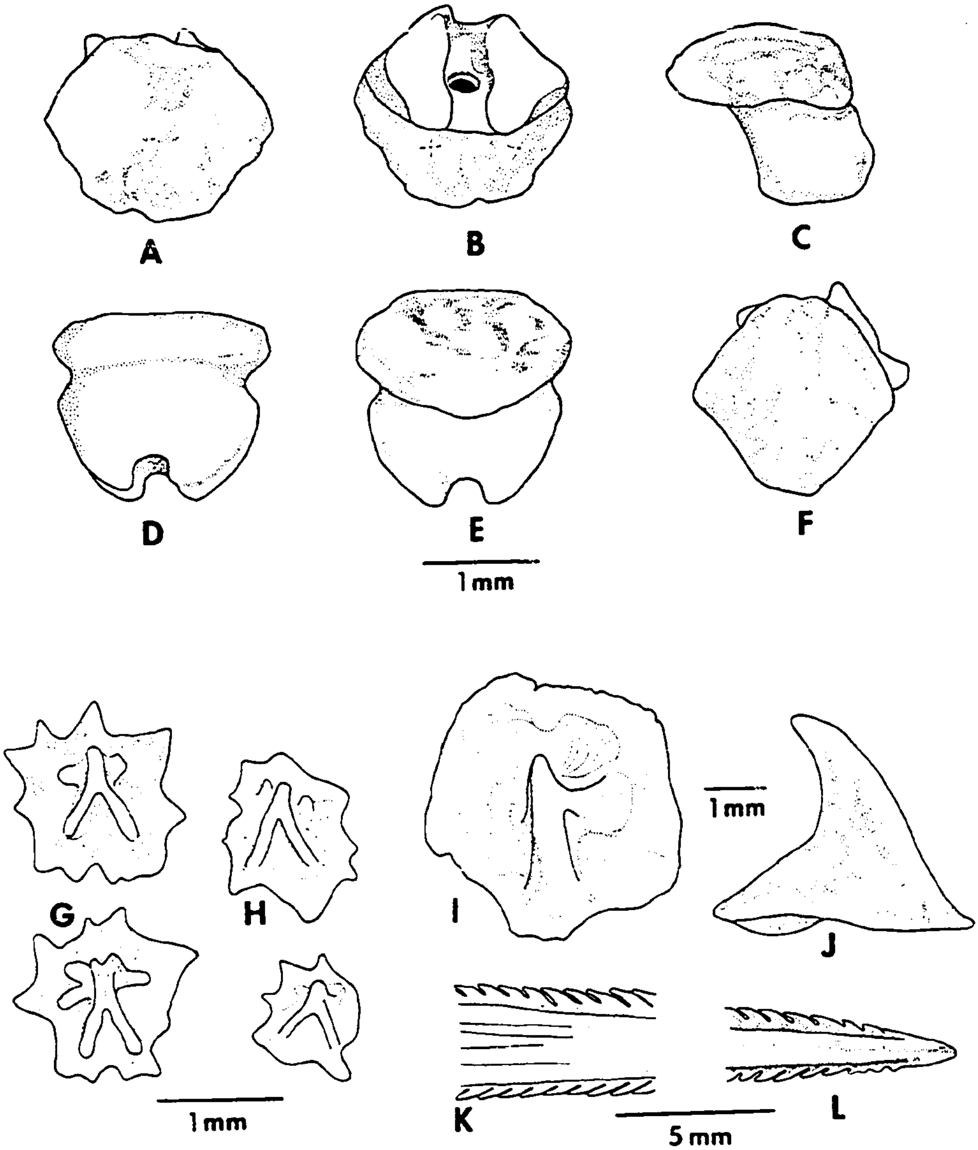

5 mm

FIG. 53

Potamotrygon henlei, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, female, 188 mm DL, MZUSP 14768. F.- Tooth from lower jaw near symphysis, apical view, MZUSP 14768. G.- Dermal denticles from disc near midline, female, MNHN 2353 (holotype). H.- Idem, MZUSP 14768. I - J.- Middorsal tail spine anterior to caudal sting, apical and lateral views, MNHN 2353. K - L.- Intermediate and distal portions of caudal sting, dorsal views, MZUSP 14768.


A
B
C
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1mm
G
H
I
J
1mm
1mm
K
L
5mm

Potamotrygon histrix (Müller & Henle, 1834)

(Figs. 54-55)

Trygon histrix Müller and Henle in Orbigny, 1834, plate 13 (folio), original illustration, Buenos Aires, indication only.

Trygon hystrix [in part] Müller and Henle, 1841: 167, 197 (original description, Buenos Aires, Surinam, Maracaibo, and Rio de Janeiro, not illustrated).

Trigon histrix [in part]. Schomburgk, 1843: 180, plate 20.

Taeniura hystrix. Jordan, 1887: 557.

Potamotrygon hystrix [in part]. Eigenmann and Eigenmann, 1891: 25.

Ellipesurus hystrix [in part]. Ribeiro, 1907: 185.

Ellipesurus histrix. Bertoni, 1939: 51.

Paratrygon hystrix [in part]. Fowler, 1948: 6.

[non] Trygon garrapa. Günther, 1870: 482.

[non] Potamotrygon humboldtii. Garman, 1877: 210.

Holotype: MNHN A-2449, by original indication, female, coll. A. d'Orbigny.

Type locality: Buenos Aires, Argentina.

Vernacular name: raya negra (Argentina).

Remarks.- The natural history plates from A. d'Orbigny's "Voyage dans l'Amérique Méridionale" were published and released on different dates as separate folios. According to Sheborn and Griffin (1934), the plate of Trygon histrix was published in 1834. The plate apparently was not numbered in print, because there are references to different numbers (11, 13 and 15) in other publications. The same plate was reprinted in Orbigny (1845), and all the fish plates from the "Voyage" were later bound together in one volume edited by Valenciennes (1847). Two references to the plate of T. histrix (Müller and Henle, 1841; Schomburgk, 1843) constitute evidence that it had been already distributed when Valenciennes issued the atlas in 1847. Schomburgk's citation demonstrates that the plate had already been named T. histrix. Whether the name had been initially credited to Müller and Henle or not, it is unknown, because I was unable to examine the original release of the plate. Access to the original plate or other historical information would permit the clarification of the authorship of the name. The plate constitutes an indication of the specific name, which should retain its spelling as T. histrix.

Müller and Henle (1841) provided a written description for T. histrix (changing the spelling to T. hystrix), and included five additional specimens, besides the one from Buenos Aires illustrated by Orbigny. One of these specimens, deposited in Leiden (RMNH 4258), was from Surinam. The other specimens, deposited in Paris, were obtained from Maracaibo, Venezuela (MNHN 2433) and from Rio de Janeiro (?) (MNHN 2434, two specimens). One remaining specimen, of unknown origin, was reported lost from the collection (MNHN A-8706) by Castex (1969a). This series of specimens has been interpreted as the type material (syntypes) of T. histrix by subsequent authors, who, therefore, added Surinam and Venezuela to the range of the species.

Müller and Henle (1841) type series consisted of heterogenous material. Castelnau (1855) pointed out that the specimens from Rio de Janeiro were distinct from the specimen illustrated by Orbigny. Castex (1969a) stated that only the specimens from Buenos Aires, Surinam, and Maracaibo had type status, due to the questionable locality data of the specimens from Rio de Janeiro. After examining these specimens, Castex concluded that they consisted of heterogenous material, and selected the specimen from Buenos Aires as the "type" (= lectotype). He also designated an "alotype" (sic), MFA 268, which lacked type status, because it was not part of an original type series. Furthermore, this proposed allotype does not belong to P. histrix, being identified as P. dumerilii by the present author. Although Castex (1969a) cleared the question on the geographic distribution of P. histrix, his taxonomic action of type designation was unnecessary, because the specimen from Buenos Aires (MNHN A-2449) is the only type (holotype) by original indication.

The holotype (fig. 54) is in bad condition, with the tail distally broken, and the ventral surface of the disc cut. The other specimens previously referred to as syntypes were identified as _Potamotrygon orbignyi_ (RMNH 4258, from Surinam), and _Potamotrygon yepezi_ (MNHN 2433, from Maracaibo). The specimens from Rio de Janeiro (MNHN 2434) could not be identified to species due to their small size and lack of pigmentation.

Diagnosis.- A species of _Potamotrygon_ from the lower Río Paraná diagnosed by the following combination of characters: disc oval; dorsal surface of disc dark brown with small light spots and irregular vermiculations; disc relatively rough with sharp denticles; tail with sharp middorsal spines, in one irregular row which continues dorsally on disc as double or triple parallel rows; teeth small with tricuspid crowns, in 27 to 40 rows in upper jaw.

Description.- Measurements and counts are given in Table 12. Disc oval, disc length 1.05-1.13 times DW. Pelvic fins dorsally covered by disc. Tail very spiny, with well-developed dorsal and ventral finfolds. No specimens with intact tails available for study; longest measured tail 1.1 in DW. Caudal sting relatively long, sting length 1.6-2.1 times tail width. Eyes relatively large, eye length 2.3-4.0 in interorbital distance, 4.7-8.7 in interocular distance. Spiracles relatively large, spiracle length 2.1-4.4 times eye length, 1.7-2.5 in interspiracular distance. Mouth relatively large, with five papillae at bottom; mouth width 1.1-1.3 times internarial distance. Preoral distance 17.6-19.5 percent of DW. Teeth relatively small (Fig. 55), with concave anterior margins and tricuspidate crowns, loosely set in quincunx, in 27/20 to 40/42 longitudinal rows, and four to ten exposed teeth in median row of lower jaw. Teeth sexually dimorphic, males with expanded and pointed central cusp. No apparent monognathic heterodonty in males or females. Nostril length 1.1-1.4 in internarial distance. Branchial basket relatively wide, its greatest width 3.5-3.8 in DW; distance between first and fifth gill slits 5.1-5.8 in DW.

Dorsal surface of disc rough, covered with sharp denticles, more developed along midline. Tail with 20 to 69 enlarged middorsal spines, with round base and sharp projecting crown; spines in irregular row which extends dorsally on disc as double or triple rows, usually forming a "V"-shaped angle edged on midline. Enlarged latero-caudal spines from tail base to distal portion.

Dorsal surface of disc dark brown, with violet tones (fide Müller and Henle, 1841, and Castex, 1964b), and scattered white spots, smaller than eye in diameter. Original illustration show light-edged vermiculations which are not conspicuous in preserved specimens. Ventral surface white with brown margins and tail, or completely dark pigmented.

Geographic distribution.- Potamotrygon histrix is known only from the lower Río Paraná in Argentina (see Fig. 101), but possibly also occurs in Río Paraguay. Citations of P. histrix for Venezuela (Fernández-Yépez, 1948; Mago-Leccia, 1970;

Brooks, Thorson and Mayes, 1981), for Guianas and Surinam (Eigenmann and Eigenmann, 1891; Goeldi, 1898; Eigenmann and Allen, 1942; Boeseman, 1948; Fowler, 1948), for Ecuador (Ovchynnyk, 1968; Saul, 1975), for Peru (Fowler, 1940, 1945; Lüling, 1945), and from Amazonas (Günther, 1870; Boulanger, 1897; Starks, 1913; Fowler, 1948) possibly represent misidentifications or compilations based on the erroneous geographic range given for the species by Müller and Henle (1841).

Additional references: Castex, 1964b (synonymy and misidentification); Castex, 1965a (misidentification); Duméril, 1865 (redescription); Eigenmann, 1907 (citation for Paraguay); Eigenmann and Kennedy, 1903 (citation for Asunción), Eigenmann and Allen, 1942 (citation for Peru); Fowler, 1940, 1945a (citations for Peru); Garman, 1913 (synonymy and redescription); Lüling, 1965 (misidentification); Ringuelet et al., 1967 (synonymy and redescription); Schomburgk, 1843 (illustration based on Orbigny's original plate).

TABLE 12

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Potamotrygon histrix*

	HOLOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	290	7	-	-	254 -465
DISC LENGTH (mm)	326		-	-	277 -489
DISC LENGTH (%)	112.0	7	109.9	3.0	105.1-113.2
TOTAL LENGTH (%)	-	-	-	-	-
INTERNAL DL (%)	97.5	4	97.3	2.0	94.4- 98.9
MOUTH TO SCAPULOCORACOID(%)	-	5	33.9	0.5	33.1- 34.3
MOUTH TO CLOACA (%)	72.7	7	73.1	3.1	70.0- 78.6
CLOACA TO STING (%)	58.6	6	52.1	3.8	48.3- 58.6
TAIL LENGTH (%)	-	-	-	-	-
TAIL WIDTH (%)	-	5	9.7	1.4	7.4- 11.1
TAIL WIDTH AT STING BASE (%)	-	4	4.0	0.6	3.2- 4.6
TAIL HEIGHT (%)	-	5	6.2	0.5	5.6- 6.8
PELVIC FIN WIDTH (%)	35.0	6	28.0	3.7	25.4- 35.0
PELVIC FIN LENGTH (%)	20.1	6	23.1	2.6	20.1- 26.6
CLASPER LENGTH (%)	-	1	26.9	-	-
STING LENGTH (%)	21.5	5	18.6	3.2	13.2- 21.5
PRECLOACAL LENGTH (%)	89.6	6	87.5	5.1	77.2- 91.3
PREORAL LENGTH (%)	18.4	6	18.6	0.7	17.6- 19.5
PRENARIAL LENGTH (%)	13.6	6	12.7	1.0	11.2- 13.6
BRANCHIAL BASKET LENGTH (%)	19.6	6	18.1	0.9	17.0- 19.6
BRANCHIAL BASKET WIDTH (%)	26.9	6	27.0	0.7	26.0- 28.1
MOUTH WIDTH (%)	11.3	6	9.4	1.2	8.1- 11.3
NOSTRIL LENGTH (%)	5.7	6	6.2	0.3	5.7- 6.6

TABLE 12

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
INTERNARIAL WIDTH (%)	8.4	6	7.8	0.3	7.3- 8.4
EYE LENGTH (%)	3.2	6	2.9	0.5	2.1- 3.5
SPIRACLE LENGTH (%)	9.8	6	8.8	0.8	7.4- 9.8
INTEROCULAR WIDTH (%)	15.2	6	17.4	1.4	15.2- 19.2
INTERSPIRACULAR WIDTH (%)	17.0	6	18.3	0.8	17.0- 19.2
PREOCULAR LENGTH (%)	26.9	6	25.9	0.6	25.2- 26.9
CRANIUM LENGTH (%)	28.0	-	-	-	-
CRANIUM WIDTH (%)	19.5	-	-	-	-
PREORBITAL WIDTH (%)	20.5	-	-	-	-
POSTORBITAL WIDTH (%)	9.4	-	-	-	-
INTERORBITAL WIDTH (%)	7.6	6	7.8	0.8	6.8- 9.4
FONTANELLE LENGTH (%)	19.2	-	-	-	-
FONTANELLE WIDTH (%)	6.7	-	-	-	-
UPPER DENTAL PLATE WIDTH (%)	7.0	7	6.3	0.4	5.9- 7.0
LOWER DENTAL PLATE WIDTH (%)	6.3	7	5.9	0.5	5.0- 6.3
PRECAUDAL VERTEBRAE	25	1	25	-	-
CAUDAL VERTEBRAE	98	1	98	-	-
CAUDAL VERTEBRAE TO BASE OF STING	78	1	78	-	-
TOTAL VERTEBRAE	123	1	123	-	-
DIPLOSPONDYLOUS VERTEBRAE	5	1	5	-	-
SYNARCUAL VERTEBRAE	3	2	3	-	-
PELVIC RADIALS ♀	25	2	26.5	-	25- 28
PROPTERYGIAL RADIALS	43	2	44.0	-	43- 45

TABLE 12

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
MESOPTERYGIAL RADIALS	12	2	12.5	-	12- 13
METAPTERYGIAL RADIALS	39	2	38.5	-	38- 39
TOTAL PECTORAL RADIALS	94	2	93.5	-	93- 94
UPPER TOOTH ROWS	37	7	32.7	4.8	26- 40
LOWER TOOTH ROWS	33	7	33.0	4.4	27- 42
LOWER MEDIAN TEETH	10	5	5.6	2.5	4- 10
MIDDORSAL SPINES	29	4	40.5	19.3	29- 69

FIG. 54

Potamotrygon histrix, dorsal view, female, 325 mm DL, MNHN 2449 (holotype).

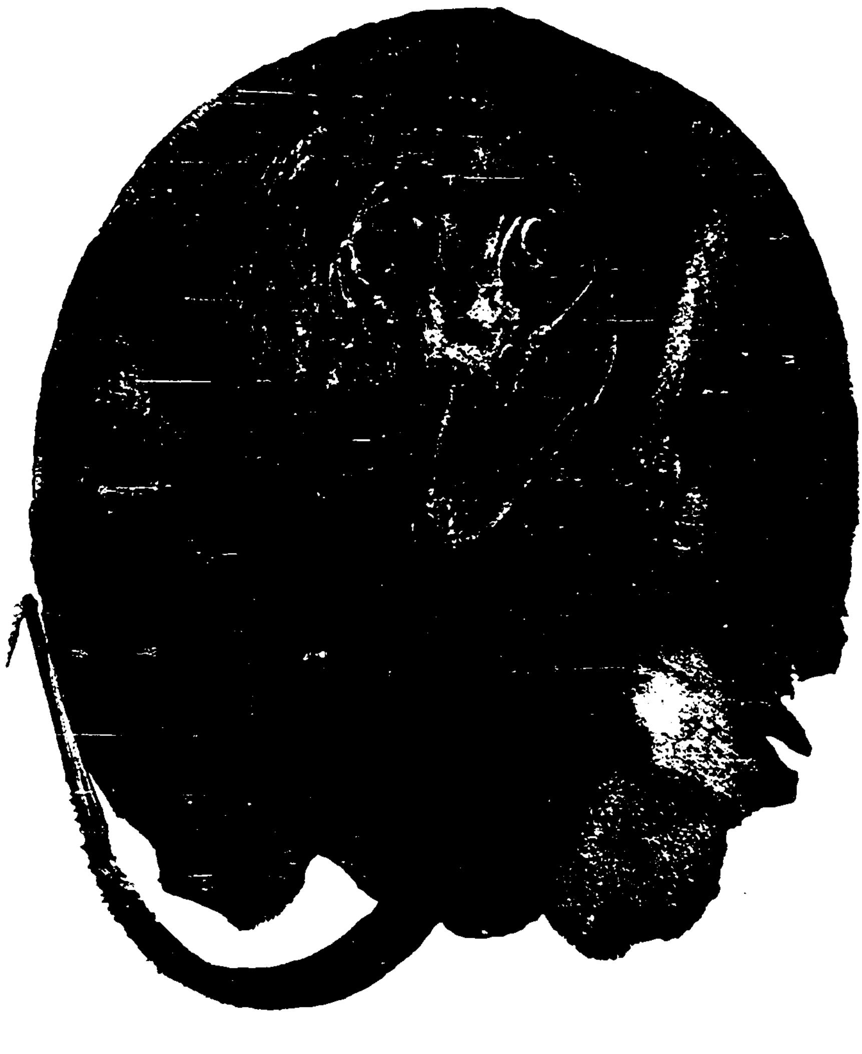
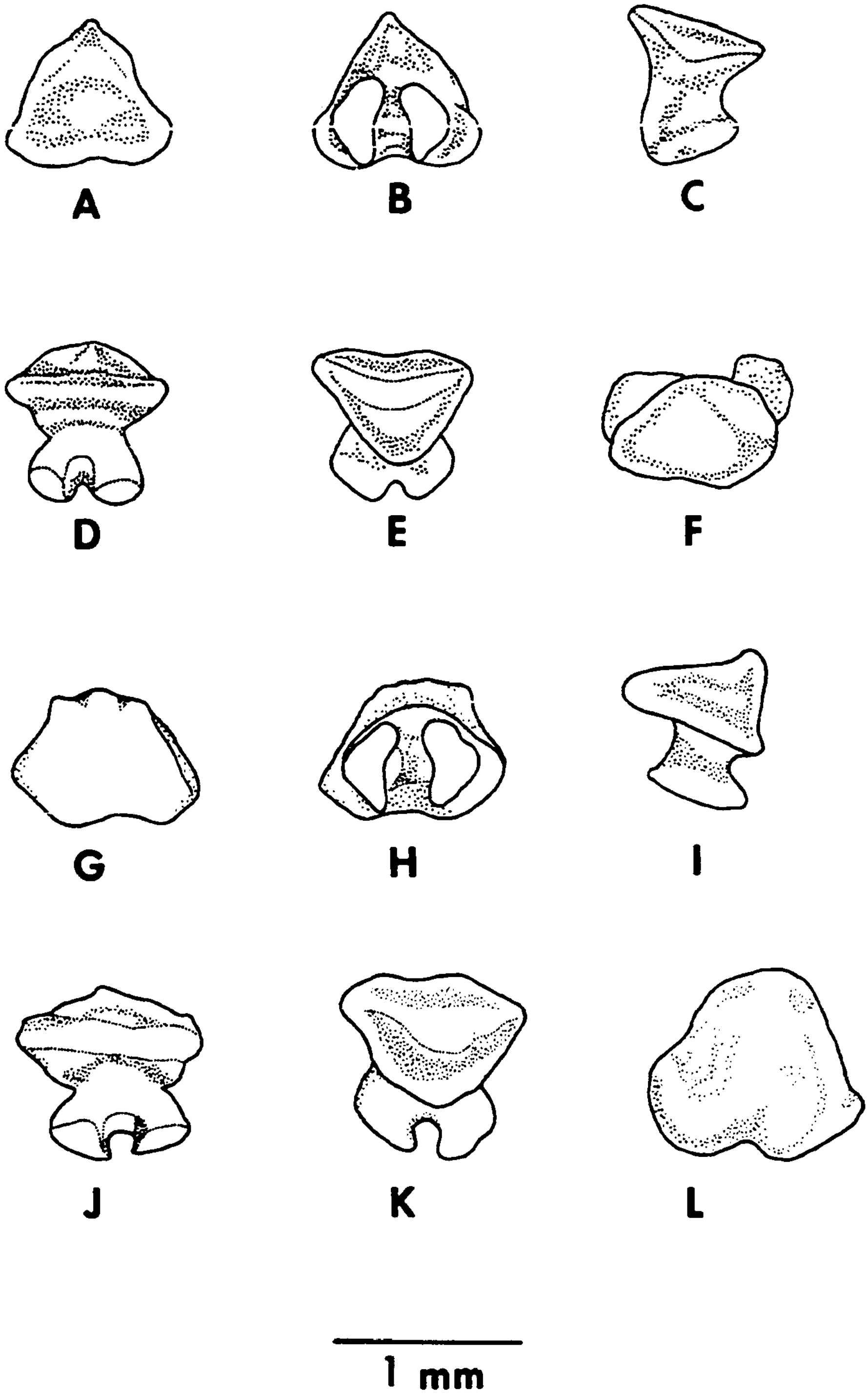


FIG. 55

Potamotrygon histrix, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, male, 277 mm DL, BMNH 1872.6.8.1. F.- Tooth from upper jaw near mouth corner, female, 473 mm DL, MFA 300. G - K.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, female, 325 mm DL, MNHN 2449 (holotype). L.- Tooth from lower jaw near symphysis, apical view, female, 473 mm DL, MFA 300.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1 mm

Potamotrygon humerosa Garman, 1913

(Figs. 18A, 26A, 56-57)

Potamotrygon humerosus Garman, 1913: 419-420 (original description, Montalegre, Brazil, not illustrated).

Holotype: MCZ 299-S, by original indication, female, coll. L. Agassiz, Thayer Expedition.

Type locality: Monte Alegre, Rio Amazonas, Pará, Brazil.

Remarks.- No holotype designation was given in the original description. Measurements, sex, locality data, and Garman's identification of the only specimen of P. humerosa found in the MCZ (MCZ 299-S) agree with those of the type. The holotype (Fig. 56) is in bad condition, partially dissected, with broken tail, and six conspicuous fish bites around disc margins. No precise disc measurements could be taken on the holotype. Castex (1967a) mistakenly reported that the type of P. humerosa was identical to P. motoro. These two species are distinct in coloration, dentition, and in the relative size of denticles and tubercles. The specific name, interpreted as an adjective, is herein changed to P. humerosa to agree in gender with Potamotrygon.

Diagnosis.- A species of Potamotrygon from the lower Amazon drainage diagnosed by the following combination of characters:

disc subcircular, with reticulate pattern of dark pigment on brown background, delimiting circular or hexagonal spaces; disc rough, with sharp denticles and sometimes with submarginal tubercles; tail with enlarged middorsal and lateral spines, irregularly distributed from tail base to insertion of caudal sting. Potamotrygon humerosa is distinguished from P. orbignyi by its relatively rougher disc and tail, with relatively larger denticles and spines at any size, and by the reticulate pattern of the interorbital region (see Fig. 26).

Description.- Measurements and counts are given in Table 13. Disc subcircular, disc length 1.01-1.14 times DW. Pelvic fins usually covered dorsally by disc. Tail relatively short, tail length 1.0-1.3 times DW; caudal sting relatively long, sting length 1.5-3.0 times tail width.

Eyes relatively large, eye length 0.8-1.9 in interorbital distance, 2.7-4.3 in interocular distance. Preocular distance 3.4-3.9 in DW, 1.2-1.6 times interocular distance. Spiracles relatively large, spiracle length 1.1-2.0 times eye length. 2.0-2.4 in interspiracular distance. Mouth relatively small, mouth width 0.8-1.1 times internarial distance. Three slender medial papillae and two small lateral papillae on floor of buccal cavity. Preoral distance 17.3-23.3 percent of DW. Teeth relatively small (Fig. 57), closely crowded in quincunx, in 23/21 to 45/47 longitudinal rows, and four to nine exposed teeth in median row of lower dental plate. Tooth crowns pointed, with large median cusp and two lateral accessory cusps. Nostril length 0.9-1.4 in internarial distance. Branchial basket relatively narrow, its greatest width 3.7-4.6 in DW; distance between first and fifth gill slits 5.5-6.5 in DW.

Dorsal surface of disc covered with sharp denticles, more developed along midline. Submarginal series of tubercles sometimes present on disc. Tail with 7 to 32 enlarged middorsal spines (Fig. 57) in irregular row. Latero-caudal spines well-developed in adults, from tail base to insertion of caudal sting.

Dorsal surface of disc light brown to dark brown, with reticulate pattern of dark pigment, delimiting circular or hexagonal spaces. Diameter of largest reticulate shape nearly equal to interocular distance. Reticulate shapes decrease in size towards disc margins. Pelvic fins dorsally with same pattern as disc. Tail dorsally brown, with lateral dark bars, and ventrally mottled with irregular white spots. Ventral surface of disc and pelvic fins white with brown margins. Central dark spot present or absent ventrally on disc.

Geographic distribution.- Northern Brazil, in the lower Amazon drainage, from Rio Tapajós to Rio Pará (see Fig. 101).

TABLE 13

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Potamotrygon humerosa*

	HOLOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	264	-	-	-	86.0-264
DISC LENGTH (mm)	294	-	-	-	91.0-294
DISC LENGTH (%)	111.3	20	107.1	4.0	101.1-114.1
TOTAL LENGTH (%)	-	5	202.0	11.4	191.8-216.0
INTERNAL DL (%)	91.2	18	93.5	3.2	87.3- 98.0
MOUTH TO SCAPULOCORACOID (%)	36.3	16	33.0	1.2	31.6- 36.3
MOUTH TO CLOACA (%)	76.8	18	66.3	3.8	58.1- 76.8
CLACA TO STING (%)	52.4	17	43.5	4.7	36.5- 52.4
TAIL LENGTH (%)	73.2*	4	114.9	11.3	102.6-126.6
TAIL WIDTH (%)	8.0	18	9.7	1.2	7.7- 11.9
TAIL WIDTH AT STING BASE (%)	4.6	17	5.2	0.7	4.1- 6.7
TAIL HEIGHT (%)	5.7	18	5.8	0.8	3.8- 7.2
PELVIC FIN WIDTH (%)	22.5	15	26.9	3.0	21.6- 32.4
PELVIC FIN LENGTH (%)	21.2	16	19.7	2.0	16.5- 22.6
CLASPER LENGTH (%)	-	9	12.8	6.2	8.6- 26.3
STING LENGTH (%)	20.0	17	24.5	4.4	18.2- 33.0
PRECLOACAL LENGTH (%)	92.0	18	85.7	3.1	81.4- 92.0
PREORAL LENGTH (%)	-	16	19.7	1.3	17.3- 23.3
PRENARIAL LENGTH (%)	-	16	14.8	1.0	13.9- 16.0
BRANCHIAL BASKET LENGTH (%)	17.9	18	16.5	0.7	15.4- 17.9
BRANCHIAL BASKET WIDTH (%)	26.4	18	23.8	1.4	21.5- 26.6
MOUTH WIDTH (%)	8.7	18	7.9	1.0	5.4- 9.7

* Tail broken on holotype.

TABLE 13

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
NOSTRIL LENGTH (%)	4.8	15	6.1	0.8	4.8- 8.3
INTERNARIAL WIDTH (%)	7.5	18	7.6	0.8	5.5- 9.7
EYE LENGTH (%)	3.8	20	5.6	1.1	3.8- 8.0
SPIRACLE LENGTH (%)	7.8	18	8.0	0.5	7.1- 9.0
INTEROCULAR WIDTH (%)	18.3	16	19.6	1.6	16.4- 21.7
INTERSPIRACULAR WIDTH (%)	17.5	18	18.3	1.3	16.2- 20.4
PREOCULAR LENGTH (%)	28.5	17	27.3	1.1	25.6- 29.0
CRANIUM LENGTH (%)	26.8	5	25.9	1.0	24.2- 26.8
CRANIUM WIDTH (%)	12.4	5	14.7	1.4	12.4- 15.9
PREORBITAL WIDTH (%)	-	4	18.5	0.4	18.1- 19.0
POSTORBITAL WIDTH (%)	8.9	5	9.0	0.2	8.8- 9.4
INTERORBITAL WIDTH (%)	8.3	18	8.2	1.2	6.5- 9.7
FONTANELLE LENGTH (%)	18.9	5	17.5	0.9	16.5- 18.9
FONTANELLE WIDTH (%)	7.6	5	6.6	0.8	5.5- 7.6
UPPER DENTAL PLATE WIDTH (%)	7.5	18	6.7	0.7	5.3- 8.3
LOWER DENTAL PLATE WIDTH (%)	7.9	18	6.1	0.7	5.3- 8.0
PRECAUDAL VERTEBRAE	30	11	30.0	1.1	28- 32
CAUDAL VERTEBRAE	108	10	97.7	6.1	91- 108
CAUDAL VERTEBRAE TO BASE OF STING	67	11	71.6	6.6	62- 83
TOTAL VERTEBRAE	138	10	127.9	5.7	120- 138
DIPLOSPONDYLOUS VERTEBRAE	6	9	8.3	2.7	5- 13
SYNARCUAL VERTEBRAE	3	11	3.4	0.8	2- 5

TABLE 13

(continued)

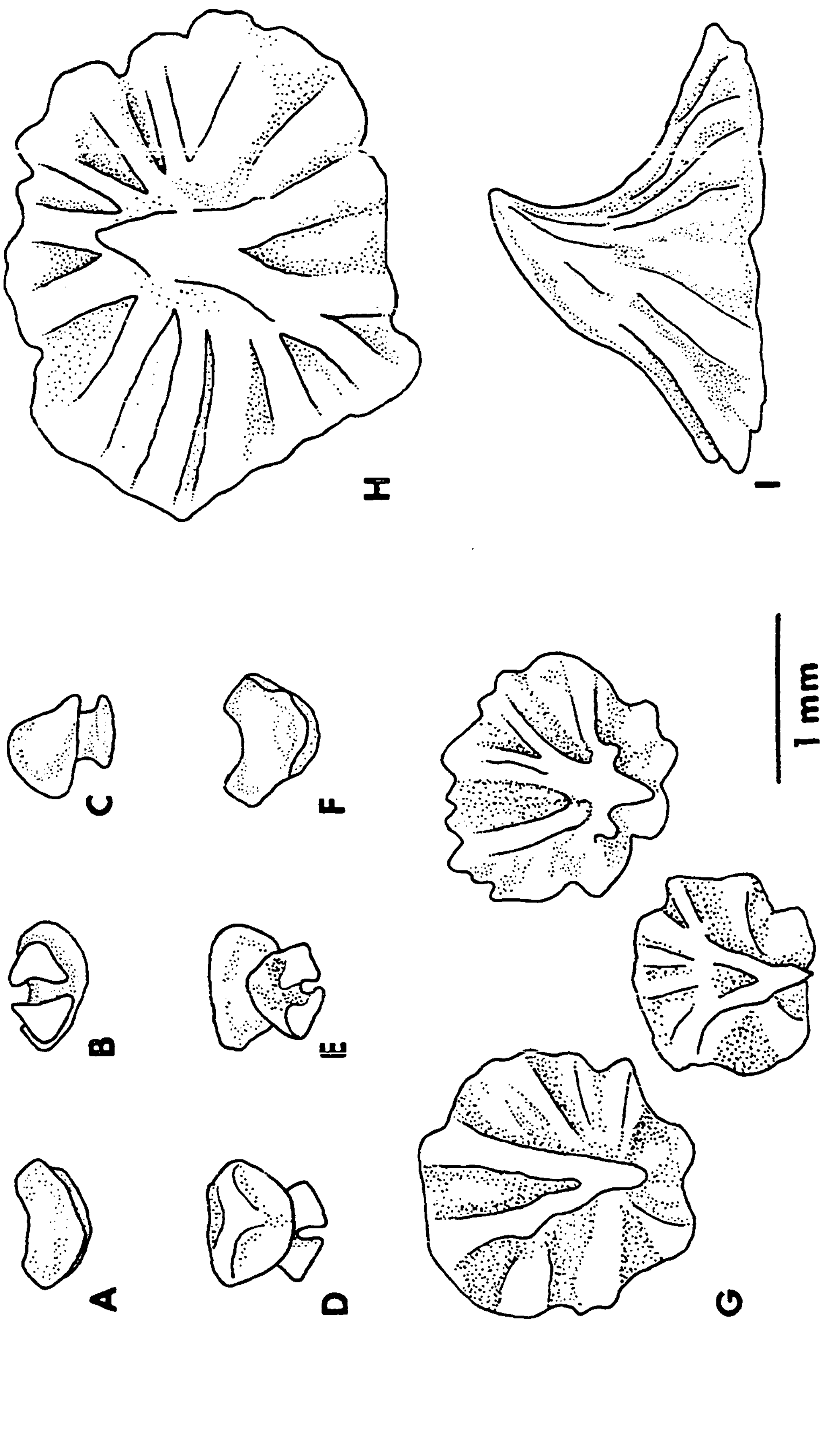
		HOLOTYPE	N	MEAN	S.D.	RANGE
PELVIC RADIALS	♂	-	5	18.4	0.5	18- 19
	♀	24	6	24.3	1.0	23- 26
PROPTERYGIAL RADIALS		43	11	43.5	1.1	42- 45
MESOPTERYGIAL RADIALS		16	11	15.9	1.1	14- 18
METAPTERYGIAL RADIALS		37	11	37.2	1.7	34- 40
TOTAL PECTORAL RADIALS		96	11	96.7	2.6	94-101
UPPER TOOTH ROWS		45	17	28.7	5.1	23- 45
LOWER TOOTH ROWS		47	18	26.8	7.3	21- 47
LOWER MEDIAN TEETH		8	16	5.5	1.5	4- 9
MIDDORSAL SPINES		20	18	12.5	6.3	7- 32

FIG. 56

Potamotrygon humerosa, dorsal view, female, 294 mm DL, MCZ 299-S (holotype).

FIG. 57

Potamotrygon humerosa, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, lingual, and labial views, female, MCZ 299-S (holotype). F.- Tooth from lower jaw near symphysis, apical view, MCZ 299-S. G.- Dermal denticles from disc near midline, MCZ 299-S. H - I.- Middorsal tail spine anterior to caudal sting, apical and lateral views, MCZ 299-S.


A
B
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1 mm

<u>Potamotrygon leopoldi</u> Castex & Castello, 1970

(Figs. 58-60)

<u>Potamotrygon leopoldi</u> Castex and Castello, 1970b: 1-16 (<u>original description</u>, <u>Rio Xingu</u>).

Holotype: IRSNB 23936, by original designation, male.

Type locality: upper Rio Xingu, below the confluence of Rio Auia-Missú, Mato Grosso, Brazil.

Remarks.- <u>Potamotrygon leopoldi</u> was described only from the holotype (Fig. 58). One additional female specimen (Fig. 59) recently collected in Rio Fresco, a tributary of Rio Xingu, was available at the MZUSP collection. There was no material for dissections, nor radiographs available for study. The following diagnosis and description are based only on these two specimens.

Diagnosis.- A species of <u>Potamotrygon</u> from Rio Xingu drainage diagnosed by the following combination of characters: dorsal surface dark gray to black with white to yellow ocelli; ocelli irregular in shape on center of disc, and circular near disc margins; ocelli extend distally on tail; triple rows of middorsal spines; teeth relatively small, in 23 to 35 longitudinal rows in upper jaw.

<u>Potamotrygon leopoldi</u> and <u>P. henlei</u> have similar color

patterns, with light ocelli on dark background, extending distally on tail, sometimes enclosing a dark spot in center. Both species have triple rows of middorsal spines. _Potamotrygon leopoldi_ has relativelly smaller teeth, in larger number of longitudinal rows than _P. henlei_ (see remarks under _P. henlei_). Additional specimens of both species are necessary for further comparative study.

Description.- Measurements and counts are given in Table 14. Disc subcircular, disc length 1.05-1.14 times DW. Pelvic fins dorsally covered by disc. Tail broken in holotype, remaining portion 1.2 in DW, with well-developed dorsal and ventral finfolds. Caudal sting large, sting length 2.0-2.4 times tail width, its insertion from cloaca 1.4-1.8 in distance from mouth to cloaca.

Eyes relatively large, eye length 2.0-2.9 in interorbital distance, 4.2-5.3 in interocular distance. Five papillae on floor of buccal cavity. Preoral distance 21.6-22.0 percent of DW. Teeth relatively small (Fig. 60), in 23/24 to 35/39 longitudinal rows, and six to eight exposed teeth in median row of lower dental plate. Median teeth rhombic in both jaws, lateral teeth triangular and less pointed. Nostrils 1.2-1.4 in internarial distance. Branchial basket relatively wide, its greatest width 3.7-4.2 in DW; distance between first and fifth gill slits 6.6-7.3 in DW. Dermal denticles more developed near center of disc. Tail with 48 to 84 middorsal spines in three parallel rows. Latero-caudal spines moderately developed near insertion of caudal sting.

Dorsal surface of disc dark gray to black, with submarginal circular yellow ocelli with white center, and irregularly shaped median ocelli, which enclose dark central spot, or form incomplete circles. Seven to fifteen submarginal ocelli on disc in row from tail base to anterior disc. Ocelli present on dorsal and lateral surfaces of tail, irregularly shaped distally on tail. Ventral surface dark pigmented, except peri-buccal region, white. Ventral margins of disc with small white spots; center of disc with or without dark spot.

Geographic distribution: Potamotrygon leopoldi is known from two specimens of Rio Xingu drainage, in the states of Pará and Mato Grosso in Brazil (see Fig. 101), possibly being endemic there.

TABLE 14

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Potamotrygon leopoldi*

	HOLOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	371	2	-	-	214 -371
DISC LENGTH (mm)	423	2	-	-	266 -423
DISC LENGTH (%)	114.0	2	109.8	-	105.6-114.0
TOTAL LENGTH (%)	-	-	-	-	-
INTERNAL DL (%)	109.7	2	100.4	-	91.1-109.7
MOUTH TO SCAPULOCORACOID(%)	35.4	2	33.6	-	31.9- 35.4
MOUTH TO CLOACA (%)	69.5	2	65.7	-	61.9- 69.5
CLOACA TO STING (%)	48.5	2	41.3	-	34.1- 48.5
TAIL LENGTH (%)	83.8*	-	-	-	-
TAIL WIDTH (%)	10.7	2	10.3	-	9.9- 10.7
TAIL WIDTH AT STING BASE (%)	6.5	2	5.4	-	4.3- 6.5
TAIL HEIGHT (%)	7.9	2	6.8	-	5.8- 7.9
PELVIC FIN WIDTH (%)	29.8	2	28.4	-	27.1- 29.8
PELVIC FIN LENGTH (%)	22.1	2	21.9	-	21.8- 22.1
CLASPER LENGTH (%)	28.4	-	-	-	-
STING LENGTH (%)	20.9	2	22.6	-	20.9- 24.3
PRECLOACAL LENGTH (%)	91.6	2	87.1	-	82.7- 91.6
PREORAL LENGTH (%)	22.0	2	21.8	-	21.6- 22.0
PRENARIAL LENGTH (%)	14.7	2	15.2	-	14.7- 15.7
BRANCHIAL BASKET LENGTH (%)	14.9	2	14.2	-	13.6- 14.9
BRANCHIAL BASKET WIDTH (%)	26.5	2	25.1	-	23.7- 26.5
MOUTH WIDTH (%)	9.5	2	9.1	-	8.8- 9.5

*Tail broken on holotype

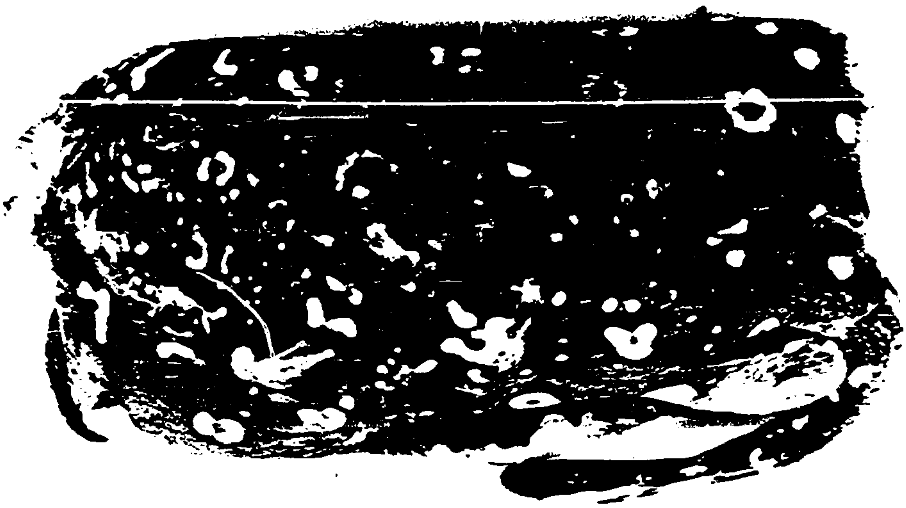
TABLE 14

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
NOSTRIL LENGTH (%)	6.9	2	6.3	-	5.8- 6.9
INTERNARIAL WIDTH (%)	8.5	2	8.3	-	8.2- 8.5
EYE LENGTH (%)	3.6	2	4.1	-	3.6- 4.6
SPIRACLE LENGTH (%)	9.3	2	8.5	-	7.2- 9.3
INTEROCULAR WIDTH (%)	19.4	2	19.5	-	19.4- 19.7
INTERSPIRACULAR WIDTH (%)	21.4	2	20.3	-	19.2- 21.4
PREOCULAR LENGTH (%)	30.3	2	28.8	-	27.4- 30.3
CRANIUM LENGTH (%)	-	-	-	-	-
CRANIUM WIDTH (%)	-	-	-	-	-
PREORBITAL WIDTH (%)	-	-	-	-	-
POSTORBITAL WIDTH (%)	-	-	-	-	-
INTERORBITAL WIDTH (%)	10.6	2	9.9	-	9.6- 10.6
FONTANELLE LENGTH (%)	-	-	-	-	-
FONTANELLE WIDTH (%)	-	-	-	-	-
UPPER DENTAL PLATE WIDTH (%)	9.4	2	8.5	-	7.6- 9.4
LOWER DENTAL PLATE WIDTH (%)	9.1	2	8.1	-	7.1- 9.1
UPPER TOOTH ROWS	35	2	29	-	23- 35
LOWER TOOTH ROWS	39	2	31.5	-	24- 39
LOWER MEDIAN TEETH	6	2	7	-	6- 8
MIDDORSAL SPINES	84	2	66	-	48- 84

FIG. 58

Potamotrygon leopoldi, A.- Dorsal view, male, 423 mm DL, IRSNB 23936 (holotype). B.- Dorsal view of tail showing triple rows of spines, and caudal ocelli, IRSNB 23936.



A

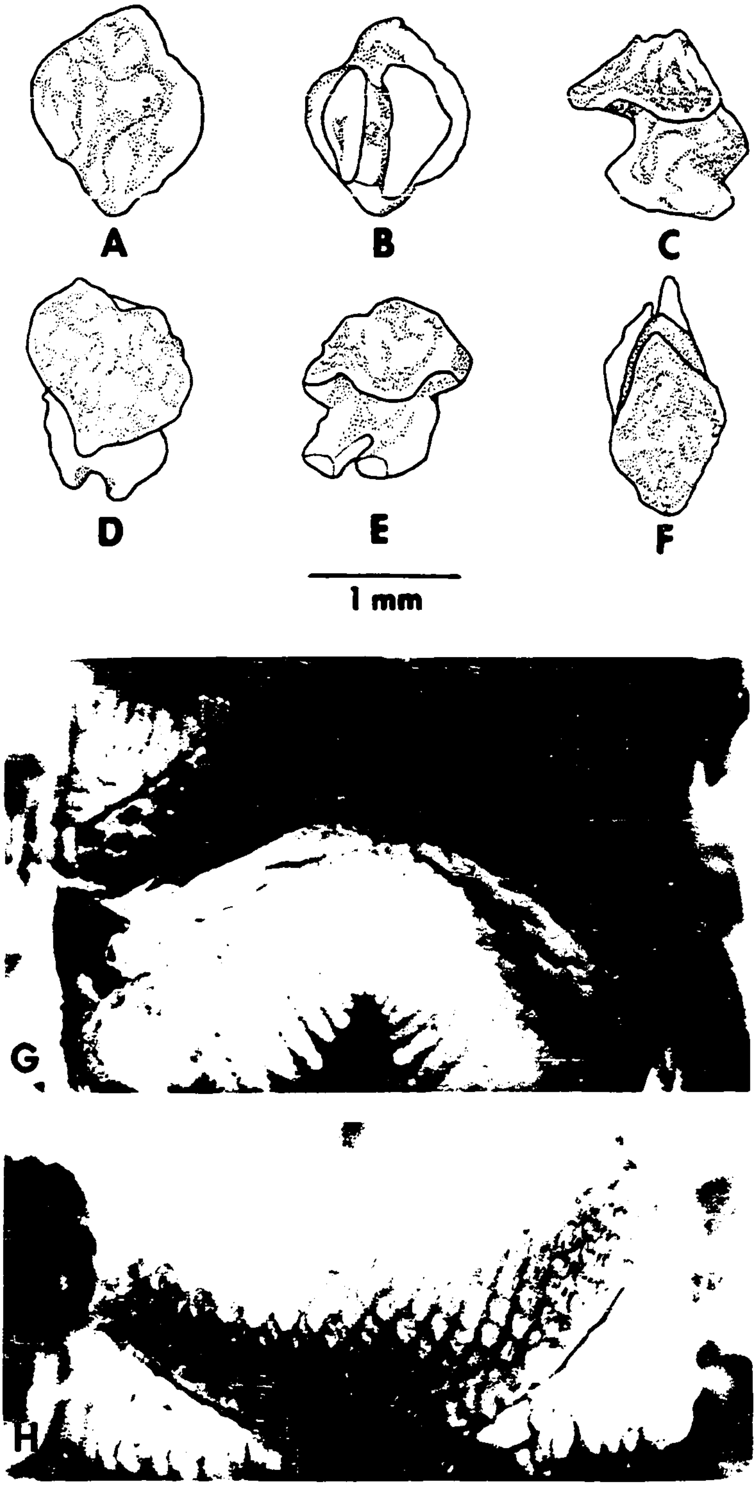
B

FIG. 59

Potamotrygon leopoldi, dorsal view, female,
226 mm DL, MZUSP (uncatalogued specimen).
Courtesy of H. Britski (MZUSP).

FIG. 60

Potamotrygon leopoldi, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, lingual, and labial views. F.- Tooth from lower jaw near symphysis, apical view. G.- Upper dental plate. H.- Lower dental plate. All from male, 423 mm DL, IRSNB 23936 (holotype).


A
B
C
D
E
F
1 mm
G
H

Potamotrygon magdalenae (Valenciennes, 1865)

(Figs. 18B, 22F, 23B, 61-63)

Taeniura magdalenae Valenciennes in Duméril, 1865: 625 (original description, Río Magdalena, not illustrated).

Potamotrygon magdalenae. Eigenmann and Eigenmann, 1891: 25.

Taenura magdalenae [sic]. Miles, 1947: 40.

Potamotrigon magdalenae [sic]. Miles, 1947: 41.

Paratrygon magdalenae. Fowler, 1970: 47.

[non] Potamotrygon magdalenae. Schultz, 1949: 29.

[non] Potamotrygon magdalenae. Fernández-Yépez and Espinosa, 1970: 13.

Holotype: MNHN 2368, by original indication, male, coll. Roulin.

TYpe locality: Río Magdalena, Colombia.

Remarks.- No collection number was given for the type in the original description. However, the specimen catalogued as type in the MNHN (MNHN 2368, see Fig. 61) corresponds in sex, measurements, and locality data with the single type described in Duméril (1865). Garman (1880) indicated that Taeniura magdalenae should be placed in the genus Potamotrygon. Schultz (1949) and Fernández-Yépez and Espinosa (1970) misidentified specimens of Potamotrygon yepezi from Lake Maracaibo as P.

magdalenae.

Diagnosis.- A species of Potamotrygon from the Río Magdalena and Río Atrato drainages diagnosed by the following combination of characters: disc oval, disc length greater than disc width; dorsal surface of disc light-brown to dark olivaceous-brown, usually mottled with small yellow spots, forming vermiculations.

Description.- Measurements and counts are given in Table 15. Disc oval, disc length 1.06-1.18 times DW. Pelvic fins usually dorsally covered by disc. Tail relatively long, tail length 1.1-2.0 times DW, with well-developed dorsal and ventral finfolds; dorsal finfold heigth 1.8-2.3 percent of DW, 2.1-3.5 in tail height. Caudal sting relatively long, sting length 1.9-2.8 times tail width.

Eyes relatively large, eye length 2.1-3.8 in interorbital distance, 6.5-8.1 in interocular distance. Preocular distance 3.3-4.0 in DW, 1.2-1.6 times interocular distance. Spiracles relatively large, spiracle length 1.3-2.5 times eye lenght, 2.3-3.6 in interspiracular distance. Mouth relatively small and curved, mouth width 0.8-1.3 times internarial distance. Mouth with five papillae at bottom (up to eight papillae fide Steindachner, 1878). Preoral distance 18.4-24.5 percent of DW. Teeth small (Fig. 62), white to brown in color, with tetragonal or hexagonal crowns, closely crowded in quincunx, in 22/22 to 39/36 longitudinal rows, and three to eleven exposed teeth in median row of lower dental plate. Teeth sexually dimorphic (Fig. 63), adult malês with pointed teeth in both jaws, females with blunt teeth. Adult males with marked heterodonty in both jaws, with pointed teeth in median rows, and blunt lateral teeth. Adult females with strong heterodonty in one or both jaws; lower jaw bearing enlarged teeth with blunt hexagonal crowns in median rows, and smaller elliptic lateral teeth. Median portion of upper dental plate concave; upper jaw with enlarged lateral teeth and smaller median teeth. Nostril length 1.1-2.3 in internarial distance. Branchial basket relatively wide, its greatest width 3.4-3.6 in DW; distance between first and fifth gill slits 5.1-6.0 in DW.

Disc relatively smooth, its dorsal surface covered with small denticles, more developed along midline, and on anterior portion of disc in adult females. Tail with four to 21 small dorsal spines in single row. Latero-caudal spines poorly developed near insertion of sting in adults, absent in juveniles.

Dorsal surface of disc and tail light brown to dark grayish-brown, usually mottled with irregular yellow spots, more evident in juveniles. Spots relatively small, usually less than eye in diameter, and decreasing in size towards disc margins. Adults with darker disc, and less conspicuous spots. Pelvic fins with same dorsal pattern as disc. Ventral surface of disc white in center, with dark-brown nargins mottled with irregular white spots. Pelvic fins and claspers dark brown distally. Ventral surface of tail dark brown.

Geographic distribution.- Northern Colombia, in Río Magdalena and Río Atrato drainages (see Fig. 101).

Additional references: Brooks and Thorson, 1976 (intestinal parasites); Brooks et al., 1979 (idem); Castex and Suilar, 1965 (redescription); Dahl, 1971 (citations for Cauca and San Jorge rivers); Eigenmann, 1910, 1912, 1921, 1922 (citations for the Magdalena and Atrato river drainages); Fowler, 1945b (citation for Honda); Mayes at al., 1978 (intestinal parasites).

TABLE 15

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Potamotrygon magdalenae*

	HOLOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	153.0	-	-	-	64.3- 230
DISC LENGTH (mm)	174.0	-	-	-	69.0- 271
DISC LENGTH (%)	113.7	36	111.3	3.1	106.1-117.8
TOTAL LENGTH (%)	222.8	20	249.1	31.9	197.2-298.5
INTERNAL DL (%)	96.2	29	98.7	2.9	90.3-104.1
MOUTH TO SCAPULOCORACOID(%)	33.8	26	35.2	1.6	30.4- 38.8
MOUTH TO CLOACA (%)	70.4	28	71.5	2.5	66.2- 78.4
CLOACA TO STING (%)	69.0	28	60.1	3.8	55.0- 69.7
TAIL LENGTH (%)	124.1	21	149.6	30.3	110.9-195.0
TAIL WIDTH (%)	10.1	28	11.1	1.1	8.9- 13.1
TAIL WIDTH AT STING BASE (%)	4.1	27	4.6	0.5	3.4- 5.8
TAIL HEIGHT (%)	7.0	28	6.1	0.7	4.7- 7.2
PELVIC FIN WIDTH (%)	29.4	28	30.5	5.5	22.8- 36.9
PELVIC FIN LENGTH (%)	32.6	29	25.5	2.5	19.0- 32.6
CLASPER LENGTH (%)	34.8	17	29.1	6.1	14.3- 34.8
STING LENGTH (%)	27.6	24	23.9	4.5	17.5- 32.9
PRECLOACAL LENGTH (%)	93.2	27	92.2	2.4	88.6- 97.6
PREORAL LENGTH (%)	23.7	29	21.5	1.6	18.4- 24.5
PRENARIAL LENGTH (%)	18.2	29	15.9	1.3	13.0- 19.2
BRANCHIAL BASKET LENGTH (%)	16.8	28	17.8	0.6	16.7- 19.3
BRANCHIAL BASKET WIDTH (%)	24.0	28	27.1	1.8	22.9- 28.9
MOUTH WIDTH (%)	9.0	28	9.2	0.7	7.5- 10.4

TABLE 15

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
NOSTRIL LENGTH (%)	5.6	23	6.0	0.7	3.6- 7.1
INTERNARIAL WIDTH (%)	8.4	28	8.4	0.5	7.5- 9.4
EYE LENGTH (%)	3.9	29	4.1	0.7	2.9- 5.8
SPIRACLE LENGTH (%)	6.4	28	7.3	0.9	5.6- 9.1
INTEROCULAR WIDTH (%)	17.8	24	19.9	1.8	17.1-24.1
INTERSPIRACULAR WIDTH (%)	19.6	27	19.9	1.0	17.7-22.7
PREOCULAR LENGTH (%)	28.0	26	27.3	1.5	24.7-30.0
CRANIUM LENGTH (%)	-	19	28.2	0.8	26.8-30.1
CRANIUM WIDTH (%)	-	19	17.8	0.4	17.1-18.7
PREORBITAL WIDTH (%)	-	19	18.4	0.5	17.4-19.6
POSTORBITAL WIDTH (%)	-	13	10.1	0.4	9.6-11.1
INTERORBITAL WIDTH (%)	9.4	27	9.9	0.6	8.6-10.5
FONTANELLE LENGTH (%)	-	19	18.3	0.8	17.4-20.2
FONTANELLE WIDTH (%)	-	19	7.5	0.5	6.5- 8.6
UPPER DENTAL PLATE WIDTH (%)	8.4	27	8.4	0.7	6.5- 9.6
LOWER DENTAL PLATE WIDTH (%)	7.5	27	8.0	0.7	6.7- 9.3
PRECAUDAL VERTEBRAE	-	27	24.1	0.8	23- 26
CAUDAL VERTEBRAE	-	26	106.1	3.7	101- 105
CAUDAL VERTEBRAE TO BASE OF STING	-	29	80.9	4.0	73- 87
TOTAL VERTEBRAE	-	25	130.3	4.0	122- 140
DIPLOSPONDYLOUS VERTEBRAE	-	23	15.3	2.0	11- 19
SYNARCUAL VERTEBRAE	-	26	1.7	0.5	1- 3

TABLE 15

(continued)

		HOLOTYPE	N	MEAN	S.D.	RANGE
PELVIC RADIALS	♂	-	10	18.8	1.0	17- 20
	♀	-	16	23.1	1.5	20- 27
PROPTERYGIAL RADIALS		-	25	42,3	1.5	40- 45
MESOPTERYGIAL RADIALS		-	30	12.4	0.8	11- 14
METAPTERYGIAL RADIALS		-	26	32.1	1.5	30- 35
TOTAL PECTORAL RADIALS		-	30	86.9	2.2	83- 92
UPPER TOOTH ROWS		23	24	28.0	4.0	22- 39
LOWER TOOTH ROWS		24	24	27.9	4.2	22- 36
LOWER MEDIAN TEETH		5	24	5.4	2.2	3- 14
MIDDORSAL SPINES		4	22	12.1	4.6	4- 21

FIG. 61

Potamotrygon magdalenae, dorsal view, male,
174 mm DL, MNHN 2368 (holotype).

FIG. 62

Potamotrygon magdalenae, A.- Exposed portions of upper and lower dental plates, male, 164 mm DL, TBT 76-38. B.- Idem, female, 182 mm DL, TBT 76-58.

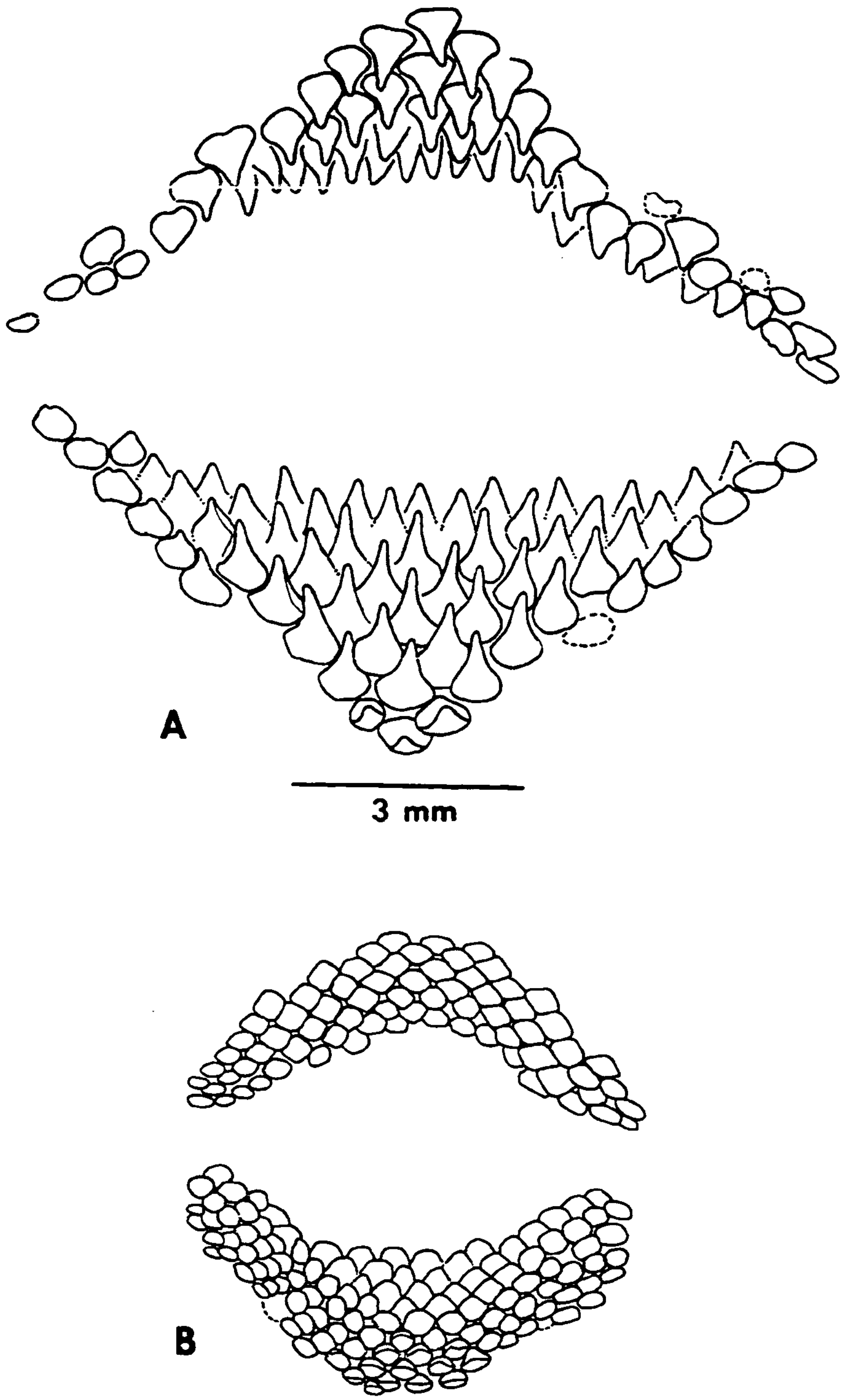
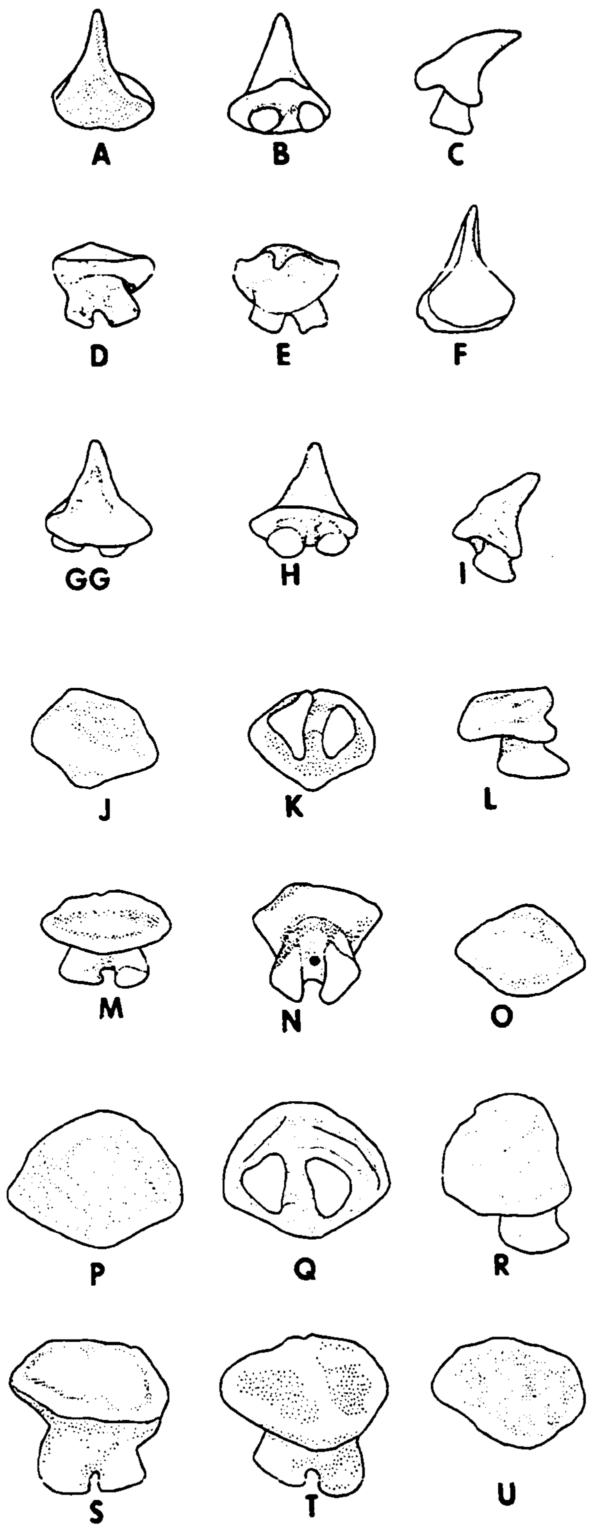

A
3 mm
B
5 mm

FIG. 63

Potamotrygon magdalenae, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, male, 164 mm DL, TBT 76-38. F.- Tooth from lower jaw near symphysis, apical view, TBT 76-38. G - I.- Tooth from upper jaw near symphysis, apical, basal, and lateral views, TBT 76-38. J - N.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, female, 182 mm DL, TBT 76-58. O.- Tooth from lower jaw near symphysis, apical view, TBT 76-58. P - T.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, male, 202 mm DL, TBT 76-39. U.- Tooth from lower jaw near mouth corner, apical view, female, 264 mm DL, TBT 76-42.


A B C
D E F
GG H I
J K L
M N O
P Q R
S T U

Potamotrygon motoro (Natterer, 1841)

(Figs. 4, 20, 24, 25, 64-68)

Raja motoro Natterer in Müller and Henle, 1841: 197 (original description, Cuiabá, not illustrated).

Taeniura motoro. Müller and Henle, 1841: 197.

Trygon (Taenura) mulleri [sic] Castelnau, 1855: 102, plate 48 (original description, Rio Crixas and Rio Araguaia).

Taenura motoro [sic]. Castelnau, 1855: 102.

Potamotrygon motoro. Garman, 1877: 211.

Ellipesurus motoro. Ribeiro, 1907: 185.

Potamotrygon laticeps Garman, 1913: 417 (original description, Tefé and Óbidos) NEW SYNONYMY.

Potamotrygon circularis [in part] Garman, 1913: 419 (original description, Coari) NEW SYNONYMY.

Paratrygon motoro. Fowler, 1948: 8.

Lectotype: ZMB 4662 (herein selected), male.

Type locality: Rio Cuiabá, Mato Grosso, Brazil.

Vernacular names: borô, raia motoro, raia maçã (Brazil); raya overa, raya pintada, yaveví-guazú (Paraguay and Argentina).

Remarks.- The type material of P. motoro consisted of three specimens from Natterer's collection, obtained in Rio Cuiabá and deposited at the Imperial Museum in Vienna. Müller and Henle (1841) mentioned additional specimens from an unreported locality, and a small specimen from Guaporé. Castex (1964b) stated that the type of P. motoro probably had been lost, but mentioned the presence of specimens without type indication in the museum of Vienna. One specimen from Cuibá (Fig. 64), originally from the Vienna collection and presently housed in Eastern Berlin, was the only type found, and herein selected as lectotype. Indications of type status are the label and catalogue information, which cite the specimen as species originalis, from Müller and Henle's collection, and collected in Cuiabá by Natterer.

Examination of the type of T. mulleri confirmed the synonymy of this species with P. motoro, as proposed by Günther (1870) and followed by most subsequent authors. The type of T. mulleri, although in bad condition, still retains characters diagnostic of P. motoro, like the dermal denticles and the typical ocelli.

Examination of the type series of P. laticeps confirmed the synonymy of this species with P. motoro, as previously suggested by Castex (1967a). All the syntypes showed no specific differences with P. motoro after their external and radiographic study. Most of the syntypes still retained the typical ocelli of P. motoro.

The type series of P. circularis consisted of heterogenous material, from which two specimens (MCZ 295-S) could be identified as *P. motoro*.

Günther (1870) mistakenly synonymized *P. dumerilii* and *P. motoro*, and was followed by Ribeiro (1907), Garman (1913), and Fowler (1948); see remarks under *P. dumerilii*.

Diagnosis.- A species of *Potamotrygon* with wide geographic distribution, ranging from Río Orinoco to Río de la Plata, diagnosed by the following combination of characters: disc subcircular; dorsal surface of disc olivaceous-brown to dark gray, with relatively large yellow to orange ocelli, greater than eye in diameter, in one to five concentric elliptic series; teeth relatively large and flat, in 18 to 39 longitudinal rows in upper jaw.

Description.- Measurements and counts are given in Table 16. Disc subcircular, disc length 0.95-1.19 times DW. Pelvic fins usually covered dorsally by disc. Tail relatively short, tail length 0.9-1.3 times DW, with well-developed dorsal and ventral finfolds. Ventral finfold length 1.2-2.2 in DW, its height nearly equal to tail height. Caudal sting relatively long, sting length 1.4-3.2 times tail width.

Eyes relatively large, eye length 1.4-4.8 in interorbital distance, 3.2-8.9 in interocular distance. Preocular distance 3.1-4.5 in DW, 1.1-1.7 times interocular distance. Spiracles relatively large, spiracle length 1.0-2.5 times eye length, 2.0-4.9 in interspiracular distance. Mouth relatively large, mouth width 0.9-1.5 times internarial distance, with five papillae at bottom. Preoral distance 20.0-26.3 percent of DW. Teeth relatively large (Figs. 66, 67), closely crowded in quincunx, with tetragonal flat crowns, in 18/20 to 39/39 longitudinal rows, and two to ten exposed teeth in median row of lower dental plate. Teeth sexually dimorphic, adult and subadult males with pointed teeth in both jaws, females with blunt teeth. Monognathic heterodonty occasionally in one or both jaws of adult specimens: adult males with pointed teeth in median rows and blunt teeth in lateral rows; adult females with relatively small teeth in median and lateral rows, and enlarged teeth in intermediate rows. Nostril length 1.1-1.8 in internarial distance. Branchial basket relatively wide, its greatest width 3.1-4.0 in DW; distance between first and fifth gill slits 5.0-7.1 in DW.

Dorsal surface of disc covered with denticles, more developed along midline. Submarginal series of tubercles occasionally on disc of adult specimens. Tail with 11 to 44 large middorsal spines, with round base and curved cusp, usually in single longitudinal row. Latero-caudal spines usually well developed in adults, from tail base to distal portion.

Dorsal surface of disc olivaceous-brown to dark gray, with yellow to orange ocelli encircled by dark ring, larger than eye in diameter, and decreasing in size towards disc margins. Ocelli occasionally with intermediate orange ring between yellow center and external dark ring. Ocelli occasionally fade in large specimens. Ocelli in one to five concentric elliptic series. Nine to 14 ocelli in half of disc, in submarginal series from tail base to anterior disc in front of eyes. Ocelli on tail limited to its basal portion, irregular in shape. Pelvic fins with dorsal pattern similar to disc, but with relatively smaller and less conspicuous ocelli. Sides of tail with alternate white and dark bars. Ventral surface of disc and pelvic fins white with brown margins. Central dark spot usually present ventrally on disc.

Geographic distribution.- *Potamotrygon motoro* has a wide distribution, ranging from Río Orinoco in Venezuela to Río de la Plata, and found throughout the Amazon drainage (see Fig. 101). Relating its distribution to that of the whole family Potamotrygonidae, it is absent only from the Atrato-Magdalena, Maracaibo, and Parnaíba drainages. Berg (1895) mistakenly considered *P. motoro* as an estuarine species restricted to the Río de la Plata.

Biological remarks.- There is considerable polychromatism in *P. motoro* (Ribeiro, 1907; Devicenzi and Teague, 1942; Achenbach and Achenbach, 1976), both geographic and intrademic. Castex (1963c, 1964b) denied ontogenetic changes in coloration for this species. Seasonal changes in coloration were observed in aquarium specimens (J. K. Langhammer, Belle Isle Aquarium, pers. comm.), and they possibly relate to the reproductive cycle. Some specimens of *P. motoro* with aberrant color patterns (Fig. 68) were used by Castex to establish new specific names (*P. alba*, *P. labratoris*, *P. pauckei* in part), while others were identified as interspecific hybrids. One specimen examined by the author (MFA 314) showed an intermediate color pattern between P. motoro and P. falkneri, but decisive evidence for hybridization is lacking.

Castex (1963c), Achenbach and Achenbach (1976), and Thorson, Langhammer and Oetinger (1983) provided data on the reproductive biology and development of P. motoro. Castex (1963c) gave maturation sizes of 310 and 350 mm of disc diameter, respectively for males and females. Achenbach and Achenbach (1976) cited that maturity generally occurs between 300 and 350 mm of disc diameter. Thorson et al. pointed that maturation occurs between 240 and 320 mm of disc width for females. Litter size of wild caught P. motoro was reported as three to 21 embryos by Achenbach and Achenbach (1976), and six to seven embryos by Thorson et al.

Additional references: Achenbach, 1969 (respiration); Achenbach, 1971 (color variability); Armburst, 1969 (photograph, behavior); Berg, 1895 (citation for Montevideo); Buen, 1950 (citations for Uruguay); Carvalho, 1955 (photograph); Carvalho, 1964 (color variability); Castello, 1972 (toxicity); Castello, 1975 (photograph); Castello, 1976 (abundance); Castex, 1963b (photograph); Castex, 1963d (photograph); Castex, 1964b (redescription and synonymy); Castex, 1967c (dermal denticles); Castex, 1967d (photographs of dental plates); Castex and Castello, 1970b (photograph); Castex and Maciel, 1963 (sperm cells); Cottrell, 1976 (photograph); Devicenzi and Teague, 1942 (color variability and biological remarks); Duméril, 1865 (redescription); Eigenmann and Eigenmann, 1891 (name only); Fowler, 1970 (name only, in Paratrygon); Garman, 1888 (lateral line system); Garman, 1913 (redescription and synonymy); Günther, 1870 (redescription and synonymy); Ihering, 1897 (citation for Rio de la Plata); Jordan, 1887 (name only, in Taeniura); Lahille, 1921 (citation for Uruguay); Lüling, 1965 (photograph, as P. hystrix); Mago-Leccia, 1971 (citation for Venezuela); Mago-Leccia, 1978 (citation for Venezuela, photograph); Perugia, 1891 (citation for Montevideo); Regan, 1905 (citation for Rio Negro); Ribeiro, 1923 (redescription); Ribeiro, 1959 (citations for Amazonas and Mato Grosso); Ringuelet et al., 1967 (redescription); Starks, 1913 (redescription); Wheeler, 1975 (photograph).

TABLE 16

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Potamotrygon motoro*

	N	MEAN	S.D.	RANGE
DISC WIDTH	60	-	-	60.0-545
DISC LENGTH (mm)	-	-	-	64.0-625
DISC LENGTH (%)	60	107.5	4.2	95.7-119.3
TOTAL LENGTH (%)	13	206.5	15.2	190.0-233.3
INTERNAL DL (%)	57	93.9	3.4	88.0-104.6
MOUTH TO SCAPULOCORACOID (%)	39	31.9	2.6	28.5- 41.8
MOUTH TO CLOACA (%)	53	64.2	3.8	57.5- 73.6
CLOACA TO STING (%)	49	46.2	4.0	39.0- 54.0
TAIL LENGTH (%)	18	124.5	16.1	97.4-131.3
TAIL WIDTH (%)	53	10.5	1.5	6.1- 14.0
TAIL WIDTH AT STING BASE (%)	50	5.1	0.9	3.2- 6.6
TAIL HEIGHT (%)	53	6.7	0.8	5.1- 9.1
PELVIC FIN WIDTH (%)	51	27.8	3.1	20.3- 37.7
PELVIC FIN LENGTH (%)	53	21.1	3.2	13.6- 30.8
CLASPER LENGTH (%)	35	18.9	9.4	7.6- 34.0
STING LENGTH (%)	44	23.5	4.5	10.7- 32.7
PRECLOACAL LENGTH (%)	53	86.9	3.7	80.1- 98.6
PREORAL LENGTH (%)	53	23.0	1.3	20.0- 26.3
PRENARIAL LENGTH (%)	53	16.8	1.4	14.7- 20.7
BRANCHIAL BASKET LENGTH (%)	53	16.4	2.9	13.9- 19.7
BRANCHIAL BASKET WIDTH (%)	51	26.9	1.4	24.6- 31.6
MOUTH WIDTH (%)	53	10.2	1.1	7.8- 13.2
NOSTRIL LENGTH (%)	53	10.2	1.1	7.8- 13.2

TABLE 16

(continued)

	N	MEAN	S.D.	RANGE
INTERNARIAL WIDTH (%)	54	8.7	0.5	7.5- 10.0
EYE LENGTH (%)	60	4.2	1.1	2.0- 6.8
SPIRACLE LENGTH (%)	54	6.3	1.1	4.9- 10.7
INTEROCULAR WIDTH (%)	38	20.3	2.4	16.5- 27.9
INTERSPIRACULAR WIDTH (%)	56	20.4	2.3	14.4- 26.5
PREOCULAR LENGTH (%)	55	27.9	2.8	22.1- 31.7
CRANIUM LENGTH (%)	11	26.7	1.1	24.9- 28.5
CRANIUM WIDTH (%)	11	18.2	1.1	15.8- 19.6
PREORBITAL WIDTH (%)	8	21.2	0.9	19.0- 22.7
POSTORBITAL WIDTH (%)	5	11.5	1.3	9.2- 12.4
INTERORBITAL WIDTH (%)	53	10.5	1.0	8.0- 13.4
FONTANELLE LENGTH (%)	14	16.7	0.9	14.5- 17.9
FONTANELLE WIDTH (%)	15	8.4	0.7	7.9- 9.4
UPPER DENTAL PLATE WIDTH (%)	48	9.2	1.2	5.6- 11.3
LOWER DENTAL PLATE WIDTH (%)	47	8.5	1.0	5.8- 10.7
PRECAUDAL VERTEBRAE	16	27.2	1.6	25- 31
CAUDAL VERTEBRAE	12	96.8	3.6	93- 101
CAUDAL VERTEBRAE TO BASE OF STING	14	71.7	3.8	63- 78
TOTAL VERTEBRAE	13	123.8	3.8	115- 128
DIPLOSPONDYLOUS VERTEBRAE	10	13.0	2.9	11- 17
SYNARCUAL VERTEBRAE	14	2.6	0.6	2- 4
PELVIC RADIALS ♂	11	19.4	0.9	18- 21
PELVIC RADIALS ♀	11	22.8	1.1	22- 24

TABLE 16

(continued)

	N	MEAN	S.D.	RANGE
PROPTERYGIAL RADIALS	19	46.8	2.3	44- 51
MESOPTERYGIAL RADIALS	19	14.4	1.4	12- 17
METAPTERYGIAL RADIALS	19	35.5	1.1	34- 38
TOTAL PECTORAL RADIALS	19	97.2	2.0	93- 101
UPPER TOOTH ROWS	45	25.2	7.7	18- 39
LOWER TOOTH ROWS	43	26.0	7.3	20- 39
LOWER MEDIAN TEETH	40	5.8	1.7	2- 10
MIDDORSAL SPINES	28	18.2	9.2	11- 44

FIG. 64

Potamotrygon *motoro*, dorsal view, ZMB 4662 (lectotype), not seen by the author. Courtesy of H. -J. Paepke (ZMB)

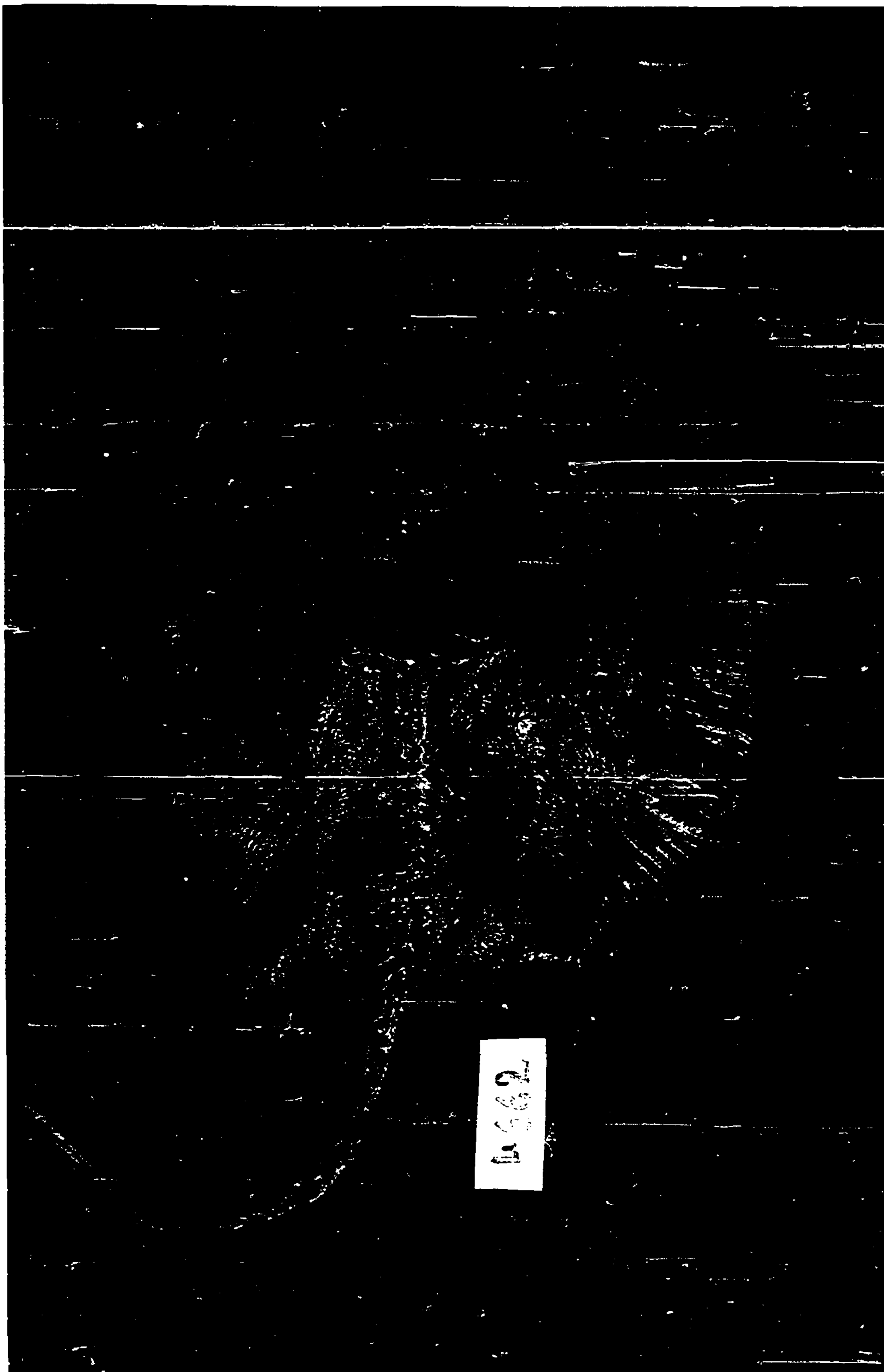


FIG. 65

Potamotrygon motoro, dorsal view, female, 217 mm DL, MCZ 52598.

FIG. 66

Potamotrygon motoro, A.- Upper and lower dental plates, subadult male, 337 mm DL, MACN (uncatalogued specimen). B.- Idem, adult male, 377 mm DL, MFA 245. Dashed lines on lower dental plates indicate the limit of the buccal integument covering the inner series of teeth.

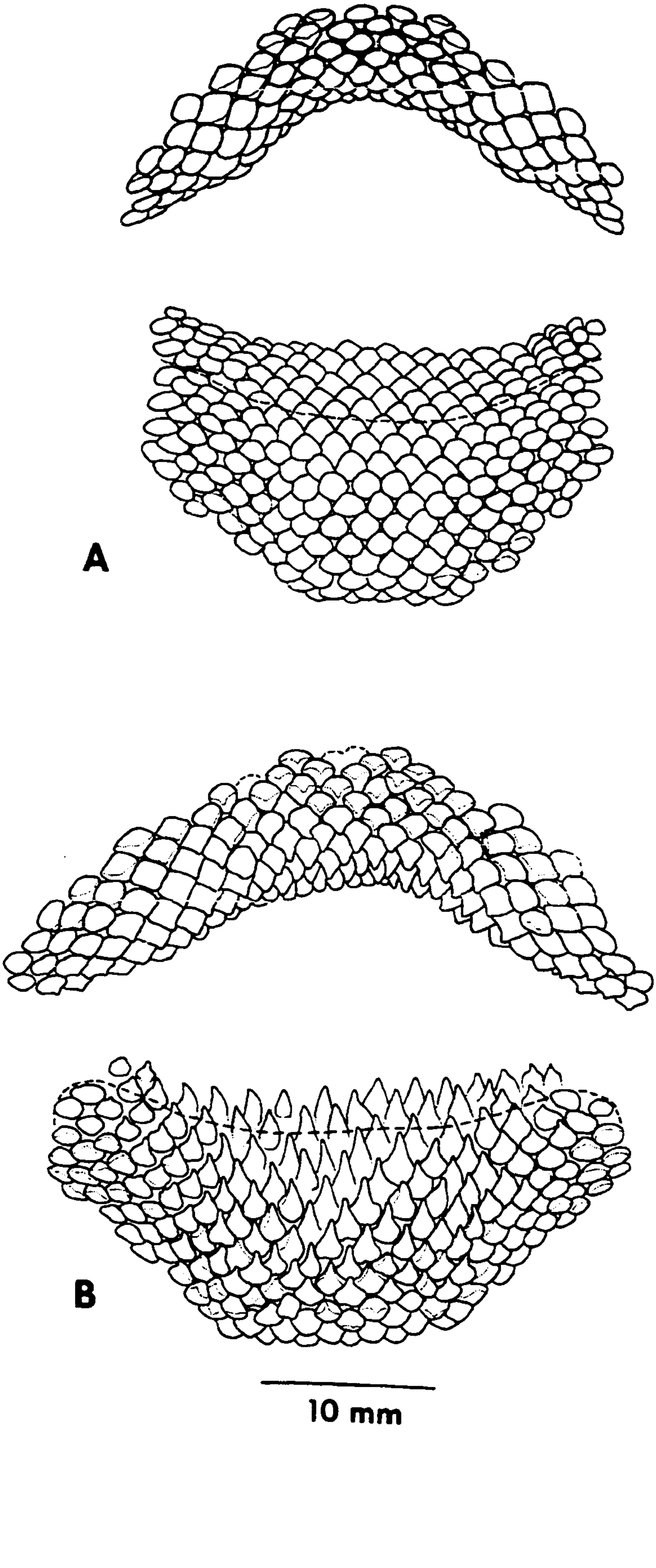

A
B
10 mm

FIG. 67

Potamotrygon motoro, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, male, 537 mm DL, AMNH (uncatalogued specimen). F.- Tooth from lower jaw near mouth corner, male, 389 mm DL, MCZ 52597.

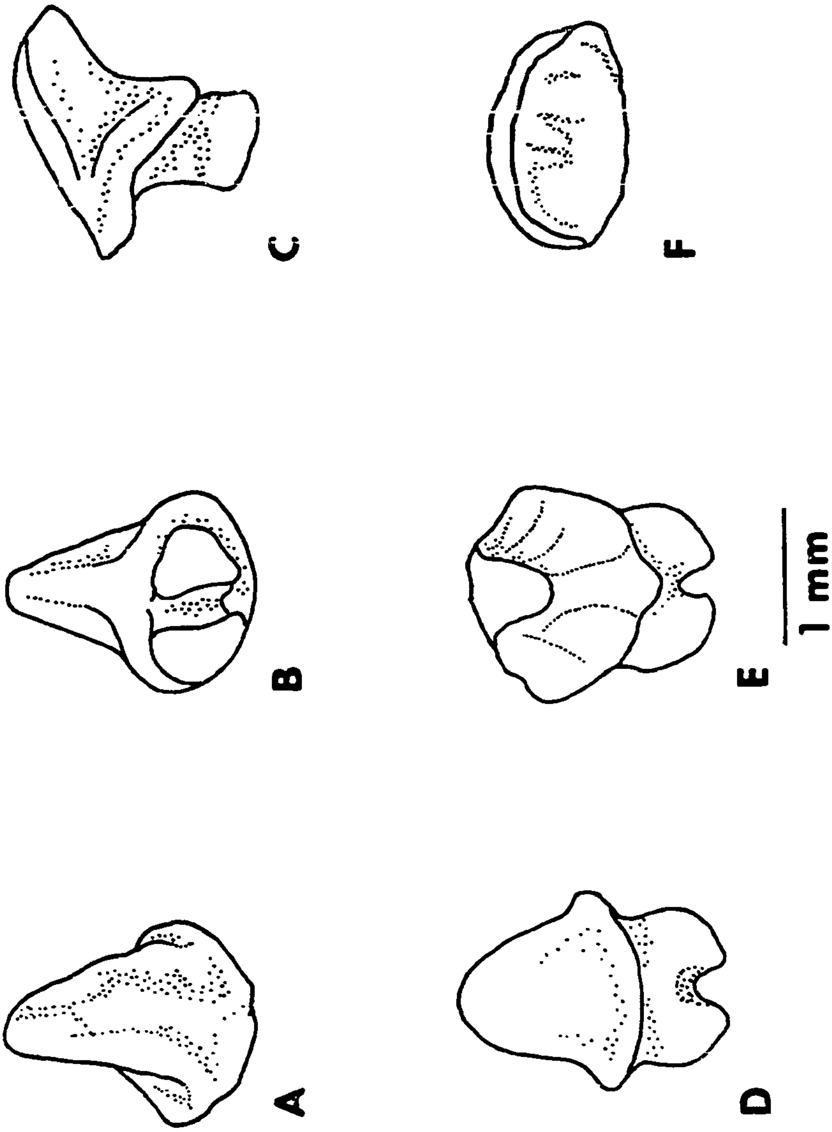
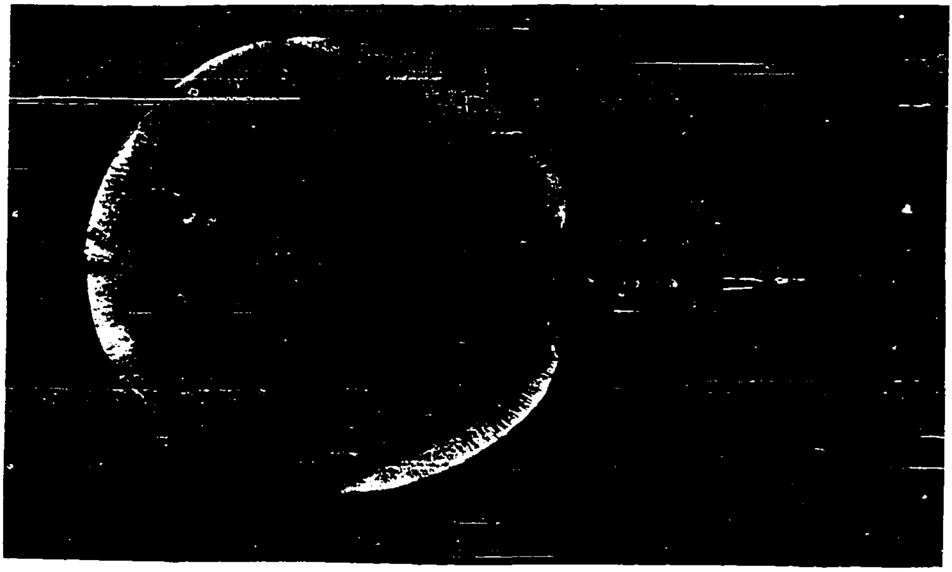

A
B
C
D
E
F
1 mm

FIG. 68

Atypical specimens of *Potamotrygon motoro*, A.- Male, 377 mm DL, MFA 245 (syntype of *Potamotrygon pauckei nomen nudum*). B.- Female, 324 mm DL, MFA 231 (type of *Potamotrygon labratoris nomen nudum*).

A



B

Potamotrygon ocellata (Engelhardt, 1912)

(Fig. 69)

Trygon hystrix ocellata Engelhardt, 1912: 647-648 (original description, Mexiana, not illustrated).

Holotype: unknown.

Neotype: MNRJ 10620 (herein selected), female, Rio Pedreira, Macapá, Brazil.

Type locality (of holotype): Southern coast of Ilha Mexiana, Brazil.

Remarks.- Engelhardt (1912) described the new variety Trygon hystrix ocellata, a name which is interpreted as subspecific according to the ICZN [art. 45(e)(i)], and therefore available at the specific rank. The name and description have been overlooked by all subsequent authors. The name P. ocellata is herein provisionally used for a single specimen (MNRJ 10620), which shows a similar color pattern to that mentioned in the original description, and does not key to any other known species. Rediscovery of the type could either prove or disprove this identification.

No holotype designation was given in the original description, and the present location of the female specimen mentioned by Engelhardt is unknown. The neotype selection is based on the agreement of color characters between specimen MNRJ 10620 and the original description, and on the relative proximity of Mexiana and Macapá. No other specimens are presently known, and the following diagnosis and description are based only on the neotype.

Diagnosis.- A species of Potamotrygon from the mouth of Rio Amazonas, with deep orange to rusty red irregular spots dorsally on disc, usually ocellated by dark rings. It is distinguished from P. motoro by its relatively redder spots and their irregular shape. Unidentified specimens (Potamotrygon sp. B) from Corantijn river drainage in Surinam resemble P. ocellata in coloration, but have relatively smaller teeth and narrower dental plates.

Description.- Measurements and counts are given in Table 17. Disc subcircular, disc length 1.06 times DW. Pelvic fins dorsally covered by disc. Tail distally broken in neotype, its length 0.8 times DW. Two caudal stings, posterior largest, its length 2.0 times tail width. Eyes relatively large, eye length 2.6 in interorbital distance, 4.5 in interocular distance. Preocular distance 3.6 in DW, 1.4 times interocular distance. Spiracles relatively large, spiracle length 1.8 times eye length, 2.8 in interspiracular distance. Mouth relatively large, mouth width 1.2 times internarial distance, with five papillae at bottom. Preoral distance 22.6 percent of DW. Teeth relatively large (Fig. 69), closely crowded in quincunx, in 24/25 longitudinal rows, and three exposed teeth in median row of lower dental plate. Tooth crowns tetragonal, without prominent cusps. Nostril length 1.1 in internarial distance. Branchial basket width 3.6 in DW; distance between first and fifth gill slits 6.6 in DW.

Dorsal surface of disc with denticles along midline. Tail with eighteen middorsal spines in single row, and relatively small lateral spines.

Dorsal surface of disc dark olivaceous-brown with irregular deep orange to rusty red spots, which decrease in size towards disc margins. Spots on center of disc ocellated by dark rings. Ventral surface of disc white, with brown edges marked with small circular spots of yellow and orange.

Geographic distribution.- Potamotrygon ocellata is known from the mouth of Rio Amazonas, in Mexiana and Macapá (see Fig. 101).

TABLE 17

MEASUREMENTS AND COUNTS ON SPECIMEN OF *Potamotrygon ocellata*

	MNRJ 10620
DISC WIDTH (100%)	190
DISC LENGTH (mm)	203
DISC LENGTH (%)	106.8
TOTAL LENGTH (%)	–
INTERNAL DL (%)	93.1
MOUTH TO SCAPULOCORACOID (%)	30.8
MOUTH TO CLOACA (%)	64.4
CLOACA TO STING (%)	40.5
TAIL LENGTH (%)	85.2*
TAIL WIDTH (%)	11.5
TAIL WIDTH AT STING BASE (%)	5.4
TAIL HEIGTH (%)	6.7
PELVIC FIN WIDTH (%)	27.7
PELVIC FIN LENGTH (%)	25.5
STING LENGTH (%)	23.8
PRECLOACAL LENGTH (%)	87.3
PREORAL LENGTH (%)	22.6
PRENARIAL LENGTH (%)	17.4
BRANCHIAL BASKET LENGTH (%)	15.1
BRANCHIAL BASKET LENGTH (%)	27.2
MOUTH WIDTH (%)	10.5
NOSTRIL LENGTH (%)	7.3

*Tail broken.

TABLE 17

(continued)

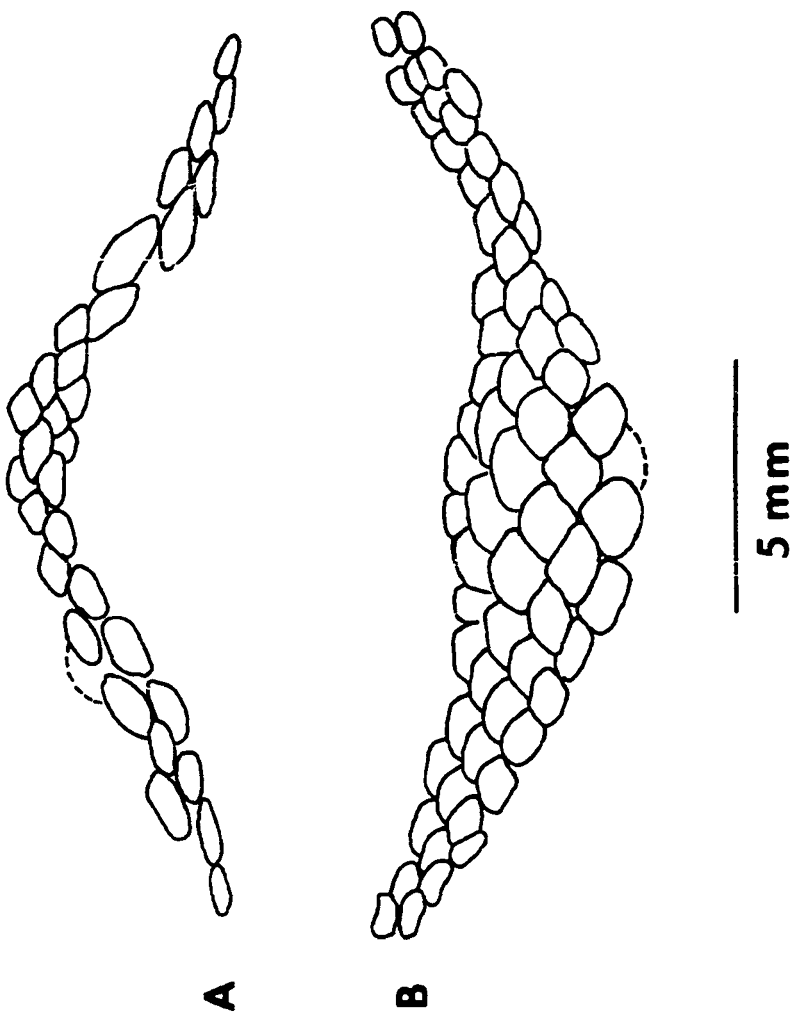
	MNRJ 10620
INTERNARIAL WIDTH (%)	8.4
EYE LENGTH (%)	4.2
SPIRACLE LENGTH (%)	7.7
INTEROCULAR WIDTH (%)	19.0
INTERSPIRACULAR WIDTH (%)	21.6
PREOCULAR LENGTH (%)	27.1
CRANIUM LENGTH (%)	27.1
CRANIUM WIDTH (%)	18.9
PREORBITAL WIDTH (%)	20.3
POSTORBITAL WIDTH (%)	8.1
INTERORBITAL WIDTH (%)	11.1
FONTANELLE LENGTH (%)	16.6
FONTANELLE WIDTH (%)	8.8
UPPER DENTAL PLATE WIDTH (%)	9.1
LOSER DENTAL PLATE WIDTH (%)	9.3
PRECAUDAL VERTEBRAE	29
CAUDAL VERTEBRAE	93
CAUDAL VERTEBRAE TO BASE OF STING	77
TOTAL VERTEBRAE	122
DIPLOSPONDYLOUS	8
SYNARCUAL VERTEBRAE	3
PELVIC RADIALS ♀	21
PROPTERYGIAL RADIALS	45

TABLE 17
(continued)

	MNRJ 10620
MESOPTERYGIAL RADIALS	13
METAPTERYGIAL RADIALS	36
TOTAL PECTORAL RADIALS	94
UPPER TOOTH ROWS	24
LOWER TOOTH ROWS	25
LOWER MEDIAN TEETH	3
MIDDORSAL SPINES	18

FIG. 69

Potamotrygon _ocellata_, A - B.- Upper and lower dental plates, female, 203 mm DL, MNRJ 10620.


A
B
5 mm

<u>Potamotrygon</u> <u>orbignyi</u> (castelnau, 1855)

(Figs. 22G, 26B, 70-74)

<u>Trygon</u> (<u>Taenura</u>) <u>d'orbignyi</u> Castelnau, 1855: 102 (original description, Tocantins).

<u>Toenura</u> <u>orbignyi</u> Castelnau, 1855, plate 49, figure 3 (original illustration).

<u>Taeniura</u> <u>orbignyi.</u> Duméril, 1865: 624.

<u>Trygon</u> <u>reticulatus</u> Günther, 1880: 9 (original description, Surinam, not illustrated) NEW SYNONYMY.

<u>Potamotrygon</u> <u>d'orbignyi</u>. Eigenmann and Eigenmann, 1891: 25.

<u>Potamotrygon</u> <u>reticulatus.</u> Eigenmann and Eigenmann, 1891: 25.

<u>Ellipesurus</u> <u>reticulatus</u>. Ribeiro, 1907: 185.

<u>Ellipesurus</u> <u>orbignyi</u>. Ribeiro, 1907: 186.

<u>Paratrygon</u> <u>reticulatus</u>. Fowler, 1948: 8.

Holotype: MNHN 2333 by original indication, female, coll. F. Castelnau.

Type locality: Rio Tocantins, Brazil.

Remarks.- Castelnau (1855) used two different spellings of the specific name (<u>d'orbignyi</u> and <u>orbignyi</u>) in the original description. The spelling <u>orbignyi</u> is the one that conforms with binominal nomenclature, and it has been correctly adopted by subsequent authors (Duméril, 1865; Günther, 1870; Ribeiro, 1907). Eigenmann and Eigenmann (1891) and Eigenmann (1910) retained the incorrect original spelling.

Garman (1877) and Schultz (1949) used Potamotrygon humboldtii, based on Pastenague de Humboldt Roulin (1829) as a senior synonym of P. orbignyi. The morphometric data given in the original description of P. humboldtii, when compared with P. orbignyi cannot support this synonymy (see comments under doubtful species).

The holotype of P. orbignyi (MNHN 2333) is in poor condition, only the skin and tail being preserved. The eyes, jaws, and pelvic fins remain intact. The tail is distally broken, and the caudal sting is missing. The size of the denticles and spines were exaggerated, and the color pattern misrepresented in the original illustration. Diagnostic characters of the holotype are the teeth, dermal denticles, middorsal spines, and the dorsal color pattern of the disc and pelvic fins.

Garman (1880) correctly pointed out that Trygon reticulatus should be placed in the genus Potamotrygon. Garman (1913) mistakenly placed T. orbignyi in the synonymy of P. histrix, and was followed by Fowler (1948) and Castex (1964b). This synonymy is incorrect because the two species are distinct, with no overlap of their geographic ranges.

Diagnosis.- A species of Potamotrygon from lower Amazon, eastern Colombia and Venezuela, and Guianas, diagnosed by the following combination of characters: disc subcircular; dorsal surface of disc brown with network of dark pigment forming hexagonal reticulations; color pattern of the interorbital region as in Fig. 26B; mouth small, its width nearly equal to internarial distance; teeth small, in 24 to 39 longitudinal rows in upper jaw.

Description.- Measurements and counts are given in Table 18. Disc subcircular, disc length 1.01-1.19 times DW. Pelvic fins usually covered dorsally by disc. Tail relatively short, tail length 0.9-1.3 times DW, with well-developed dorsal and ventral finfolds. Ventral finfold length 1.2-2.8 in tail width. Caudal sting relatively long, 1.4-2.9 times tail width.

Eyes relatively large, eye length 1.4-2.8 in interorbital distance, 3.5-6.9 in interocular distance. Preocular distance 3.2-4.4 in DW, 1.1-1.6 times interocular distance. Spiracles relatively large, spiracle length 1.0-2.3 times eye length, 1.6-3.2 in interspiracular distance. Mouth relatively small, mouth width 0.8-1.2 times internarial distance. Preoral distance 17.6-25.5 percent of DW. Teeth relatively small (Figs. 73-74), white to caramel in color, crowded in quincunx, in 25/23 to 39/38 longitudinal rows, and three to eight exposed teeth in median row of lower dental plate. Anterior margin of tooth crowns concave, posterior margin with central cusp and two small accessory cusps. Teeth sexually dimorphic, mature males with enlarged central cusp, juvenile males and females with smaller central cusp. Nostril length 0.9-1.6 in internarial distance. Branchial basket relatively wide, its greatest width 3.6-4.5 in DW; distance between first and fifth gill slits 5.3-7.5 in DW.

Dorsal surface of disc covered with stellate denticles, with round base, prominent central cusp, and usually five small accessory cusps. Denticles more developed along midline, and on anterior portion of disc of adults. Tail of adults and subadults with 9 to 26 relatively small middorsal spines, usually in a single irregular row. Latero-caudal spines small or absent. Juveniles with smooth disc and tail.

Dorsal surface of disc light brown with mesh of dark pigment forming reticulate pattern, delimiting hexagonal spaces larger than eye in diameter. Reticulations more or less sharp, usually less conspicuous in darker specimens. Posterior margin of spiracles spotted with dark pigment. Small yellow spots above orbits and around disc margins. Pelvic fins dorsally with same pattern as disc, but with relatively smaller reticulations. Tail laterally with alternate white and dark bars. Ventral surface of disc white with brown margins; central dark spot usually present ventrally on disc.

Geographic distribution.- Potamotrygon orbignyi has wide distribution, ranging from Río Orinoco drainage in Venezuela, through Colombian Amazon, Guianas, Surinam, to the lower Amazon (see Fig. 102). There are few records above Manaus, and the species seems to be less abundant in the upper Amazon.

Specimens from Peruvian Amazon (CAS, two uncatalogued specimens; IU 16138; SU 36845) could only be tentatively identified as *P. orbignyi*, due to their small size and faded color pattern.

Additional references: Castex, 1964b (redescription, as *P. reticulatus*); Eigenmann, 1910 (citation for Río Orinoco); Garman, 1913 (redescription, as *P. reticulatus*).

TABLE 18

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Potamotrygon orbignyi*

	HOLOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)		51	-	-	110.0-285
DISC LENGTH (mm)		51		-	127.0-313
DISC LENGTH (%)		49	108.5	3.5	101.6-119.6
TOTAL LENGTH (%)		22	207.4	13.0	189.3-226.8
INTERNAL DL (%)		51	-	-	110.0-285
MOUTH TO SCAPULOCORACOID(%)		43	32.6	1.9	27.2-37.0
MOUTH TO CLOACA (%)		49	66.2	3.1	59.0-73.5
CLOACA TO STING (%)		48	48.0	4.5	39.8-57.4
TAIL LENGTH (%)		22	116.0	13.5	92.3-137.2
TAIL WIDTH (%)		50	10.5	1.3	7.3- 12.9
TAIL WIDTH AT STING BASE(%)		49	5.3	0.6	4.1- 7.1
TAIL HEIGHT (%)		48	6.3	0.7	5.0- 8.8
PELVIC FIN WIDTH (%)		48	27.6	2.8	22.1- 33.9
PELVIC FIN LENGTH (%)		49	21.4	2.9	14.6- 26.7
CLASPER LENGTH (%)		27	14.3	6.1	9.9- 31.2
STING LENGTH (%)		33	24.1	3.4	15.4- 31.1
PRECLOACAL LENGTH (%)		48	86.8	2.8	82.0- 94.3
PREORAL LENGTH (%)		45	21.1	2.1	17.6- 25.5
PRENARIAL LENGTH (%)		47	16.1	1.7	13.0- 20.2
BRANCHIAL BASKET LENGTH (%)		48	16.5	1.1	13.2- 18.7
BRANCHIAL BASKET WIDTH (%)		48	24.5	1.3	22.2- 27.6
MOUTH WIDTH (%)		48	8.0	0.5	6.4- 10.4
NOSTRIL LENGTH (%)		42	5.9	0.7	4.3- 7.4

TABLE 18

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
INTERNARIAL WIDTH (%)		49	7.7	0.7	6.5- 10.5
EYE LENGTH (%)		49	4.7	0.7	3.3- 6.8
SPIRACLE LENGTH (%)		50	7.6	1.6	5.3- 10.8
INTEROCULAR WIDTH (%)		44	19.8	1.8	16.7- 22.8
INTERSPIRACULAR WIDTH (%)		49	18.2	1.8	14.7- 22.0
PREOCULAR LENGTH (%)		47	27.1	1.8	22.5- 30.8
CRANIUM LENGTH (%)		8	26.7	1.9	23.4- 29.4
CRANIUM WIDTH (%)		8	16.7	1.0	15.4- 18.7
PREORBITAL WIDTH (%)		6	19.7	1.3	18.0- 21.2
POSTORBITAL WIDTH (%)		5	10.3	0.7	9.4- 11.2
INTERORBITAL WIDTH (%)		48	9.0	0.8	7.3- 11.1
FONTANELLE LENGTH (%)		15	17.3	1.5	14.6- 20.8
FONTANELLE WIDTH (%)		15	7.6	1.1	5.8- 10.6
UPPER DENTAL PLATE WIDTH (%)		46	6.6	0.9	5.0- 9.4
LOWER DENTAL PLATE WIDTH (%)		45	6.2	0.9	4.9- 7.8
PRECAUDAL VERTEBRAE		9	28.1	0.9	27- 30
CAUDAL VERTEBRAE		9	98.8	3.5	96- 107
CAUDAL VERTEBRAE TO BASE OF STING		10	75.0	5.6	69- 85
TOTAL VERTEBRAE		8	127.1	3.1	124- 134
DIPLOSPONDYLOUS VERTEBRAE		7	11.5	2.8	8- 17
SYNARCUAL VERTEBRAE		6	2.3	0.5	2- 3
PELVIC RADIALS ♂		6	19.1	1.1	18- 21
PELVIC RADIALS ♀		2	25.0	-	25- 25

TABLE 18

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
PROPTERYGIAL RADIALS	-	9	44.2	2.3	41- 49
MESOPTERYGIAL RADIALS	-	9	14.1	0.7	12- 15
METAPTERYGIAL RADIALS	-	10	37.0	1.9	34- 41
TOTAL PECTORAL RADIALS	-	9	95.4	3.7	89-101
UPPER TOOTH ROWS	35	44	30.7	4.0	24- 39
LOWER TOOTH ROWS	34	45	29.2	4.4	22- 43
LOWER MEDIAN TEETH	7	41	5.3	1.5	3- 8
MIDDORSAL SPINES	20	32	18.0	4.5	10- 26

FIG. 70

Potamotrygon orbignyi, Dorsal view, female, 260 mm DL, MNHN 2333 (holotype).

FIG. 71

Potamotrygon _orbignyi_, dorsal view, male, RMNH 4258 [from Müller and Henle's (1841) heterogenous type series of _Potamotrygon_ _histrix_].

FIG. 72

Potamotrygon orbignyi, Dorsal view, male, 189 mm DL, BMNH 1926.3.2.1.

FIG. 73

Potamotrygon orbignyi, A.- Exposed portions of upper and lower dental plates, male, 313 mm DL, ANSP 135813. B.- Idem, female, 271 mm DL, ANSP 135812.

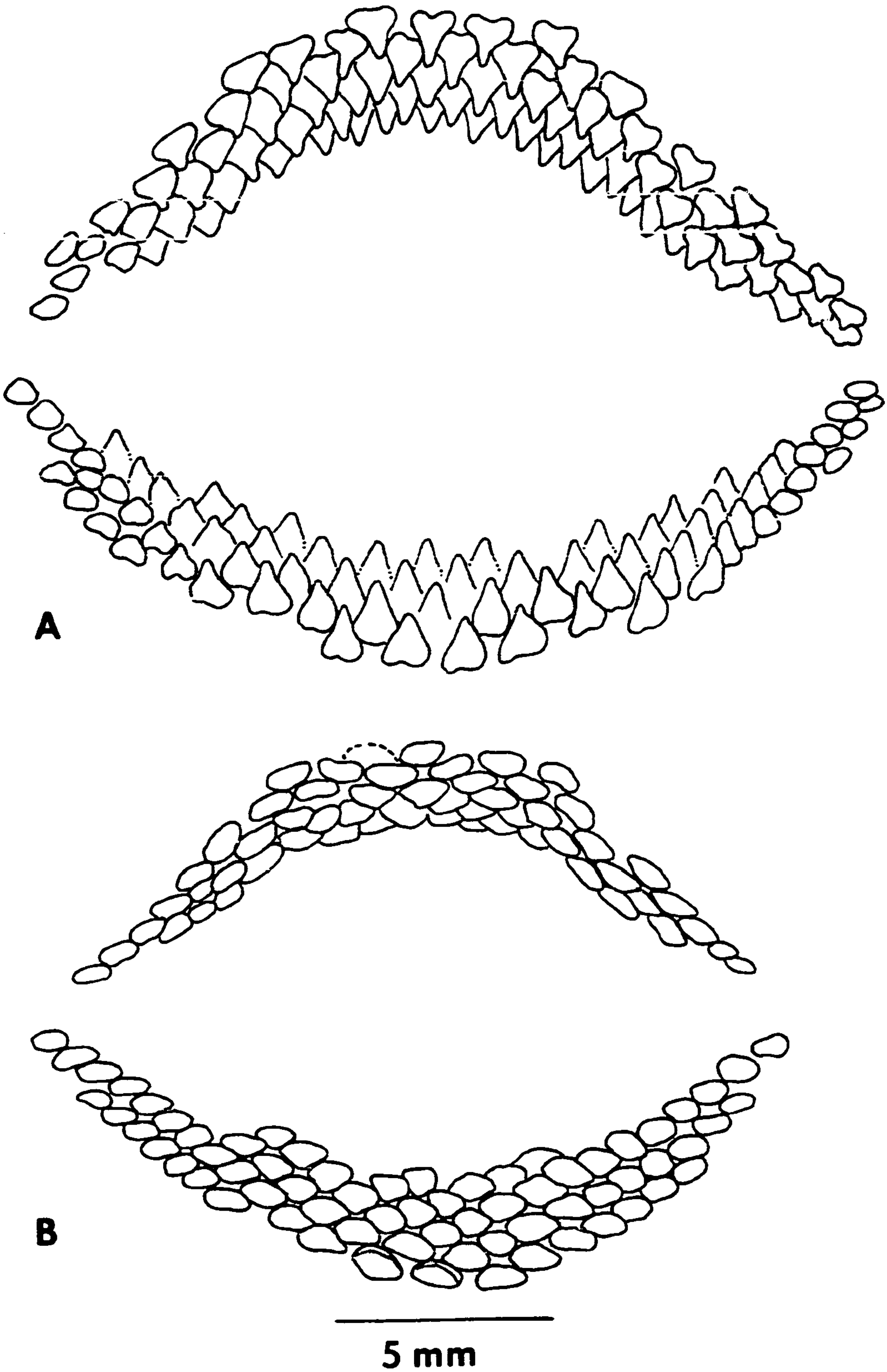
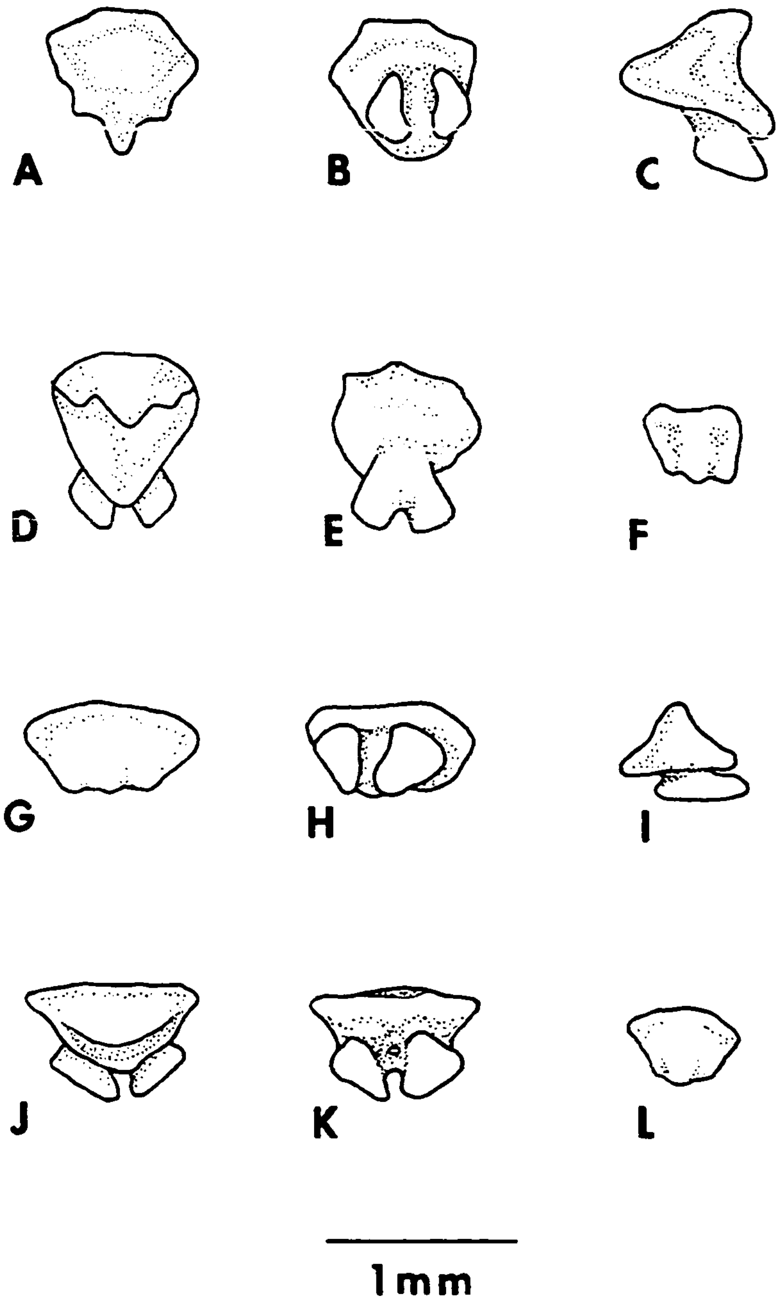

A
B
5 mm

FIG. 74

Potamotrygon orbignyi, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, lingual, and labial views, male, 229 mm DL, BMNH 1870.3.10.1 (type of *Trygon reticulatus*). F.- Tooth from lower jaw near mouth corner, BMNH 1870.3.10.1. G - K.- Tooth from upper jaw near symphysis, apical, basal, lateral, lingual, and labial views, female, 260 mm DL, MNHN 2333 (holotype). L.- Tooth from lower jaw near mouth corner, MNHN 2333.


A
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1mm

Potamotrygon schroederi Fernández-Yépez, 1957

(Figs. 21I, 75-77)

Potomatrygon schreoederi [sic] Fernández-Yépez, 1957: 8.

Potamotrygon schroederi Fernández-Yépez, 1957: 10, figure 1 (original description, Boca Apurito).

Holotype: collection of Augustín Fernández-Yépez, number 51289, by original indication, female, coll. J. Marrero.

Type locality: Boca Apurito, Río Apure, Venezuela.

Vernacular names: raya guacamaya, raya guayanesa (Venezuela).

Remarks.- Holotype not examined, its present location unknown (F. Mago-Leccia and T. B. Thorson, pers. comm.). This species was first photographed and reported from Puerto Carreño, Río Orinoco, by Fernández-Yépez (1949b), under the vernacular name raya guacamaya. Castex and Yagolkowski (1970) redescribed P. schroederi based on a single specimen from Manaus, Brazil, extending the geographic range of the species.

Diagnosis.- A species of Potamotrygon from Río Orinoco and Rio Negro drainages, diagnosed by the following combination of characters: disc oval; dorsal surface of disc dark grayish-brown with yellow to orange spots, forming irregularly-shaped figures which decrease in size towards disc margins; teeth small, with concave anterior margin, in 36 to 53 longitudinal rows in upper jaw.

Description.- Measurements and counts are given in Table 19. Disc oval, disc length 1.06-1.12 times DW. Pelvic fins broad, partially covered dorsally by disc. Tail relatively short, tail length 0.9 times DW in intact juvenile specimen. Other examined specimens with broken tails. Tail with well-developed dorsal and ventral finfolds, height of dorsal finfold 2.0 in tail height. Caudal sting (Fig. 77) relatively long, sting length 1.4-3.2 times tail width.

Eyes relatively large, eye length 1.5-2.2 in interorbital distance, 3.7-5.1 in interocular distance. Preocular distance 3.2-3.6 in DW, 1.3-1.6 times interocular distance. Spiracles relatively large, spiracle length 1.5-2.4 times eye length, 1.9-3.0 in interspiracular distance. Mouth relatively large, mouth width 1.0-1.5 times internarial distance. All examined specimens (also specimen of Castex and Yagolkowski, 1970) with five buccal papillae, contrary to original description, which stated papillae lacking. Preoral distance 18.0-20.7 percent of DW. Teeth relatively small (Fig. 76), loosely set in quincunx, in 36/35 to 53/50 longitudinal rows, and four to seven exposed teeth in median row of lower dental plate. Tooth crowns reniform, with concave anterior margin, without prominent cusps except in mature males. Teeth sexually dimorphic, adult and subadult males with pointed central cusp and two small accessory cusps; females with blunt teeth.

Branchial basket relatively wide, its greatest width 3.9-4.4 in DW; distance between first and fifth gill slits 5.9-6.8 in DW.

Dorsal surface of disc covered with denticles (Fig. 77), more developed along midline. Denticles "Y"-shaped on midline, with central cusp and small accessory cusps pointing posteriorly. Submarginal tubercles occasionally on disc of adults. Tail with seven to 29 middorsal spines (Fig. 77) in one irregular row. Largest caudal spines form tubercles in adults. Latero-caudal spines well developed in adults, near insertion of caudal sting.

Dorsal surface of disc dark grayish-brown (with blue tones when alive *fide* Fernández-Yépez), mottled with groups of small yellow to orange spots, more or less fused forming larger blotches of various shapes, circular to brain-shaped. Blotches decrease in size towards disc margins, and continue dorsally on tail. Dorsal surface of pelvic fins dark with smaller orange blotches than disc. Sides of tail with alternate white and dark bars. Ventral surface white with dark-pigmented margins of disc and pelvic fins. Central dark spot present or absent ventrally on disc.

Geographic distribution.- (See Fig. 102) *Potamotrygon schroederi* was firstly reported and described from the mid Orinoco drainage in Venezuela, and subsequently recorded from Rio Negro in Brazil. The species probably is rare in Rio Orinoco (Fernández-Yépez, 1957; F. Mago-Leccia, pers. comm.), and no specimens from Venezuela were available for study. The species seems to be more abundant in Rio Negro, from its upper portion down to Manaus. Although the Rio Negro and Orinoco are interconnected by the Canal de Casiquiare, more specimens from both drainages are needed, to evaluate possible intraspecific variation in this species.

Additional references: Mago-Leccia, 1970 (photograph); Mago-Leccia, 1978 (name only).

TABLE 19

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Potamotrygon schroederi*

	HOLOTYPE*	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	524	7	-	-	134.0- 385
DISC LENGTH (mm)	600	7	-	-	144.0- 413
DISC LENGTH (%)	114.5	7	108.4	2.3	106.3-112.1
TOTAL LENGTH (%)	-	1	189.5	-	-
INTERNAL DL (%)	104.0	7	92.8	3.2	88.9- 96.1
MOUTH TO SCAPULOCORACOID (%)	-	5	32.9	1.3	30.8- 34.1
MOUTH TO CLOACA (%)	-	7	65.9	1.5	63.6- 67.5
CLOACA TO STING (%)	-	6	42.1	6.0	36.3- 51.1
TAIL LENGTH (%)	85.5	1	98.1	-	-
TAIL WIDTH (%)	12.9	7	10.3	1.3	9.2- 13.0
TAIL WIDTH AT STING BASE(%)	7.0	6	5.9	0.7	5.0- 7.0
TAIL HEIGHT (%)	-	7	6.2	0.5	5.1- 6.9
PELVIC FIN WIDTH (%)	28.6	7	29.0	1.9	27.1- 33.0
PELVIC FIN LENGTH (%)	25.6	7	25.5	3.3	20.7- 31.0
CLASPER LENGTH (%)	-	3	22.2	-	10.2- 29.5
STING LENGTH (%)	18.4	6	23.3	4.2	19.0- 30.3
PRECLOACAL LENGTH (%)	-	7	85.3	2.0	81.7- 87.8
PREORAL LENGTH (%)	-	7	19.9	0.9	18.0- 20.7
PRENARIAL LENGTH (%)	-	7	13.6	1.1	12.0- 14.6
BRANCHIAL BASKET LENGTH (%)	-	7	15.6	0.7	14.7- 16.4
BRANCHIAL BASKET WIDTH (%)	-	7	24.2	1.1	22.3- 25.6

*Holotype measurements and counts *fide* Fernández-Yépez, 1957.

TABLE 19

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
MOUTH WIDTH (%)	-	7	9.2	1.0	7.3- 10.5
NOSTRIL LENGTH (%)	-	5	7.0	0.6	6.1- 8.1
INTERNARIAL WIDTH (%)	-	7	6.6	0.3	6.3- 7.1
EYE LENGTH (%)	-	6	4.5	0.8	3.4- 5.3
SPIRACLE LENGTH (%)	-	7	7.9	0.7	6.5- 8.8
INTEROCULAR WIDTH (%)	-	5	19.2	2.0	16.8- 21.7
INTERSPIRACULAR WIDTH (%)	-	7	19.7	1.6	16.9- 21.6
PREOCULAR LENGTH (%)	30.5	6	28.2	0.3	27.7- 28.9
CRANIUM LENGTH (%)	-	1	28.1	-	-
CRANIUM WIDTH (%)	-	1	16.6	-	-
PREORBITAL WIDTH (%)	-	1	18.9	-	-
POSTORBITAL WIDTH (%)	-	1	9.7	-	-
INTERORBITAL WIDTH (%)	-	7	8.2	0.8	6.6- 9.1
FONTANELLE LENGTH (%)	-	1	19.2	-	-
FONTANELLE WIDTH (%)	-	1	7.3	-	-
UPPER DENTAL PLATE WIDTH (%)	-	6	8.2	1.2	6.0- 9.7
LOWER DENTAL PLATE WIDTH (%)	-	5	7.7	0.9	6.0- 8.4
PRECAUDAL VERTEBRAE	-	1	26	-	-
CAUDAL VERTEBRAE	-	1	94	-	-
CAUDAL VERTEBRAE TO BASE OF STING	-	1	64	-	-
TOTAL VERTEBRAE	-	1	120	-	-
DIPLOSPONDYLOUS VERTEBRAE	-	1	6	-	-
SYNARCUAL VERTEBRAE	-	1	3	-	-

TABLE 19

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
PELVIC RADIALS	-	1	23/22	-	-
PROPTERYGIAL RADIALS	-	1	44/43*	-	-
MESOPTERYGIAL RADIALS	-	1	14/18*	-	-
METAPTERYGIAL RADIALS	-	1	38/36*	-	-
TOTAL PECTORAL RADIALS	-	1	96/97*	-	-
UPPER TOOTH ROWS	-	7	43.8	5.9	36-53
LOWER TOOTH ROWS	-	6	41.3	5.9	35-50
LOWER MEDIAN TEETH	-	7	5.0	1.0	4- 7
MIDDORSAL SPINES	-	6	20.0	7.5	7-29

*Left and right side counts of one female specimen.

FIG. 75

Potamotrygon schroederi, dorsal view, male, 413 mm DL, INPA (uncatalogued specimen).

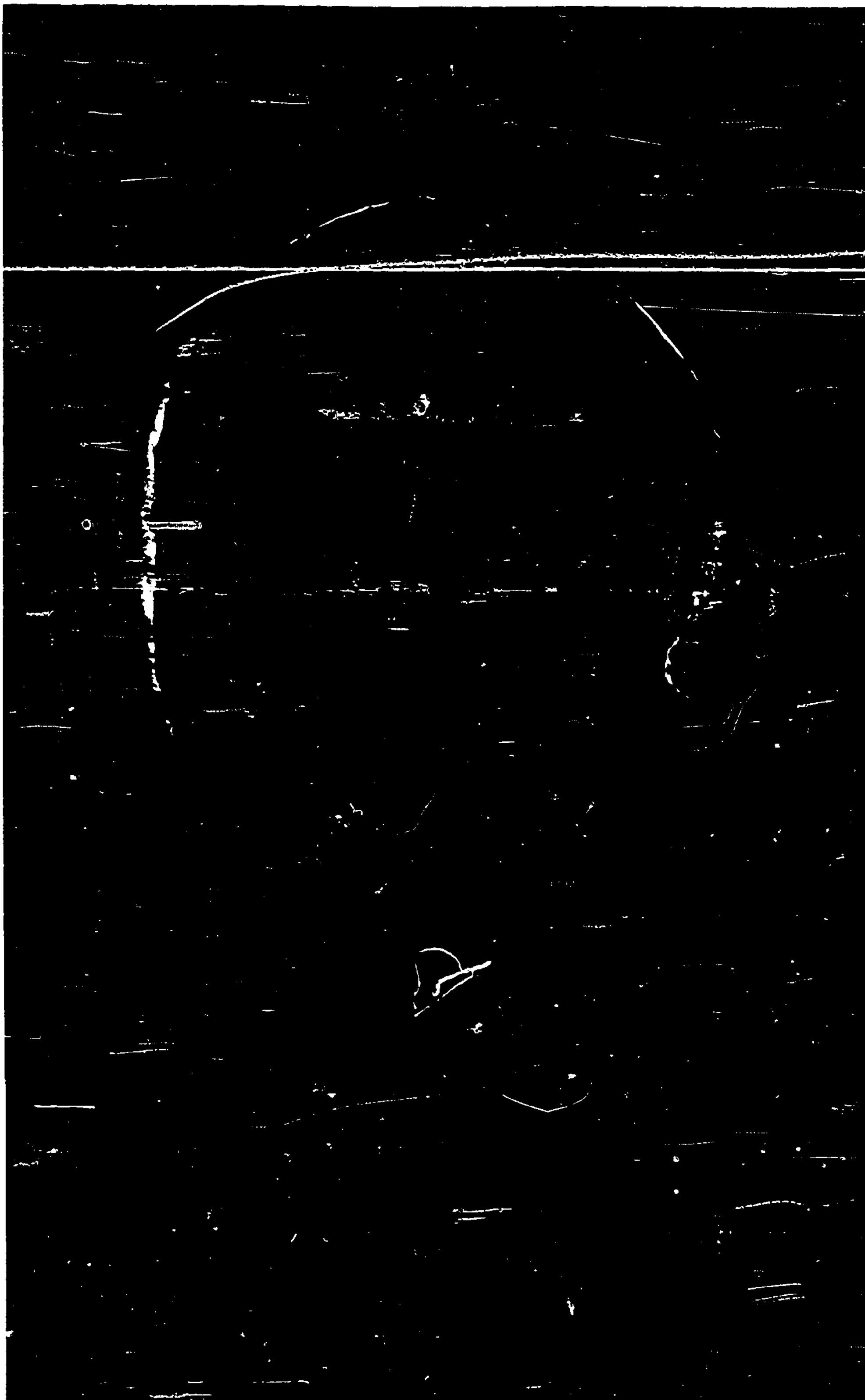
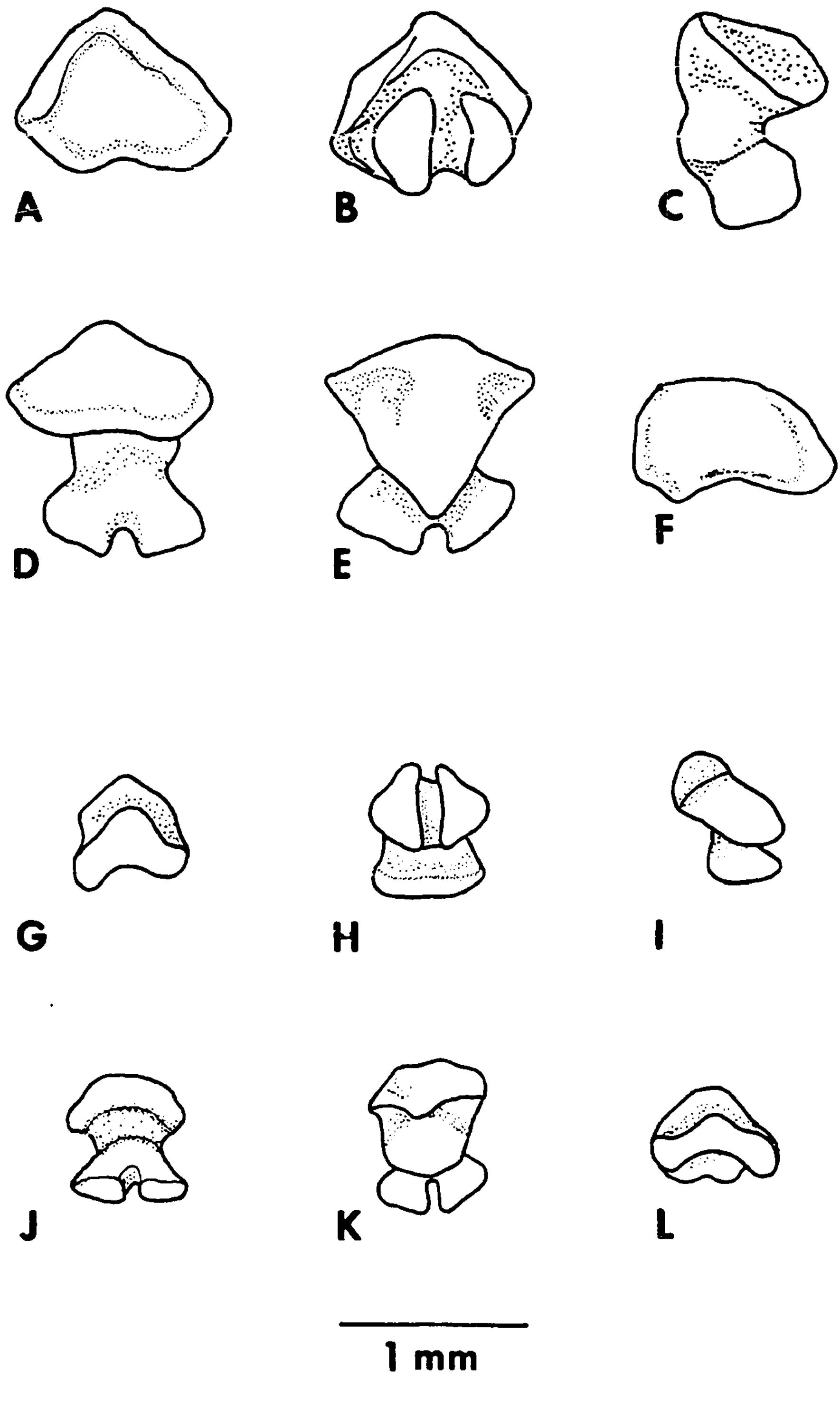


FIG. 76

Potamotrygon schroederi, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, male, 413 mm DL, INPA (uncatalogued specimen). F.- Tooth from upper jaw near mouth corner, apical view, INPA (same specimen). G - K.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views, female, 231 mm DL, MZUSP 19209. L.- Tooth from lower jaw near symphysis, apical view, MZUSP 19209.


A
B
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I
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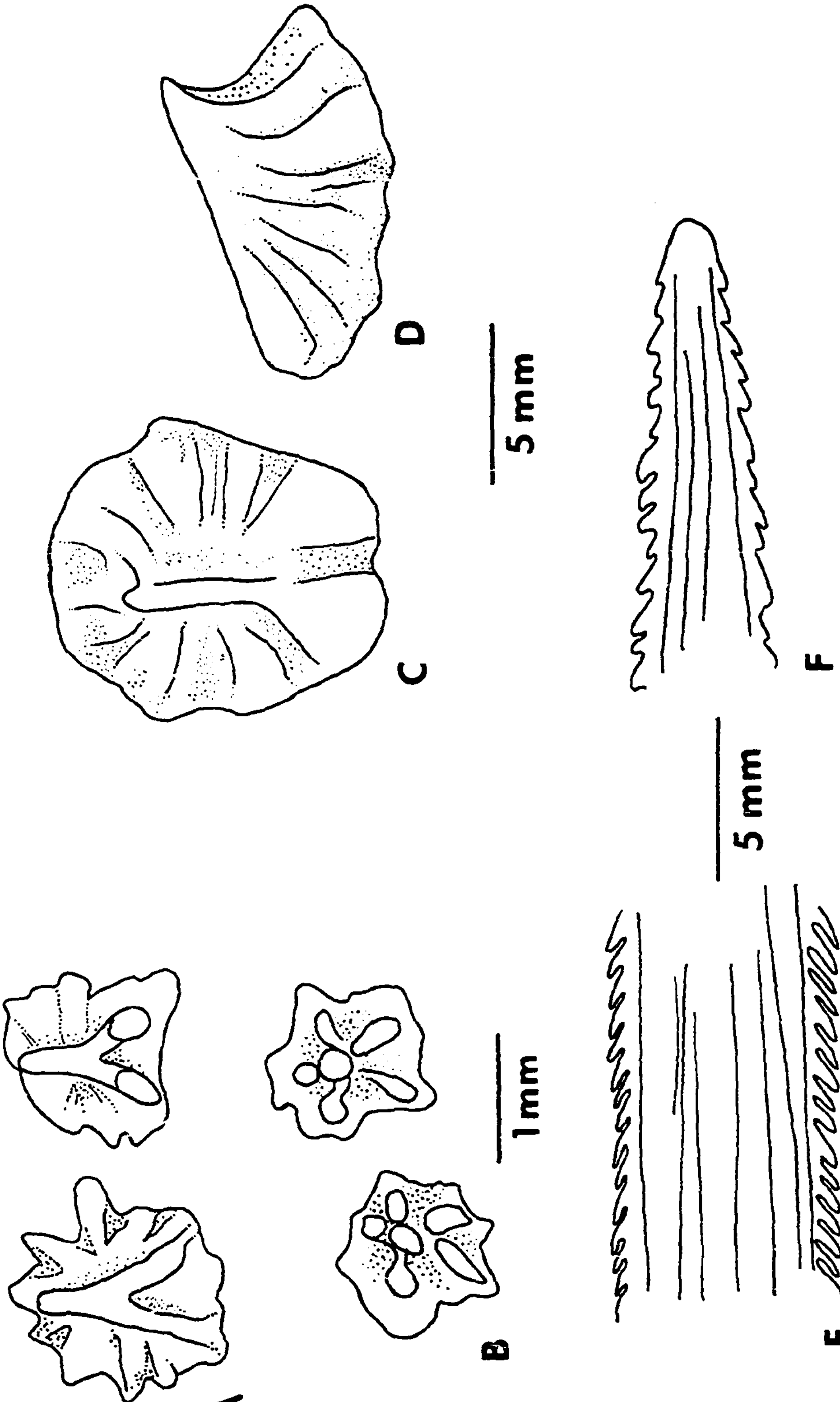
L
1 mm

FIG. 77

<u>Potamotrygon</u> <u>schroederi</u>, A.- Dermal denticles from tail base, near midline. B.- Dermal denticles from disc, near midline. C - D.- Middorsal tail spine, anterior to caudal sting, apical and lateral views. E - F.- Intermediate and distal portions of caudal sting, dorsal view. All from male, 413 mm DL, INPA (uncatalogued specimen).


A
B
C
D
E
F
1 mm
5 mm
5 mm

Potamotrygon schuemacheri Castex, 1964

(Figs. 21G, 78)

Potamotrygon schuhmacheri Castex, 1964a: 92-94 (original description, Río Colastiné).

Potamotrygon schühmacheri Castex, ibidem.

Potamotrygon schuemacheri. Taniuchi, 1982: 29.

Holotype: MFA 269, by original designation, male, coll. Castex.

Type locality: Río Colastiné Sur, Santa Fe, Argentina.

Remarks.- The specific name had two different spellings in the original publication (Castex, 1964a), being used without the umlaut mark in the title, and with the umlaut in the descriptive text. Castex kept using both spellings in his subsequent publications, as *schühmacheri* (Castex, 1964b, 1967a, 1967b), and as *schuhmacheri* (Castex, 1967d). Taniuchi (1982) emended the specific name to *schuemacheri*. Although it was an improper latinization by deletion of the second "h", this spelling should be retained according to the first reviser principle. The two forms originally used by Castex should be treated as incorrect original spellings [article 32(c) of the ICZN].

Castex (1964b, 1967b) mistakenly cited Castex and Martínez Achenbach as authors of the specific name. There is no co-authorship in the original publication of the name (Castex, 1964a), nor any evidence that Martínez Achenbach is also responsible for the name.

The holotype was lebelled as syntype and tagged with number 293 in the MFA collection. This specimen corresponds with the description and illustrations of the holotype given by Castex (1964a, 1964b). Since no additional specimens were mentioned by Castex, and since no specimen with number 269 was found in the collection, it is concluded that the holotype was mislabelled, and that it should retain the number given in the original description (MFA 269). The holotype (Fig. 78) has a cut-off tail, lacking the distal portion and caudal sting. A square piece of skin was removed from the dorsal surface. The jaws are missing.

Potamotrygon schuemacheri is known only from the holotype. One additional specimen (USNM 181767) from Paraguay resembles the holotype in coloration. Due to the lack of other comparative material, and the absence of important structures of the holotype (jaws and tail) which are usually diagnostic, no definite identification could be given for USNM 181767. Its proportional measurements and counts are given along with those of the holotype for comparative purposes. The following diagnosis and description are based only on the holotype.

Diagnosis.- A species of *Potamotrygon* from the lower Rio Paraná with subcircular disc; dorsal surface of disc with reticulate pattern of dark pigment, delimiting irregular yellowish-brown spaces with dark center, which decrease in size towards disc margins.

Description.- Measurements and counts are given in Table 20. Disc subcircular, disc length 1.06 times DW. Tail shorter than disc (*fide* Castex, 1964a, 1964b), with curved middorsal spines in single row. Latero-caudal spines relatively small, at base of tail. Eyes relatively large, eye length 2.2 in interorbital distance, 4.5 in interocular distance. Mouth relatively small, mouth width 1.1 times internarial distance. Five slender papillae at bottom of buccal cavity, one anteriorly placed near dental plate, four others posteriorly (*fide* Castex 1964a). Teeth pointed, in eight and sixteen tranverse rows respectively in upper and lower jaws (*fide* Castex, 1964a). Nostril length 1.3 in internarial distance. Branchial basket relatively wide, its greatest width 4.0 in DW; distance between first and fifth gill slits 5.8 in DW.

Disc completely covered dorsally with small denticles, which decrease in size towards disc margins. Dorsal surface of disc yellowish-brown with irregular reticulate pattern of dark pigment, delimiting light spaces with dark center. Reticulate figures of various shapes, irregular in center of disc, more circular and smaller towards disc margins. Dorsal surface of pelvic fins with same pattern as disc, but with relatively smaller reticulation. Ventral surface of disc and pelvic fins grayish, with many small white spots and dark margins.

Geographic distribution.- Potamotrygon schuemacheri is known only from Río Colastiné, a branch of Río Paraná in Santa Fe, Argentina (see Fig. 102). Castex (1964a) mentioned that the holotype was collected during the flooding season, therefore he supposed that the typical habitat of this species would be upper in Río Paraná and Río Paraguay drainages. The specimen similar to the holotype reported here, from Asunción, Paraguay, if definitely identified as P. schuemacheri could support Castex's view.

TABLE 20

MEASUREMENTS AND COUNTS ON HOLOTYPE AND PROBABLE SPECIMEN OF *Potamotrygon schuemacheri*

	HOLOTYPE	USNM 181767
DISC WIDTH (100%)	237	193
DISC LENGTH (mm)	252	210
DISC LENGTH (%)	106.3	108.8
TOTAL LENGTH (%)	-	187.0
INTERNAL DL (%)	94.9	96.3
MOUTH TO SCAPULOCORACOID (%)	32.3	32.5
MOUTH TO CLOACA (%)	68.7	68.9
CLOACA TO STING (%)	-	48.7
TAIL LENGTH (%)	-	93.7
TAIL WIDTH (%)	12.8	12.1
TAIL WIDTH AT STING BASE (%)	-	5.3
TAIL HEIGTH (%)	6.0	7.0
PELVIC FIN WIDTH (%)	25.7	28.9
PELVIC FIN LENGTH (%)	22.4	22.7
CLASPER LENGTH (%)	25.3	-
STING LENGTH (%)	-	22.7
PRECLOACAL LENGTH (%)	83.9	89.6
PREORAL LENGTH (%)	18.4	20.3
PRENARIAL LENGTH (%)	14.0	14.6
BRANCHIAL BASKET LENGTH (%)	17.2	16.8
BRANCHIAL BASKET WIDTH (%)	24.5	26.5
MOUTH WIDTH (%)	8.2	7.5

TABLE 20

(continued)

	HOLOTYPE	USNM 181767
NOSTRIL LENGTH (%)	6.3	7.3
INTERNARIAL WIDTH (%)	8.1	7.7
EYE LENGTH (%)	4.0	4.4
SPIRACLE LENGTH (%)	7.5	7.8
INTEROCULAR WIDTH (%)	18.3	19.3
INTERSPIRACULAR WIDTH (%)	18.4	19.2
PREOCULAR LENGTH (%)	25.5	28.4
CRANIUM LENGTH (%)	25.7	25.1
CRANIUM WIDTH (%)	15.8	15.8
PREORBITAL WIDTH (%)	18.4	20.6
POSTORBITAL WIDTH (%)	9.7	10.4
INTERORBITAL WIDTH (%)	8.9	8.7
FONTANELLE LENGTH (%)	16.4	14.4
FONTANELLE WIDTH (%)	6.5	6.9
UPPER DENTAL PLATE WIDTH (%)	-	3.7
LOWER DENTAL PLATE WIDTH (%)	-	3.8
PRECAUDAL VERTEBRAE	25	29
CAUDAL VERTEBRAE	-	90
CAUDAL VERTEBRAE TO BASE OF STING	-	72
TOTAL VERTEBRAE	-	119
DIPLOSPONDYLOUS VERTEBRAE	-	8
SYNARCUAL VERTEBRAE	2	5
PELVIC RADIALS	18/19	23

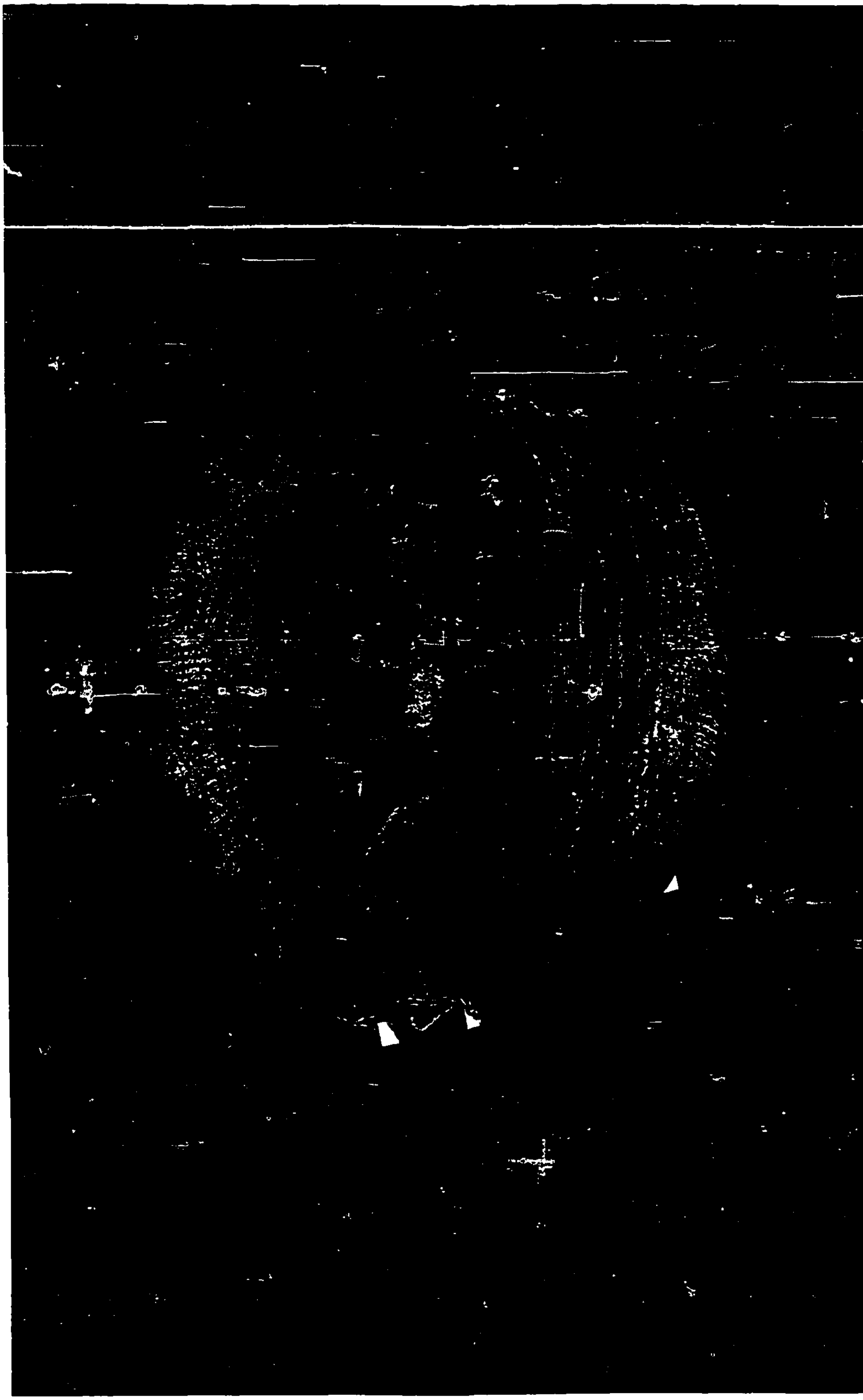
TABLE 20

(continued)

	HOLOTYPE	USNM 181767
PROPTERYGIAL RADIALS	44	47
MESOPTERYGIAL RADIALS	13	14
METAPTERYGIAL RADIALS	36	35
TOTAL PECTORAL RADIALS	93	96
UPPER TOOTH ROWS	-	31
LOWER TOOTH ROWS	-	23
LOWER MEDIAN TEETH	-	4
MIDDORSAL SPINES	-	-

FIG. 78

Potamotrygon schuemacheri, Dorsal view, male, 252 mm DL, MFA 269 (holotype).



Potamotrygon scobina Garman, 1913
(Figs. 22D, 79-81)

Potamotrygon scobina Garman, 1913: 418 (original description, Cameta, not illustrated).

Holotype: MCZ 602-S by original indication, male, coll. L. Agassiz, Thayer Expedition.

TYpe locality: Cametá, Rio Tocantins, Pará, Brazil.

Remarks.- No holotype designation was given in the original description. Sex, measurements, locality data, and Garman's identification of the only specimen of *P. scobina* found in the MCZ (MCZ 602-S) agree with those of the type. The holotype has the tail broken and the caudal sting missing. A square of skin was removed from the dorsal surface.

Castex (1967a) mistakenly identified the type of *P. scobina* as *P. motoro*. These two species are distinct in coloration, dentition, and in the shape and distribution of the caudal spines.

Diagnosis.- A species of *Potamotrygon* from the mid and lower Amazon drainage, diagnosed by the following combination of characters: disc subcircular; disc dorsally light brown to rusty brown, with small white to light yellow spots; teeth with flat, wider than long crowns; middorsal tail spines low relative to basal diameter, in irregular parallel rows.

Potamotrygon scobina is distinguished from P. motoro by its relatively smaller teeth, less pointed middorsal spines, distributed in parallel rows instead of single row, and by lack of large ocelli on disc.

Description.- Measurements and counts are given in Table 21. Disc subcircular, disc length 1.03-1.10 times DW. Tail apparently short, but no specimens with intact tails available for study. Caudal sting (Fig. 81) relatively long, sting length 2.0 times tail width.

Eyes relatively small, eye length 2.1-2.5 in interorbital distance, 3.9-5.2 in interocular distance. Spiracles relatively small, spiracle length 1.5-1.8 times eye length, 2.3-3.2 in interspiracular distance. Mouth relatively small, mouth width nearly equal to internarial distance. Three slender medial papillae and two reduced lateral papillae on floor of buccal cavity. Anteromedian papilla bifid in holotype, entire in other specimens. Preoral distance 22.6-26.5 percent of DW. Teeth small (Figs. 80-81), closely crowded in quincunx, in 30/32 to 36/40 longitudinal rows, and six to eight exposed teeth in median row of lower dental plate. Tooth crowns white, wider than long, with blunt edges. Sexual dimorphism in dentition unknown, due to lack of mature males available for study. Nostril length 1.4-1.7 in internarial distance. Branchial basket relatively narrow, its greatest width 3.9-4.0 in DW; distance between first and fifth gill slits 6.8-6.9 in DW.

Dorsal surface of disc covered with small denticles (Fig. 81), more developed medially and anteriorly on disc. Tail with 21 to 32 small middorsal spines (Fig. 81), low relative to basal diameter, in irregular parallel rows. Latero-caudal spines moderately developed near insertion of sting.

Dorsal surface of disc light brown to rusty brown, with many small white to light yellow circular spots; spots less than eye in diameter, decreasing in size towards disc margins. Pelvic fins with same dorsal pattern as disc. Ventral surface of disc and pelvic fins white with brown margins. Tail ventrally brown with irregular white spots.

Geographic distribution.- Northern Brazil, in the mid and lower Amazon drainage, from Manaus to Belém (see Fig. 102).

TABLE 21

MEASUREMENTS AND COUNTS ON SPECIMENS OF <u>Potamotrygon scobina</u>

	HOLOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	230.0	-	-	-	205- 270
DISC LENGTH (mm)	253	-	-	-	212- 290
DISC LENGTH (%)	110.0	4	106.3	2.9	103.4-110.0
TOTAL LENGTH (%)	-	2	192.8	-	191.3-194.4
INTERNAL DL (%)	98.2	4	94.6	2.8	91.7- 98.2
MOUTH TO SCAPULOCORACOID(%)	31.5	4	30.0	1.1	28.9- 31.5
MOUTH TO CLOACA (%)	65.2	4	64.3	1.2	63.1- 65.5
CLOACA TO STING (%)	-	2	54.0	-	53.7- 54.3
TAIL LENGTH (%)	-	2	101.3	-	100.0-102.7
TAIL WIDTH (%)	-	3	11.9	0.1	11.8- 12.0
TAIL WIDTH AT STING BASE(%)	-	2	5.6	-	-
TAIL HEIGTH (%)	6.7	4	6.4	0.4	5.8- 6.7
PELVIC FIN WIDTH (%)	23.8	4	24.8	1.7	23.0- 27.0
PELVIC FIN LENGTH (%)	20.7	4	22.7	2.5	20.3- 25.3
CLASPER LENGTH (%)	11.6	3	11.4	0.5	10.8- 11.9
STING LENGTH (%)	-	1	24.2	-	-
PRECLOACAL LENGTH (%)	91.7	4	88.8	2.6	86.3- 91.7
PREORAL LENGTH (%)	26.5	4	24.5	1.7	22.6- 26.5
PRENARIAL LENGTH (%)	21.0	4	18.6	2.1	8.1- 8.9
BRANCHIAL BASKET LENGTH(%)	-	3	14.6	0.1	14.4- 14.7
BRANCHIAL BASKET WIDTH (%)	-	3	25.2	0.4	24.9- 25.7
MOUTH WIDTH (%)	9.9	4	8.9	0.6	8.3- 9.9
NOSTRIL LENGTH (%)	-	3	5.1	0.6	4.7- 5.9

TABLE 21

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
INTERNARIAL WIDTH (%)	8.9	4	8.4	0.3	8.1- 8.9
EYE LENGTH (%)	3.6	4	3.9	0.3	3.6- 4.3
SPIRACLE LENGTH (%)	6.5	4	6.3	0.4	5.8- 6.8
INTEROCULAR WIDTH (%)	18.9	4	17.7	0.9	16.5-18.9
INTERSPIRACULAR WIDTH (%)	16.8	4	17.4	1.1	16.2-18.7
PREOCULAR LENGTH (%)	30.2	4	28.0	1.9	26.3-30.2
CRANIUM LENGTH (%)	26.3	3	25.1	1.0	24.4-26.3
CRANIUM WIDTH (%)	17.8	3	16.9	0.8	16.2-17.8
PREORBITAL WIDTH (%)	18.5	3	17.9	0.6	17.3-18.5
POSTORBITAL WIDTH (%)	9.3	3	9.6	0.3	9.3- 9.8
INTERORBITAL WIDTH (%)	9.0	4	9.0	0.6	8.9- 9.9
FONTANELLE LENGTH (%)	17.3	3	16.5	0.6	16.1-17.3
FONTANELLE WIDTH (%)	7.8	3	7.5	0.2	7.3- 7.8
UPPER DENTAL PLATE WIDTH(%)	8.1	4	7.9	0.4	7.4- 8.4
LOWER DENTAL PLATE WIDTH(%)	7.4	4	7.6	0.2	7.4- 7.9
PRECAUDAL VERTEBRAE	27	3	26.6	-	25- 28
CAUDAL VERTEBRAE	-	2	99.0	-	97- 101
CAUDAL VERTEBRAE TO BASE OF STING	-	2	71.5	-	69- 74
TOTAL VERTEBRAE	-	2	125.5	-	122- 129
DIPLOSPONDYLOUS VERTEBRAE	-	2	12.5	-	11- 14
SYNARCUAL VERTEBRAE	2	3	2.0	-	2- 2
PELVIC RADIALS ♂	22	2	21.5	-	21- 22
PELVIC RADIALS ♀	-	1	28.5	-	28- 29*

*Left and right side counts of one Female specimen.

TABLE 21

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
PROPTERYGIAL RADIALS	44	3	41.6	-	38- 44
MESOPTERYGIAL RADIALS	12	3	12.0	-	12- 12
METAPTERYGIAL RADIALS	32	3	32.0	-	31- 33
TOTAL PECTORAL RADIALS	89	3	86.3	-	81- 89
UPPER TOOTH ROWS	36	4	33.7	2.8	30- 36
LOWER TOOTH ROWS	40	4	36.2	4.3	32- 40
LOWER MEDIAN TEETH	-	4	5.7	0.9	5- 7
MIDDORSAL SPINES	-				

FIG. 79

Potamotrygon scobina, dorsal view, male, 253 mm DL, MCZ 602-S (holotype).

FIG. 80

Potamotrygon scobina, A.- Exposed portions of upper and lower dental plates, male, 241 mm DL, MZUSP 14792. B.- Idem, female, 290 mm DL, AMNH 3883.

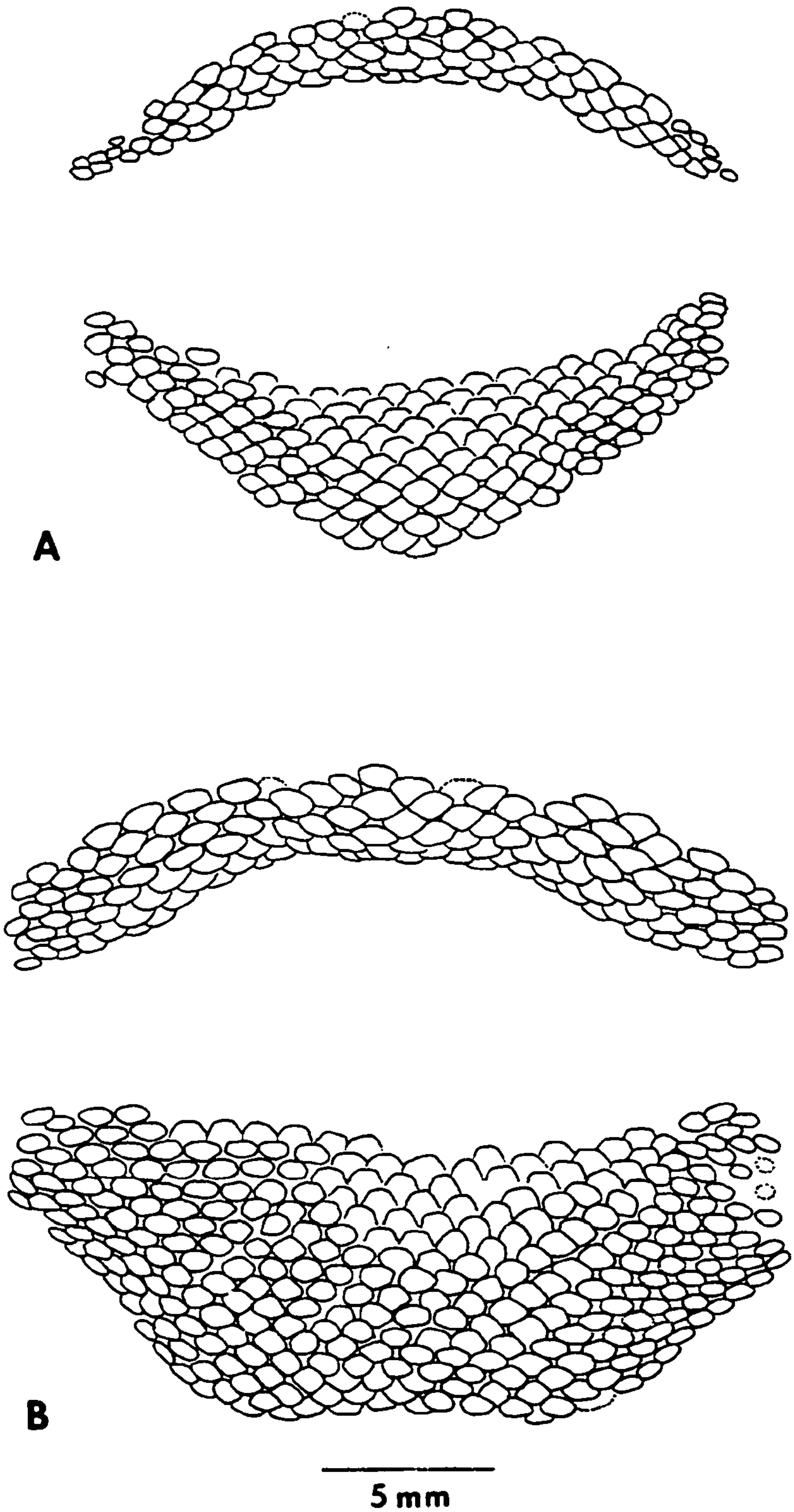
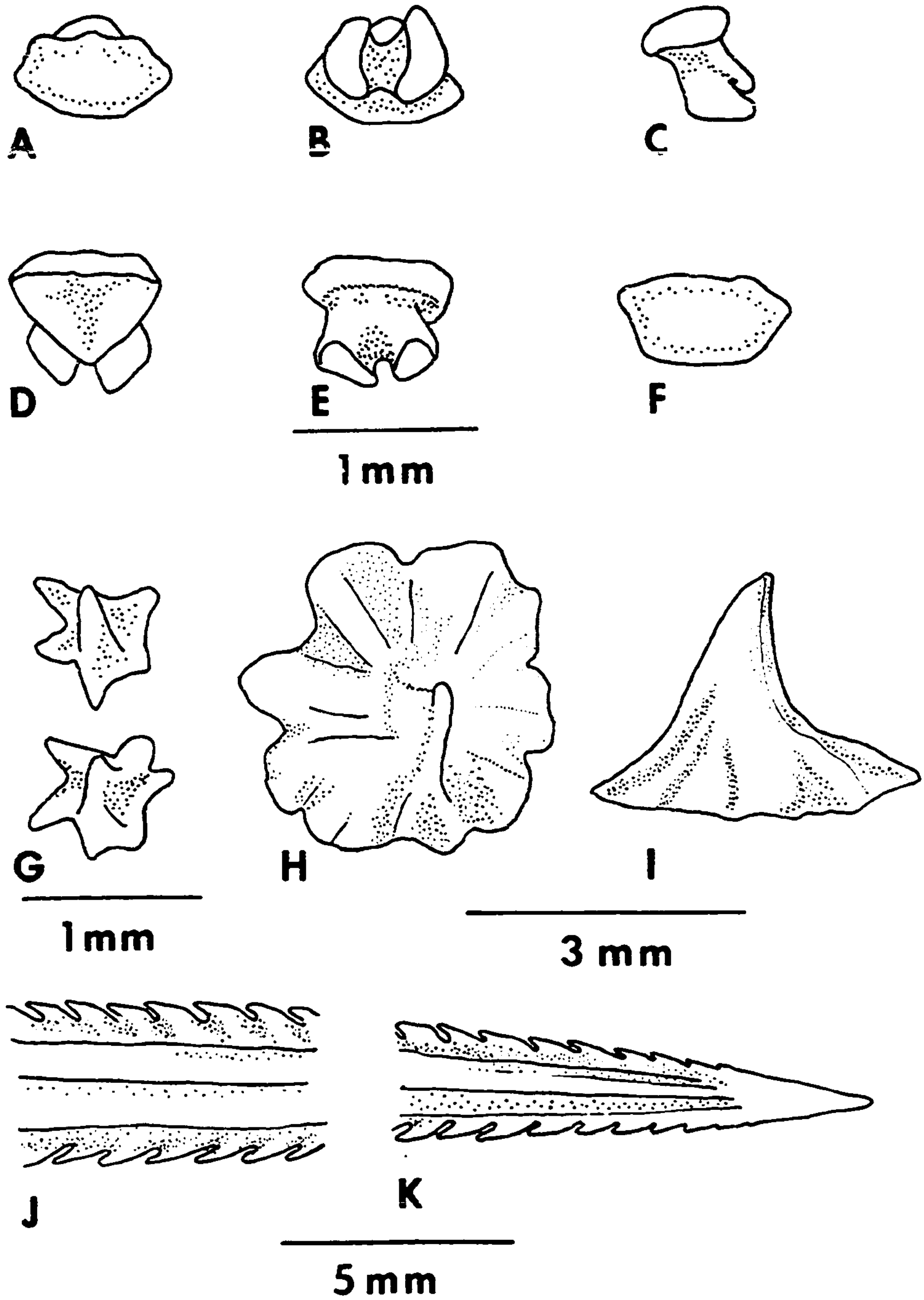

A
B
5 mm

FIG. 81

Potamotrygon scobina, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, labial, and lingual views. F.- Tooth from lower jaw near symphysis, apical view. G.- Dermal denticles from disc near midline, apical view. H - I.- Mid-dorsal tail spine anterior to caudal sting, apical and lateral views. J - K.- Dorsal views of intermediate and distal portions of caudal sting. All from male, 241 mm DL, MZUSP 14792.


A
B
C
D
E
F
1mm
G
H
I
1mm
3 mm
J
K
5mm

Potamotrygon signata Garman, 1913

(Figs. 22B, 82)

Potamotrygon signatus Garman, 1913: 420 (original description, San Gonçallo, not illustrated).

Paratrygon signatus. Fowler, 1948: 10.

Lectotype: MCZ 600-S (herein selected), male, coll. I. St. John, Thayer Expedition.

Paralectotype: USNM 153589 (formerly MCZ 560-S), male, coll. I. St. John, Thayer Expedition.

Type locality: São Gonçalo, Rio Parnaíba, Piauí, Brazil.

Remarks.- The specific name, interpreted as an adjective, is herein changed to feminine to agree in gender with _Potamotrygon_ (article 30 of the ICZN). No holotype designation was given in the original description. The lectotype selection is based on size and maturity of the specimen (it was the only adult male among the syntypes), and the more precise locality data given for it. Only one specimen from Rio Poty (of the two mentioned by Garman) was found, and selected as paralectotype. Two immature males of _P. motoro_ (MCZ 604-S) from Amazonas were misidentified and labelled as types of _P. signata_.

Diagnosis.- A species of _Potamotrygon_ from Rio Parnaíba drainage diagnosed by the following combination of characters: disc oval; dorsal surface brown mottled with yellow spots, occasionally forming a network; teeth relativelly small, with wider than long flat crowns, in 27 to 36 longitudinal rows in upper jaw.

Description.- Measurements and counts are given in Table 22. Disc oval, disc length 1.06-1.16 times DW. Tail relatively short, tail length 1.1 times DW. caudal sting relatively long, sting length 1.9-2.9 times tail width.

Eyes relatively small, eye length 1.8-3.0 in interorbital distance, 3.4-5.2 in interocular distance. Spiracles relatively large, spiracle length 1.4-1.9 times eye length, 2.1-3.0 in interspiracular distance. Mouth relatively large, mouth width 1.0-1.2 times internarial distance. Five papillae at floor of buccal cavity. Preoral distance 26.2-31.3 percent of DW. Teeth relatively small, white to caramel in color, with crowns wider than long and flattened in females, males with pointed crowns. Teeth closely crowded in quincunx, in 27/22 to 26/34 longitudinal rows, and three to nine exposed teeth in median row of lower dental plate. Nostril length 1.2-2.0 in internarial distance. Branchial basket relatively narrow, its greatest width 3.7-4.0 in DW; distance between first and fifth gill slits 5.5-5.9 in DW.

Disc rough, dorsally covered with dermal denticles, more developed on midline. Tail of adults and subadults with 16 to 31 middorsal spines, in double or triple irregular rows. Latero-caudal spines well developed near caudal sting.

Dorsal surface of disc olivaceous-brown, darker on midline, mottled with small, oval or irregular yellow spots, which occasionally form labyrinthic network. Spots decrease in size towards disc margins; largest spots less than eye in diameter. Bright yellow ocelli ocasionally on disc. Tail with dorsal yellow vermiculations. One juvenile specimen from Rio Poti drainage (MZUSP 19233) with yellow pigment forming reticulate pattern on disc, and distinct yellow spots only on disc margins. Dorsal pattern of lines pictured by Fowler (1941, 1948) possibly caused by fungal attack on specimen ANSP 69344, not corresponding with real color pattern. Ventral surface white with brown margins. Tail ventrally white mottled with brown spots.

Geographic distribution.- Northern Brazil, in Piauí state (see Fig. 102). Potamotrygon signata is possibly endemic to the Rio Parnaíba drainage. It is not known whether an isolated population remains in the upper Parnaíba, above the dam of Boa Esperança. Records of this species for the state of Ceará (Fowler, 1941, 1948) probably are erroneous, as noted by Menezes (1953). The states of Piauí and Ceará are separated by a platform (Chapada do Ipiapaba) with elevations above 500 m. Although Rio Poty, a tributary of Rio Parnaíba, has its headwaters in the state of Ceará, its upper course is intermittent and marked by falls.

Biological remarks.- Some of the specimens of *P. signata* studied showed remarkable similarity in coloration, external morphology, and dentition to *P. castexi*. The small series of specimens studied showed great variability in coloration and tooth morphology. Further sampling is necessary to confirm the identity of P. signata, or to reveal possible additional species in Rio Parnaíba drainage. According to zoologists from Piauí, a second species of *Potamotrygon* might be present in Rio Parnaíba.

Menezes (1953) reported that the stingrays are abundant in Rio Poti, but periodically disappear. A sampling program carried out by the present author during the rainy season in Rio Poti, from Teresina to the upper course, revealed very few stingrays. Nevertheless, local fishermen reported that the stingrays are abundant there in the dry season. These facts suggest that the stingrays migrate downstreams during the rainy season, and return to the upper course in the dry period.

TABLE 22

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Potamotrygon signata*

	LECTOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	186	5	-	-	145.0- 274
DISC LENGTH (mm)	204	5	-	-	155- 318
DISC LENGTH (%)	109.6	5	110.9	3.5	106.8-116.0
TOTAL LENGTH (%)	189.7*	1	202.3	-	- - -
INTERNAL DL (%)	96.7	4	94.2	3.5	89.4- 97.1
MOUTH TO SCAPULOCORACOID(%)	31.2	5	32.2	0.7	31.2- 33.0
MOUTH TO CLOACA (%)	65.3	5	64.7	3.4	59.0- 68.6
CLACA TO STING (%)	51.0	4	49.3	4.5	42.8- 53.2
TAIL LENGTH (%)	97.3*	1	113.2	-	- - -
TAIL WIDTH (%)	11.5	5	11.9	2.0	8.5- 13.2
TAIL WIDTH AT STING BASE(%)	3.8	4	5.6	1.4	3.8- 7.3
TAIL HEIGTH (%)	7.0	5	6.7	0.9	5.4- 8.1
PELVIC FIN WIDTH (%)	27.9	5	28.9	1.9	26.7- 31.0
PELVIC FIN LENGTH (%)	26.6	5	25.4	3.0	23.4- 30.0
CLASPER LENGTH (%)	32.3	3	21.4	-	10.8- 32.3
STING LENGTH (%)	26.0	4	26.3	1.1	25.2- 28.0
PRECLOACAL LENGTH (%)	87.6	4	85.5	2.2	83.1- 87.6
PREORAL LENGTH (%)	21.5	5	22.2	3.3	18.4- 25.7
PRENARIAL LENGTH (%)	17.2	5	17.4	2.2	14.9- 19.2
BRANCHIAL BASKET LENGTH (%)	18.1	5	17.2	0.4	16.9- 18.1
BRANCHIAL BASKET WIDTH (%)	26.6	5	25.4	0.6	24.9- 26.6
MOUTH WIDTH (%)	10.1	5	9.3	1.0	7.9- 10.1

*Tail distally broken on lectotype.

TABLE 22

(continued)

	LECTOTYPE	N	MEAN	S.D.	RANGE
NOSTRIL LENGTH (%)	3.9	5	5.6	0.9	3.9- 6.2
INTERNARIAL WIDTH (%)	7.9	5	8.6	1.0	7.4- 9.9
EYE LENGTH (%)	3.9	5	4.2	0.6	3.6- 5.2
SPIRACLE LENGTH (%)	5.7	5	7.4	1.2	5.7- 8.8
INTEROCULAR WIDTH (%)	17.61	5	18.3	1.8	15.5-20.4
INTERSPIRACULAR WIDTH (%)	17.6	5	19.3	1.4	17.6-21.4
PREOCULAR LENGTH (%)	31.3	5	28.9	2.3	26.2-31.3
CRANIUM LENGTH (%)	26.4	4	26.2	0.7	25.2-27.1
CRANIUM WIDTH (%)	16.9	4	17.3	0.6	16.7-18.0
PREORBITAL WIDTH (%)	19.3	4	19.4	0.2	19.3-19.9
POSTORBITAL WIDTH (%)	10.6	3	10.8	-	9.6-12.2
INTERORBITAL WIDTH(%)	8.6	5	9.7	1.2	8.6-11.2
FONTANELLE LENGTH (%)	17.0	4	16.6	0.6	15.7-17.0
FONTANELLE WIDTH (%)	7.4	4	7.8	0.5	7.2- 8.4
UPPER DENTAL PLATE WIDTH(%)	6.5	5	7.4	1.1	6.4- 8.7
LOWER DENTAL PLATE WIDTH(%)	5.8	5	6.7	1.3	5.4- 8.6
PRECAUDAL VERTEBRAE	24	5	25.8	1.3	24- 27
CAUDAL VERTEBRAE	105	4	99.0	4.0	96- 105
CAUDAL VERTEBRAE TO BASE OF STING	75	4	71.0	3.2	67- 75
TOTAL VERTEBRAE	129	4	124.5	3.0	123- 129
DIPLOSPONDYLOUS VERTEBRAE	-	2	8.0	-	-
SYNARCUAL VERTEBRAE	2	4	2.0	0.0	-

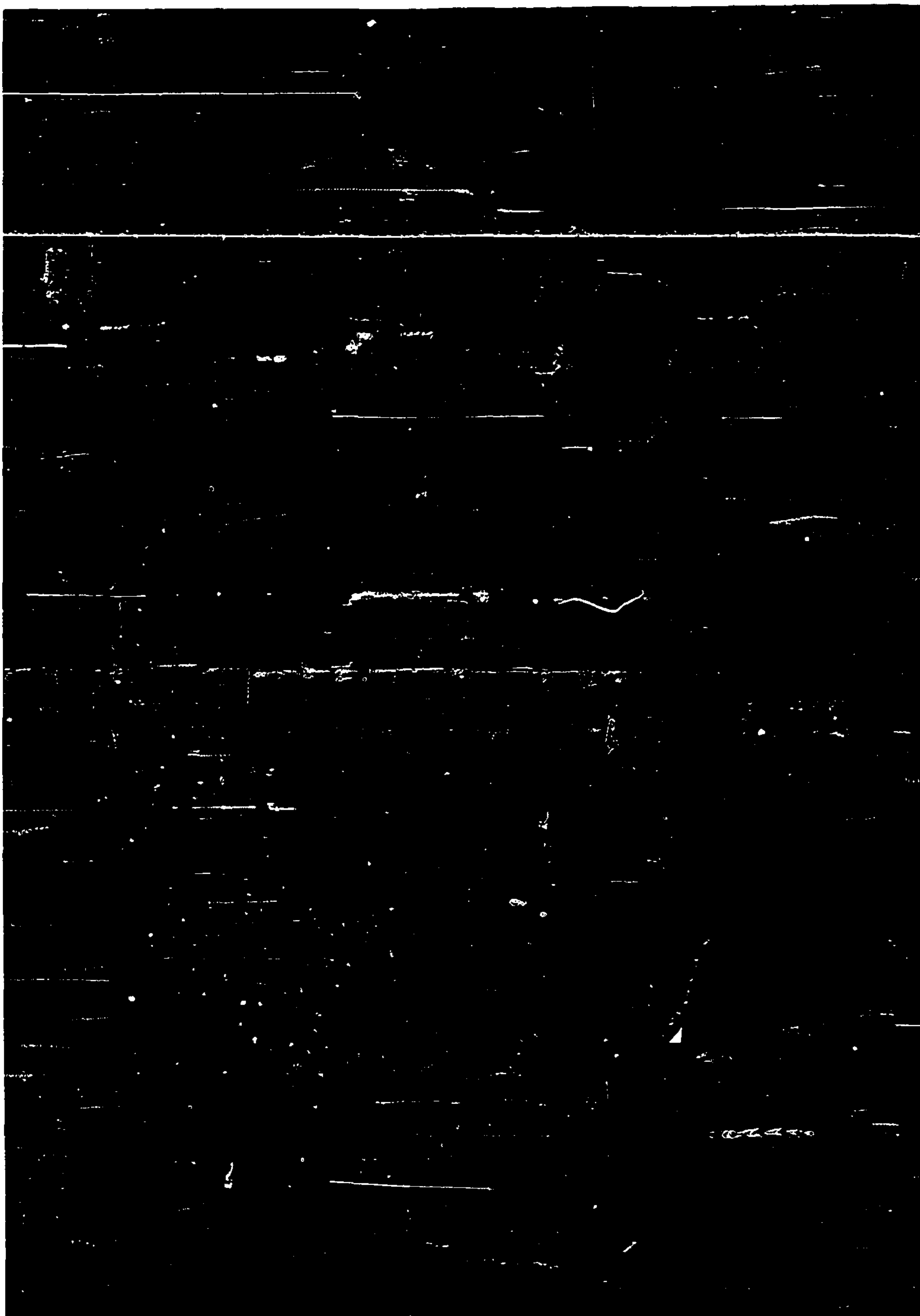
TABLE 22

(continued)

	LOCTOTYPE	N	MEAN	S.D.	RANGE
PELVIC RADIALS	17	3	19.0	-	17-20
	-	2	26.0	-	25-27
PROPTERYGIAL RADIALS	44	5	44.4	4.7	37-48
MESOPTERYGIAL RADIALS	14	5	13.0	1.2	11-14
METAPTERYGIAL RADIALS	36	5	36.8	0.4	36-37
TOTAL PECTORAL RADIALS	94	5	94.2	4.5	87-99
UPPER TOOTH ROWS	27	5	30.4	3.5	27-36
LOWER TOOTH ROWS	22	5	29.2	5.0	22-34
LOWER MEDIAN TEETH	9	5	6.4	2.6	3- 9
MIDDORSAL SPINES	22	4	24.0	6.4	16-31

FIG. 82

Potamotrygon signata, dorsal view, female,
318 mm DL, MZUSP 19234.



Potamotrygon yepezi Castex & Castello, 1970

(Figs. 20C, 83-84)

Trygon hystrix [in part]. Müller and Henle, 1841: 167. Duméril, 1865: 608.

Potamotrygon hystrix [in part]. Garman, 1913: 422.

Potamotrygon magdalenae [in part]. Schultz, 1949: 24, 29. Fernández-Yépez, 1970: 9.

Potamotrygon yepezi Castex and Castello, 1970a: 17 (original description, Maracaibo).

Holotype: USNM 121662 by original designation, male, coll. L. P. Schultz. Type locality of holotype: Río Palmar, Maracaibo drainage, Venezuela.

Paratypes (by original designation): USNM 121659 (two specimens); USNM 121660; USNM 121663; USNM 121664; USNM 121665; USNM 121667; USNM 121668 (two specimens).

Remarks.- Müller and Henle (1841) included one specimen of P. yepezi (MNHN 2433) in their heterogenous material of P. histrix. Schutz (1949), and subsequently Fernández-Yépez and Espinosa (1970) misidentified specimens of P. yepezi as P. magdalenae. Castex and Castello (1970a) recognized the specimens collected by Schultz as distinct from P. magdalenae, and described them as a new species. Although these authors did not refer to the original description of P. magdalenae, they had comparative material of this species.

Diagnosis.- A species of Potamotrygon from Lake Maracaibo drainage diagnosed by the following combination of characters: disc oval; dorsal surface of disc light brown to dark grayish-brown, usually with scattered small black spots, occasionally mottled with yellow spots; teeth small, in 22 to 27 longitudinal rows in upper jaw.

Description.- Measurements and counts are given in Table 23. Disc oval, disc length 1.05-1.17 times DW. Pelvic fins broad, usually covered dorsally by disc. Tail relatively long, tail length 1.1-1.4 times DW, with well-developed dorsal and ventral finfolds. Maximum height of dorsal finfold 0.9-2.2 in tail height. Caudal sting relatively long, sting length 1.6-2.8 times tail width.

Eyes relatively large, eye length 1.8-2.9 in interorbital distance, 3.6-6.0 in interocular distance. Preocular distance 3.4-4.3 in DW, 1.2-1.5 times interocular distance. Spiracles relatively small, spiracle length 1.0-2.0 times eye length, 2.4-3.4 in interspiracular distance. Mouth relatively large, mouth width 0.8-1.3 times internarial distance. Five buccal papillae, two extreme papillae smaller than medial and paramedial papillae. Preoral distance 20.9-26.4 percent of DW. Teeth white to caramel in color, relatively small, closely crowded in quincunx (Fig. 84), in 22/19 to 27/28 longitudinal rows, and four to seven exposed teeth in median row of lower dental plate. Teeth sexually dimorphic, subadult and adult males with pointed teeth in both jaws, females with blunt teeth. No apparent monognathic heterodonty in males or females, except for decrease in tooth size from midline towards lateral margins of dental plates. Nostril length 1.0-1.4 in internarial distance. Branchial basket relatively wide, its grestest width 3.4-4.1 in DW; distance between first and fifth gill slits 5.5-6.7 in DW.

Dorsal surface of disc relatively smooth, occasionally with enlarged stelliform denticles on midline. Tail of subadults and adults with seven to 23 middorsal spines in single row. Latero-caudal spines moderately developed near insertion of caudal sting, or entirely lacking.

Dorsal color pattern variable, with light brown to dark grayish-brown background, usually with small scattered black spots, occasionally mottled with irregular yellow spots, more conspicuous in lighter specimens. Ventral surface of disc white to light yellow, with brown margins and occasional dark spots. Central dark spot present or absent ventrally on disc. Tail and pelvic fins dorsally with same pattern as disc. Tail with alternate white and brown lateral bars in lighter specimens. Pelvic fins ventrally white, with dark posterior margins. Ventral surface of tail white mottled with irregular brown spots, or entirely brown in darker specimens.

Geographic distribution.- *Potamotrygon yepezi* is endemic to the Maracaibo drainage in Venezuela (see Fig. 102).

TABLE 23

MEASUREMENTS AND COUNTS ON SPECIMENS OF *Potamotrygon yepezi*

	HOLOTYPE	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	167	43	-	-	69.6- 349
DISC LENGTH (%)	182	29	-	-	82.0- 391
DISC LENGTH (%)	108.9	27	109.2	2.3	105.3-117.8
TOTAL LENGTH (%)	226.3	17	235.0	23.7	209.2-321.0
INTERNAL DL (%)	96.4	24	95.5	2.5	90.9- 99.4
MOUTH TO SCAPULOCORACOID (%)	32.9	29	32.2	0.7	31.1- 33.9
MOUTH TO CLOACA (%)	67.3	26	67.3	2.3	62.9- 71.7
CLOACA TO STING (%)	61.3	25	58.7	5.9	49.7- 74.1
TAIL LENGTH (%)	129.3	17	132.3	9.7	110.9-149.5
TAIL WIDTH (%)	11.7	25	11.0	0.9	8.6- 13.5
TAIL WIDTH AT STING BASE(%)	5.2	25	5.4	1.0	3.3- 8.5
TAIL HEIGHT (%)	6.5	24	6.8	0.7	5.4- 8.5
PELVIC FIN WIDTH (%)	36.2	26	32.3	2.5	26.3- 36.2
PELVIC FIN LENGTH (%)	25.1	26	24.2	2.0	21.2- 29.3
CLASPER LENGTH (%)	34.0	13	27.7	7.0	14.4- 34.0
STING LENGTH (%)	24.1	32	25.1	3.9	17.9- 33.6
PRECLOACAL LENGTH (%)	91.0	24	91.1	5.1	83.0-110.8
PREORAL LENGTH (%)	23.6	26	23.2	1.3	20.9- 26.4
PRENARIAL LENGTH (%)	16.8	26	16.6	1.4	14.0- 19.7
BRANCHIAL BASKET LENGTH (%)	16.1	29	15.9	0.8	14.6- 17.9
BRANCHIAL BASKET WIDTH (%)	25.6	28	26.0	1.1	24.0- 29.1
MOUTH WIDTH (%)	10.2	26	9.7	1.2	8.0- 13.1
NOSTRIL LENGTH (%)	-	13	6.6	0.4	6.1- 7.5

TABLE 23

(continued)

		HOLOTYPE	N	MEAN	S.D.	RANGE
INTERNARIAL WIDTH (%)		9.1	26	8.6	0.5	7.6-10.2
WYE LENGTH (%)		5.0	27	4.4	0.7	3.4- 5.9
SPIRACLE LENGTH (%)		6.4	26	7.4	1.0	6.1- 9.6
INTEROCULAR WIDTH (%)		-	15	20.0	1.4	17.8-22.6
INTERSPIRACULAR WIDTH (%)		21.6	25	21.0	0.7	19.1-22.7
PREOCULAR LENGTH (%)		27.7	26	27.2	1.2	23.0-28.9
CRANIUM LENGTH (%)		26.5	25	26.3	1.1	23.9-28.4
CRANIUM WIDTH (%)		19.2	24	18.2	0.5	17.3-19.3
PREORBITAL WIDTH (%)		19.9	24	18.8	0.9	17.3-21.6
POSTORBITAL WIDTH (%)		11.3	6	10.4	0.9	9.1-11.3
INTERORBITAL WIDTH (%)		9.6	25	10.2	0.5	9.3-11.0
FONTANELLE LENGTH (%)		17.8	10	17.9	0.8	16.4-18.9
FONTANELLE WIDTH (%)		8.7	10	8.0	0.3	7.3- 8.7
UPPER DENTAL PLATE WIDTH (%)		8.0	25	8.2	0.7	7.0- 9.8
LOWER DENTAL PLATE WIDTH (%)		7.2	24	7.7	0.6	6.6- 9.2
PRACAUDAL VERTEBRAE		25	24	24.6	1.8	21- 28
CAUDAL VERTEBRAE		-	24	99.9	3.5	92- 108
CAUDAL VERTEBRAE TO BASE OF STING		85	23	76.3	4.0	70- 86
TOTAL VERTEBRAE		-	24	124.5	4.1	117-132
DIPLOSPONDYLOUS VERTEBRAE		-	19	15.3	1.8	14- 18
SYNARCUAL VERTEBRAE		-	22	3.1	2.5	1- 4
PELVIC RADIALS	♂	20	9	19.7	0.6	19- 22
	♀	-	16	23.5	1.3	21- 25

TABLE 23

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
PROPTERYGIAL RADIALS	45	25	43.3	1.2	41- 46
MESOPTERYGIAL RADIALS	13	31	12.6	3.5	10- 14
METAPTERYGIAL RADIALS	34	24	33.1	1.4	30- 36
TOTAL PECTORAL RADIALS	92	26	89.4	2.7	85- 96
UPPER TOOTH ROWS	25	6	25.0	1.8	22- 27
LOWER TOOTH ROWS	22	16	22.2	2.3	19- 28
LOWER MEDIAN TEETH	5	5	5.4	1.1	4- 7
MIDDORSAL SPINES	7	7	13.4	5.1	7- 23

FIG. 83

Potamotrygon yepezi, dorsal view, female, 131.0 mm DL, MCNG 775-20.

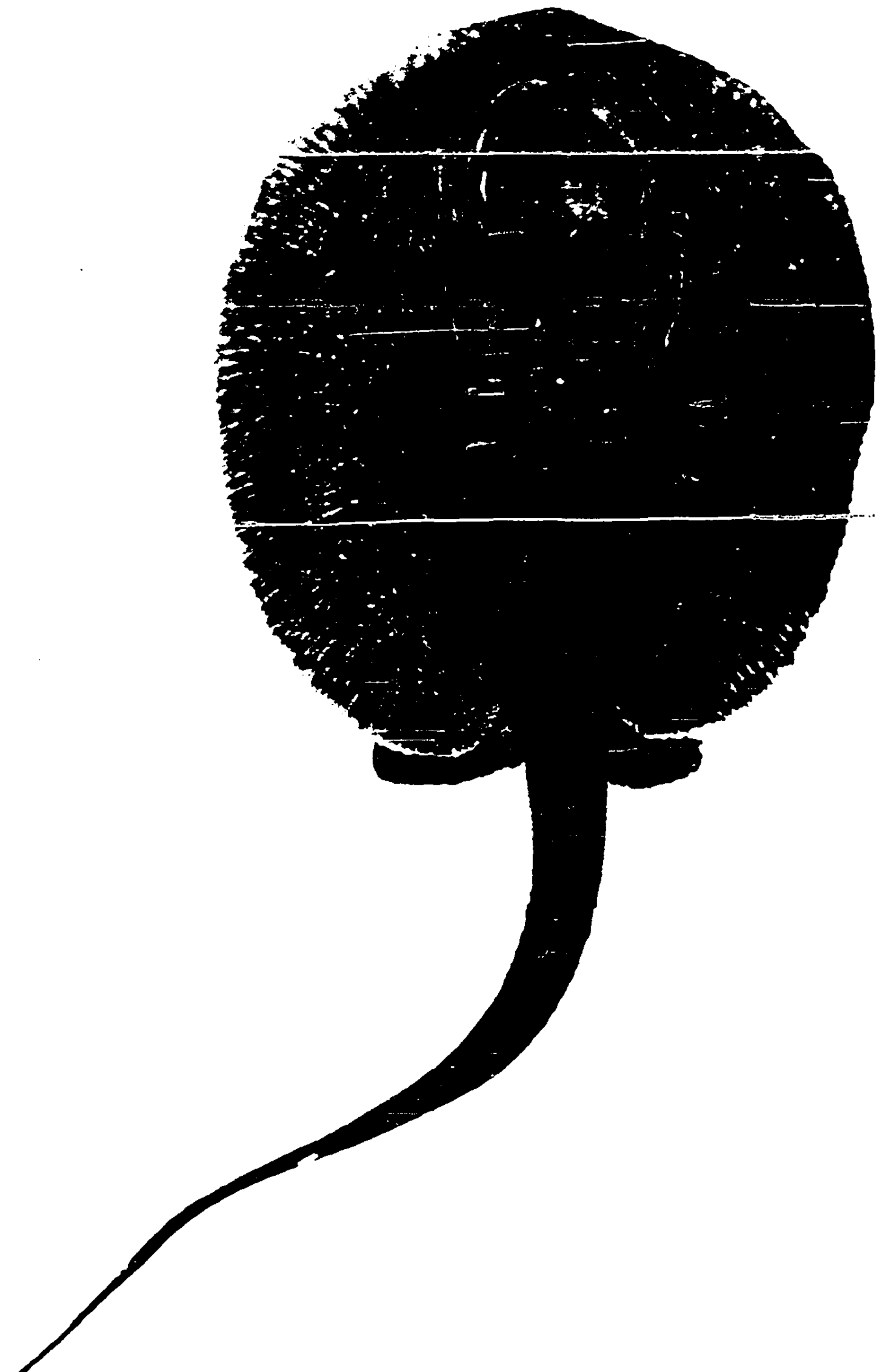
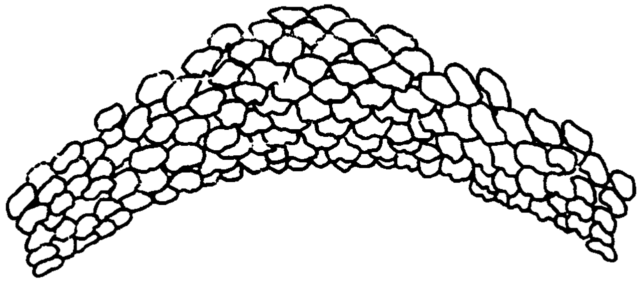


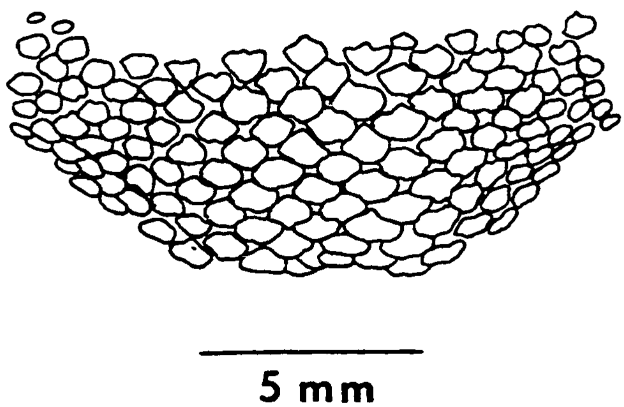
FIG. 84

Potamotrygon yepezi, A - B.- Exposed portions of upper and lower dental plates, male, 181 mm DL, VIMS 06064.

A



B



COMMENTS ON UNIDENTIFIED SPECIMENS OF *POTAMOTRYGON*

The following accounts refer to specimens of the genus *Potamotrygon* which could not be keyed into any of the existing species descriptions. These specimens may belong to undescribed species, or may represent divergent morphs of known species. The lack of adequate study material (small sample sizes, geographically restricted samples, or the lack of adult specimens) precluded comparative studies necessary to make decisions at the species level, or to adequately describe new species.

Potamotrygon sp. A.- This series of specimens (see material examined) was obtained in several localities of Rio Amazonas (Solimões) and its tributary Rio Ucayali, from Contamana (Peru) down to Óbidos (Brazil). It also includes material from the vicinity of Puerto Maldonado, Madre de Diós, Peru (Rio Madeira drainage). The specimens are similar in color to *P. motoro*, their dorsal pattern formed by yellow ocelli on brown background. The ocelli are relatively smaller than in *P. motoro*, and do not vary in size as in the latter species, all the ocelli being nearly equal to eye in diameter. The dentition of these specimens differs from that of *P. mo-*

toro in showing relatively smaller teeth with tricuspidate crowns, in larger number of longitudinal rows (up to 42 rows in the upper jaw). The radiographic study of these specimens revealed that they have relatively narrower mandible, and the cranial fontanelle relatively more constricted than P. motoro.

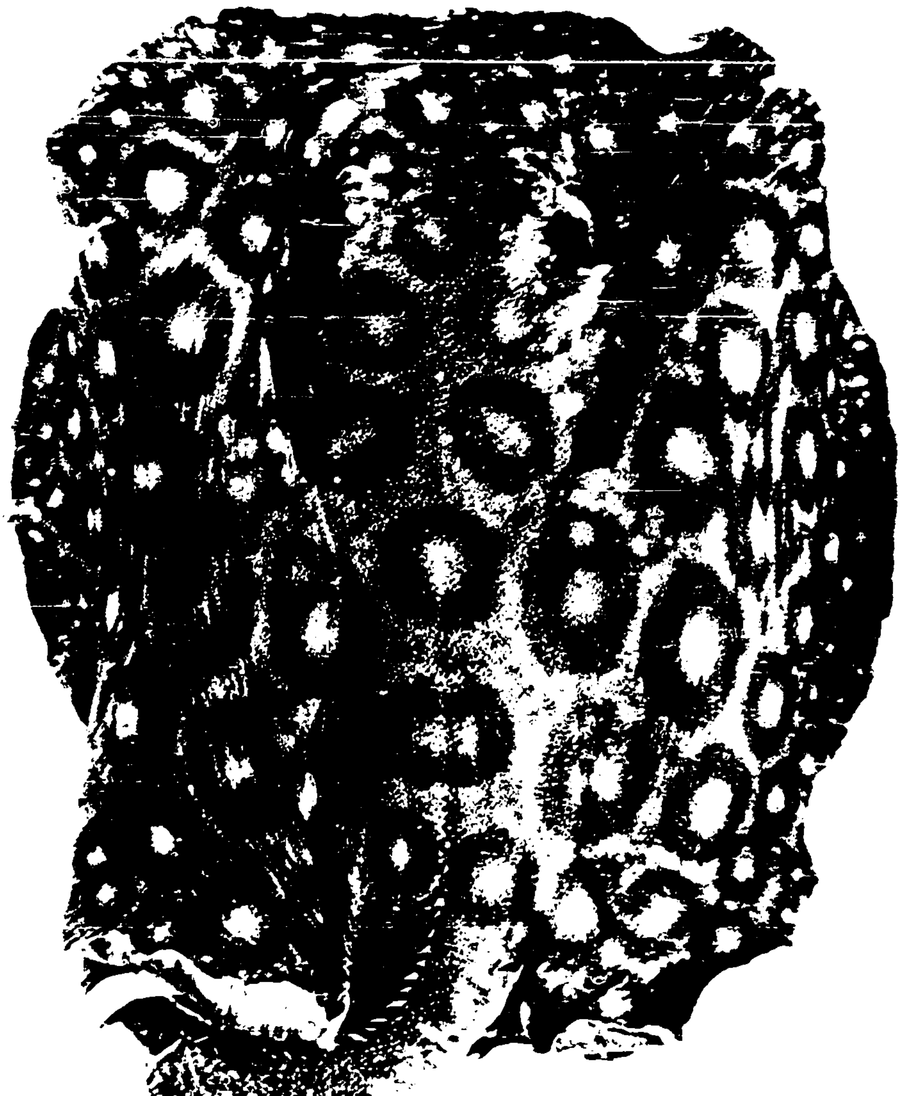
The present material is composed only of small specimens, less than 220 mm DW, most with faded color patterns. There are two possibilities concerning the status of this material: (1) the characters seen in these juvenile specimens represent intraspecific variations of P. motoro, or (2) it represents an undescribed species of Potamotrygon. Any decision would depend on larger series of specimens of various ontogenetic stages for comparative purposes.

Potamotrygon sp. B.- These specimens (see material examined) were obtained in several localities of Corantijn river drainage in Surinam. They resemble P. motoro and P. ocellata in having an ocellated color pattern on disc (Fig. 85), but unlike P. motoro, the ocelli have irregular contours (instead of rounded), and are more intensily colored in orange or red as in P. ocellata. The dorsal background coloration is darker than in P. motoro, being nearly black in all specimens. The buccal cavity is dark-pigmented, and has orange spots in some specimens, a condition not seen in P. motoro. The teeth are relatively smaller and in greater number than in P. motoro and P. ocellata (up to 45 rows in the upper jaw). The middorsal tail spines are relatively smaller, sharper, and less curved than in *P. motoro*. These specimens show slightly higher counts of pectoral-fin radials (98 to 103) than *P. motoro* and *P. ocellata*.

The decision on whether *Potamotrygon* sp. B represents an undescribed species or a geographic morph of *P. motoro* or *P. ocellata* would depend on larger series of specimens of the three forms, from Guianas to Amapá, to detect possible clinal variation of the discussed characters.

FIG. 85

Potamotrygon sp. B, dorsal view, female, 420 mm DL, RMNH (uncatalogued specimen).



Paratrygon Duméril, 1865

Trygon [in part]. Müller and Henle, 1841: 196; Schomburgk, 1843: 183; Duméril, 1865: 592, 594; Günther, 1870: 476.

Himantura [in part]. Duméril, 1865: 592.

Paratrygon Duméril, 1865: 594.

Disceus Garman, 1877: 208.

?*Elipesurus* [in part]. Garman, 1913: 424-425.

Ellipesurus [in part]. Ribeiro, 1907: 184.

Type species: *Trygon aiereba* Müller and Henle, 1841 (non Marcgrave) by monotypy.

Etymology: *Paratrygon*, from Greek = close to trygon.

Remarks.- Duméril (1865) established *Paratrygon* as a subgenus of *Trygon*, for the single species *Trygon aiereba* Müller and Henle. Günther (1870) used *Paratrygon* in the generic category, by citing *Paratrygon aiereba* in the synonymy of *Trygon orbicularis*. Duméril (1865) mistakenly included Aiereba Marcgrave, 1648 (a doubtful pre-Linnaean vernacular) and *Raja orbicularis* (a binomen established for Aiereba) in the synonymy of *Paratrygon aiereba*. This synonymy induced subsequent authors (Günther, 1870; Eigenmann, 1912; Castex, 1964b, 1968; Castex and Castello, 1969; Bailey, 1969) to regard Paratrygon as a genus established for the Aiereba of Marcgrave. Based on this wrong synonymy, Eigenmann (1912) and Fowler (1948, 1970) respectively selected Raja orbicularis and Raja ajereba, two binomina based on Aiereba Marcgrave, as type species of Paratrygon. Trygon aiereba Müller and Henle was the only species originally included in Paratrygon, therefore it is the type species by monotypy. Although Müller and Henle (1841: 160) initially referred to Trygon aiereba as a doubtful species based on Aiereba Marcgrave, the description they provided on page 196 did not correspond with Marcgrave's specimen, but with a new species. Since page 196 is part of the addenda containing reinterpretations of previous pages and new synonymies, and since no page priority rule exists in the ICZN, the description of Trygon aiereba on page 196 can be considered original and valid. It is convenient to note that Aiereba, Raja ajereba, and Raja orbicularis were not formally cited as synonyms of Trygon aiereba on page 196.

Garman (1877) established the new monotypic genus Disceus for Trygon strogylopterus Schomburgk, and included T. aiereba in the synonymy. Garman (1913) redescribed Disceus, and removed T. strogylopterus from the synonymy, placing it as a doubtful species in the genus Elipesurus. Ribeiro (1907, 1923) also cited T. strogylopterus in Elipesurus. Since T. strogylopterus is a junior synonym of T. aiereba, Elipesurus is also a subjective synonym of Paratrygon.

Jordan (1887), Eigenmann and Eigenmann (1891), Eigenmann (1910, 1912), and Rosa (unpublished, see Appendix C) considered _Paratrygon_ as the senior synonym of _Disceus_. Castex (1964b, 1968) and Castex and Loza (1964) stated that _P. aiereba_ could not be identified from the original description, and therefore considered _Paratrygon_ as a _nomen dubium_. Bailey (1969) also considered _Paratrygon_ doubtful, and maintained that _Elipesurus_ should be used as a senior synonym of _Disceus_. The review of the original description of _P. aiereba_ (see Appendix C) indicated that this species is identifiable, and identical to _T. strogylopterus_, _Disceus strogylopterus_, and to _Disceus thayeri_, therefore _Paratrygon_ is the senior synonym of _Disceus_. As discussed earlier in the text (see also comments on doubtful species and Appendix B), _Elipesurus_ should be treated as a _nomen dubium_, and I reject its synonymy with _Paratrygon_ and _Disceus_.

Diagnosis.- A presently monotypic genus of Potamotrygonidae diagnosed by the following combination of characters: tail relativelly short, less than two times disc width, broad at base and distally filiform, lacking dorsal and ventral finfolds; caudal sting relatively small, usually less than two times tail width; disc nearly circular with concave anterior margin, lacking anteromedian prominence; eyes very small, nonpedunculate; preocular distance relatively large, nearly 1.5 times distance from mouth to coracoid bar; pelvic fins dorsally covered by disc; 101 to 118 pectoral-fin radials.

Paratrygon aiereba (Müller & Henle, 1841)

(Figs. 86-96)

Trygon aiereba Müller and Henle, 1841: 196 (not 160, non Marcgrave), original description, Brazil, not illustrated.

Trygon strogylopterus Schomburgk, 1843: 183, plate 22 (original description, Rio Branco).

Trygon (Himantura) strogylopterus. Duméril, 1865: 592.

Trygon (Paratrygon) aiereba. Duméril, 1865: 594.

Trygon strongyloptera. Günther, 1870: 482.

Paratrygon aiereba. Günther, 1870: 482.

Disceus strongylopterus. Garman, 1877: 208.

Paratrygon strongylopterus. Eigenmann and Eigenmann, 1891: 24.

Ellipesurus strongylopterus. Ribeiro, 1907: 184.

Elipesurus strongylopterus. Garman, 1913: 425.

Disceus thayeri Garman, 1913, 426, plate 34 (original description, Rio Pará and Manaus).

Potamotrygon strongylopterus. Castex, 1964b: 22.

Disceus strogylopterus. Castex and Castello, 1969: 21.

[non] Disceus thayeri. Nieuwenhuizen, 1974: 370.

Holotype: originally deposited in München Zoologisches Museum, reported lost by Castex and Castello (1969) and by Dr. F. Terofal (pers. comm.).

Type locality: Brazil.

Diagnosis.- See generic diagnosis.

Description.- Measurements and counts are given in Table 24. Disc nearly circular, disc length 1.0-1.2 times DW; anterior margin of disc concave, lacking median prominence. Pelvic fins covered dorsally by disc, relatively narrow, their posterior margins 3.7-5.3 in DW. Tail relatively short, tail length 1.1-1.9 times DW; tail anteriorly flattened with lateral folds, distally filiform lacking dorsal and ventral finfolds. Distal portion of tail arbitrarily restored in original illustration of Disceus thayeri (Garman, 1913, plate 34). Caudal sting relatively short, sting length 1.0-2.1 times tail width.

Eyes very small, non pedunculate, their length 2.1-6.5 in interorbital distance, 4.2-11.5 in interocular distance. Spiracles relatively small, with conspicuous knob-shaped process on posterior margin; spiracle length 1.1-4.9 times eye length, 1.8-5.0 in interspiracular distance. Mouth relatively small, mouth width 0.9-1.4 times internarial distance. Buccal papillae small, two to nine in number, or papillae entirely lacking. Preoral distance relatively long, 30.6-37.2 percent of DW. Teeth relatively small (Figs. 90, 91) crowded in quincunx, in 15/15 to 35/33 longitudinal rows, and three to seven exposed teeth in median row of lower dental plate. Teeth sexually dimorphic, mature males with pointed teeth, females with blunt teeth. Branchial basket relatively broad and short, its greatest width 3.7-4.9 in DW; distance between first and fifth gill slits 6.6-11.1 in DW.

Anterior subpleural portion of lateral line system reticulate (see Garman, 1888 for detailed description and illustration of lateral line system of Paratrygon, as Disceus strongylopterus).

Neurocranium (Figs. 92, 93; see also Garman, 1913, plate 70, as Disceus thayeri) relatively short, cranium length 5.2-5.6 in DW. Nasal capsules transversely elliptic, with median indentation between them in juveniles and adults. Embryos with median rostral projection (Fig. 93) between nasal capsules. Preorbital processes short, preorbital width equal to or less than cranium width at nasal capsules. Postorbital processes inconspicuous in embryos, small in juveniles and adults; postorbital width 2.4-2.6 in cranium length. Cranial fontanelle relatively short, its length 8.4-9.6 in DW, posteriorly narrow, with moderate constriction at orbital level.

Anterior portion of vertebral column with coalescent vertebrae forming two synarcual plates. Distal portion of vertebral column in intact tails with 21 to 24 diplospondylous vertebrae.

Branchial skeleton (Fig. 94; see also Garman, 1913, plate

70, as Disceus thayeri) with segmented basihyal (four or five segments), hypobranchial entire and relatively short, less than fifth ceratobranchial in length. Pseudohyoid ventrally fused to first ceratobranchial, first and second ceratobranchials fused to each other, other ceratobranchials free from each other. Basibranchial plate nearly elliptic in dorsal view, with blunt anterior and posterior margins. Five opercular cartilages (sensu Garman, 1913) on outer edges of pseudohyoid and ceratobranchials one to four. Opercular cartilages not entirely formed in embryonic specimen dissected.

Scapulocoracoid relatively wide, its maximum width greater than distance from mouth to coracoid bar. Lateral face of scapulocoracoid with large anteroventral fenestra and small postventral fenestra. Coracoid bar relatively thick, its maximum diameter in median cross section nearly equal to distance between mesocondyle and metacondyle.

Pelvic girdle (Fig. 94; see also Garman, 1913, plate 54, as Disceus thayeri) thick, with relatively short prepubic process, its length nearly equal to distance between lateral faces of ischiopubic bar, its tip nearly reaching half of distance between coracoid bar and cloaca. Three or four obturator foramina and one iliac process on each side of pelvic girdle. Internal margin of pelvic girdle nearly semicircular, anterior margins concave with abrupt angle towards lateral margins, lacking prepelvic processes.

Pectoral fins plesodic, with 101 to 118 radials (mode = 110). Propterygium arched and thick, reaching anterior level of nasal capsules. Anterior segment of propterygium with three or four branching radials. Antorbital cartilage short, triangular in dorsal view. Mesopterygium relatively long, its length greater than distance between procondyle and metacondyle of scapulocoracoid, with 19 to 29 radials; anterior and posterior portions of mesopterygium usually detached from main basal element. Metapterygium distally segmented, with 36 to 44 radials. Pelvic fins with 23 to 24 radials in females, and 18 to 21 radials in males.

Claspers relatively short and stout (Figs. 95, 96), their length 14.8-17.0 percent of DW in mature males. Clasper straight in lateral view, broadly elliptic in cross section. Clasper groove anteriorly oblique and distally parallel to midline. Dorsal pseudosiphon oblique to midline, its length nearly half of clasper width at level of terminal cartilages. Axial cartilage straight in dorsal view, slightly arched in lateral view, anteriorly broad and articulated with pelvic basipterygium by two basal elements, distally cylindrical. Beta cartilage proximally triangular in cross section, articulated with first basal element, distally flat reaching level of dorsal marginal cartilage. Dorsal marginal cartilage oblique to midline, anteriorly with curved dorsal expansion, forming outer wall of clasper groove. Dorsal terminal 1 cartilage fusiform in lateral view, proximally articulated with dorsal marginal cartilage, ventrally attached to axial cartilage. Dorsal terminal 2 cartilage elongate, quadrangular in dorsal view, proximally articulated with ventral marginal cartilage, laterally attached to axial cartilage, distally grooved forming roof and floor of ventral pseudosiphon. Ventral covering piece elongate in outer lateral view, distally attached to dorsal terminal 1 and axial cartilages.

Dorsal surface of disc relatively smooth, covered with small denticles. Tail naked, or dorsally and laterally with spines of circular base and perpendicularly projecting crown, from tail base to insertion of caudal sting.

Dorsal surface of disc light brown to grayish-brown, with irregular network of dark pigment; tail dorsally brown. Ventral surface of disc and tail white, with brown margins of disc and pelvic fins.

Geographic distribution.- Northern Bolivia, eastern Peru, northern Brazil (Amazonas and Pará), and Venezuela, in Río Orinoco drainage (see Fig. 99). Paratrygon aiereba is probably endemic to the Amazon and Orinoco river drainages, occurring from Río Ucayali to Rio Tocantins, and in major tributaries of Rio Amazonas.

Biological remarks.- Paratrygon aiereba attains larger body sizes than other species of the family, with the possible exception of Plesiotrygon iwamae and Potamotrygon brachyura. The largest specimen examined by the author was a female (UMMZ 204320) with 920 mm in disc length (field measurement taken by Dr. Reeve Bailey). One specimen photographed in Rio Trombetas, Brazil (Fig. 89) measured approximately 770 mm in disc length.

Additional references: Fernández-Yépez, 1949a (citation for Venezuela, as *Disceus thayeri*); Gray, 1851 (name only, as *Trygon aiereba*); Mangum at al., 1978 (ionic concentrations in body fluids, as "unidentified genus"); Müller and Troschel, 1848 (redescription, as *Trygon strogylopterus*); Myers, 1949 (classification in vicarious category according to salt tolerance, as *D. thayeri*).

TABLE 24

MEASUREMENTS AND COUNTS ON SPECIMENS OF Paratrygon aiereba

	HOLOTYPE*	N	MEAN	S.D.	RANGE
DISC WIDTH (100%)	193.0	24	-	-	108.0-870
DISC LENGTH (mm)	-	24		-	121.0-920
DISC LENGTH (%)	-	24	111.7	3.7	105.1-119.6
TOTAL LENGTH (%)	248.2	11	239.6	30.0	207.0-287.4
INTERNAL DL (%)	-	21	100.8	3.4	94.5-108.3
MOUTH TO SCAPULOCORACOID (%)	22.2	13	22.7	2.0	19.8- 25.7
MOUTH TO CLOACA (%)	60.5	22	56.5	3.0	52.3- 63.2
CLOACA TO STING (%)	-	18	24.1	3.5	19.0- 31.1
TAIL LENGTH (%)	139.4	10	145.1	24.8	108.8-189.2
TAIL WIDTH (%)	-	20	6.8	1.0	5.1- 9.3
TAIL WIDTH AT STING BASE(%)	-	19	3.1	0.9	2.0- 4.6
TAIL HEIGHT (%)	-	20	3.3	0.6	2.1- 4.6
PELVIC FIN WIDTH (%)	-	18	21.0	1.6	18.8- 26.8
PELVIC FIN LENGTH (%)	-	19	17.8	2.2	15.6- 26.5
CLASPER LENGTH (%)	-	9	10.9	4.1	7.0- 17.0
STING LENGTH (%)	-	15	10.9	2.7	6.2- 14.1
PRECLOACAL LENGTH (%)	93.3	21	89.8	3.4	84.6- 97.5
PREORAL LENGTH (%)	33.3	21	32.8	1.8	30.2- 37.2
PRENARIAL LENGTH (%)	30.0	21	30.1	1.9	26.6- 33.8
BRANCHIAL BASKET LENGTH(%)	-	19	11.3	1.5	9.0- 15.0
BRANCHIAL BASKET WIDTH (%)	-	19	22.4	1.8	20.2- 23.6
MOUTH WIDTH (%)	-	19	9.8	0.7	8.1- 10.9

*Holotype measurements fide Müller and Henle (1841) and Duméril (1865).

TABLE 24

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
NOSTRIL LENGTH (%)	-	13	1.4	0.3	0.8- 2.1
INTERNARIAL WIDTH (%)	-	20	8.4	0.7	7.0- 9.7
EYE LENGTH (%)	-	19	1.9	0.5	1.1- 3.1
SPIRACLE LENGTH (%)	-	20	4.3	1.1	2.9- 6.4
INTEROCULAR WIDTH (%)	13.1	18	13.3	1.6	11.0-17.0
INTERSPIRACULAR WIDTH (%)	-	22	14.2	2.8	10.1-20.2
PREOCULAR LENGTH (%)	33.3	21	33.3	2.1	30.8-37.6
CRANIUM LENGTH (%)	-	4	18.4	0.4	17.8-19.0
CRANIUM WIDTH (%)	-	4	12.5	0.7	11.6-13.3
PREORBITAL WIDTH (%)	-	3	11.2	-	10.8-12.1
POSTORBITAL WIDTH (%)	-	3	7.2	-	7.0- 7.5
INTERORBITAL WIDTH (%)	-	19	7.3	1.0	5.9- 9.8
FONTANELLE LENGTH (%)	-	4	11.1	0.7	10.4-11.8
FONTANELLE WIDTH (%)	-	4	5.0	0.4	4.4- 5.3
UPPER DENTAL PLATE WIDTH (%)	-	17	5.5	0.6	3.7- 6.2
LOWER DENTAL PLATE WIDTH (%)	-	17	5.4	0.4	4.6- 6.1
PRECAUDAL VERTEBRAE	-	8	33.6	2.7	28- 37
CAUDAL VERTEBRAE	-	4	91.0	2.3	89- 93
CAUDAL VERTEBRAE TO BASE OF STING	-	6	63.6	3.6	58- 69
TOTAL VERTEBRAE	-	4	124.7	1.8	122- 126
DIPLOSPONDYLOUS VERTEBRAE	-	2	22.5	-	21- 24
SYNARCUAL VERTEBRAE	-	8	5.2	2.8	1- 8
PELVIC RADIALS ♂	-	3	19.6	-	18- 21
PELVIC RADIALS ♀	-	3	23.3	-	23- 24

TABLE 24

(continued)

	HOLOTYPE	N	MEAN	S.D.	RANGE
PROPTERYGIAL RADIALS	-	14	47.0	2.4	44- 51
MESOPTERYGIAL RADIALS	-	14	23.7	2.7	19- 29
METAPTERYGIAL RADIALS	-	14	40.0	3.3	36- 44
TOTAL PECTORAL RADIALS	-	14	110.2	4.9	101-118
UPPER TOOTH ROWS	-	15	22.4	6.2	15- 35
LOWER TOOTH TOWS	-	16	21.8	6.0	15- 33
LOWER MEDIAN TEETH	-	9	4.5	0.8	3- 6

FIG. 86

Paratrygon aiereba, dorsal view, male, ZMB 4632 (type of *Trygon strogylopterus*), not seen by the author. Courtesy of H. -J. Paepke (ZMB).


4632

FIG. 87

Paratrygon aiereba, dorsal view, female, 305 mm DL, MCZ 297-S (syntype of Disceus thayeri).

FIG. 88

Paratrygon aiereba, dorsal view, female, 318 mm DL, MCZ 563-S (syntype of Disceus thayeri).

563

FIG. 89

Paratrygon aiereba, dorsal view,
adult specimen with approximately
770 mm DL, not seen by the author.
Photographed in Rio Trombetas,
Pará, Brazil, by R. M. C. Castro
(formerly at MZUSP).

FIG. 90

Paratrygon aiereba, upper and lower dental plates, female, MCZ 297-S (syntype of Disceus thayeri). Dashed line on lower dental plate indicates limit of buccal integument covering inner series of teeth.

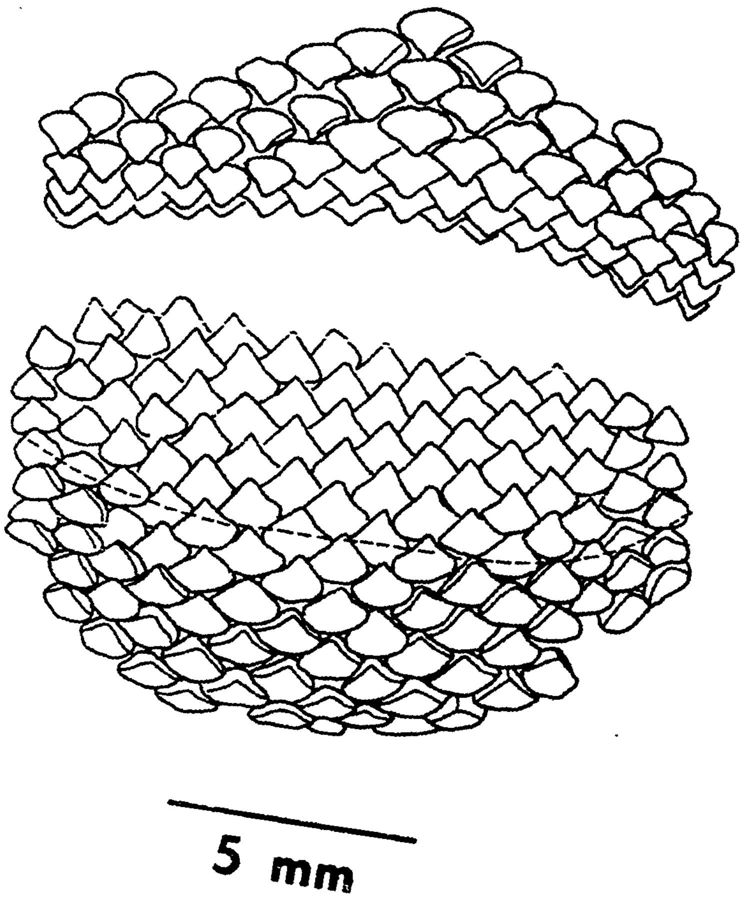

5 mm

FIG. 91

Paratrygon aiereba, A - E.- Tooth from upper jaw near symphysis, apical, basal, lateral, lingual, and labial views, female, 305 mm DL, MCZ 297-S (syntype of *Disceus thayeri*). F.- Tooth from upper jaw near symphysis, apical view, juvenile male, 315 mm DL, INPA (uncatalogued specimen).

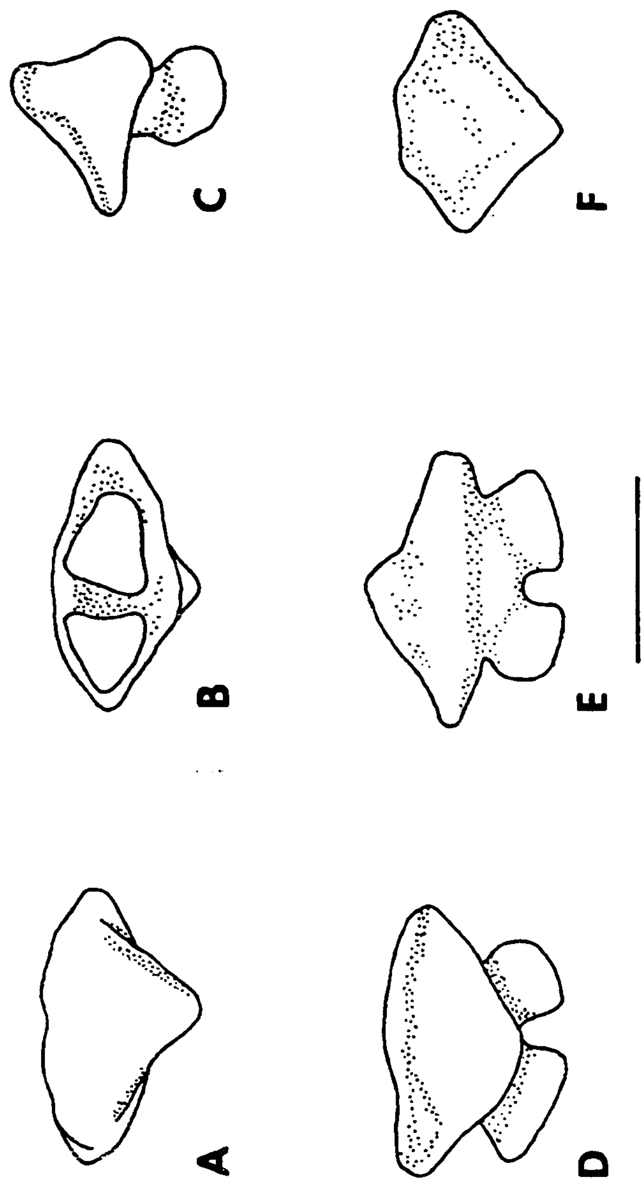

A
B
C
D
E
F
1 mm

FIG. 92

<u>Paratrygon</u> <u>aiereba</u>, dorsal view of skeleton, from radiograph, female, 318 mm DL, MCZ 563-S (syntype of <u>Disceus</u> <u>thayeri</u>). Pelvic girdle shown by transparency under vertebral column.

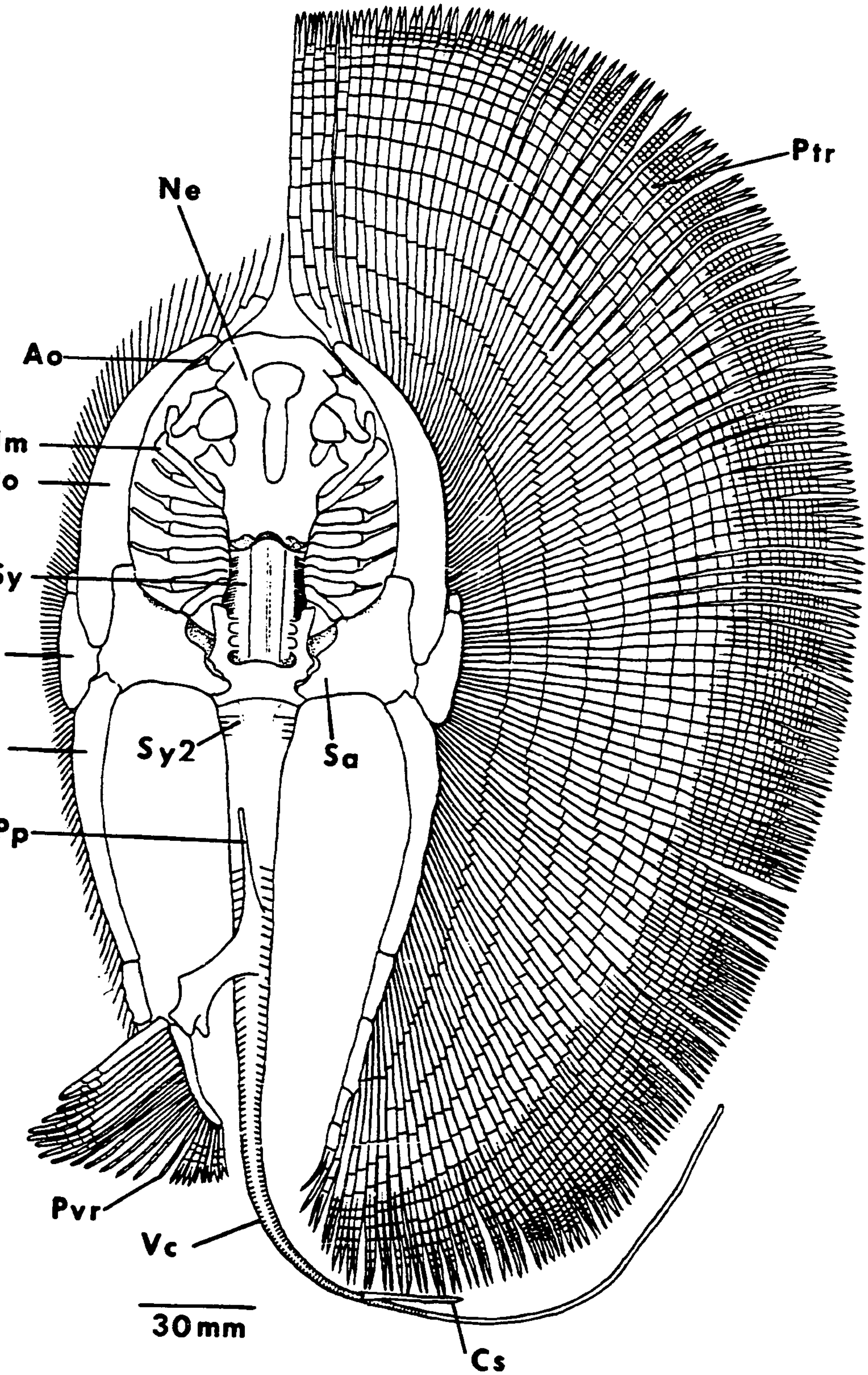
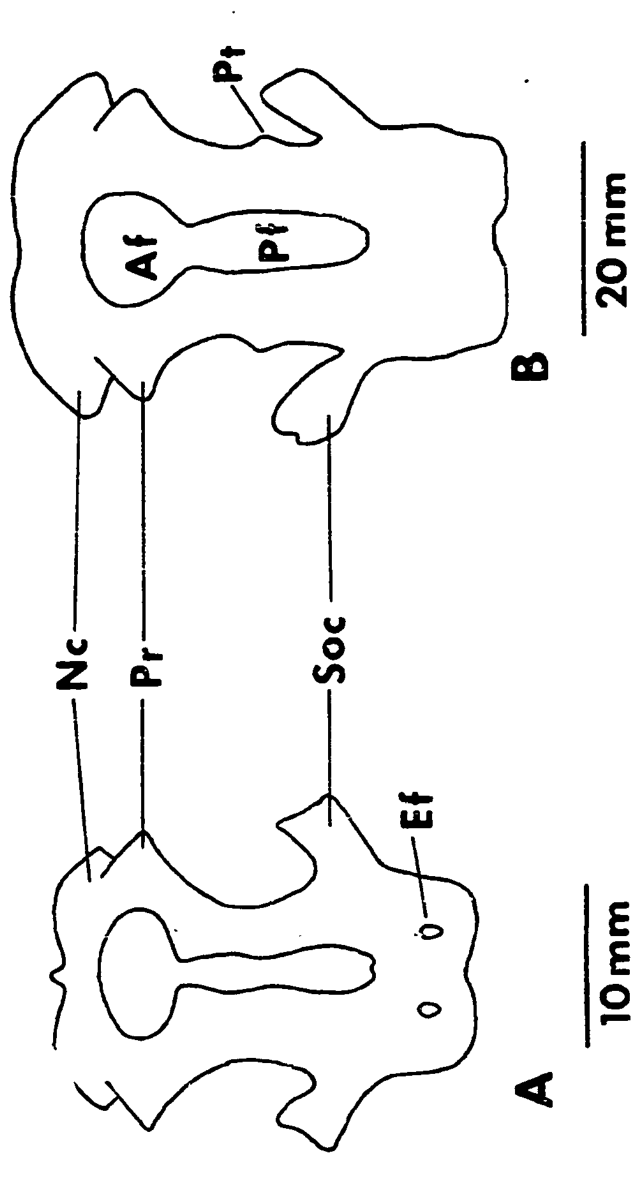

Ptr
Ne
Ao
Hm
Po
Sy
Ms
Sy2
Sa
Pp
Pvr
Vc
30mm
Cs

FIG. 93

<u>Paratrygon</u> <u>aiereba</u>, A.- Dorsal view of neurocranium from dissection, female, 160 mm DL, INPA (uncatalogued embryonic specimen). B.- Dorsal view of neurocranium from radiograph, female, 318 mm DL, MCZ 563-S (syntype of <u>Disceus</u> <u>thayeri</u>).



Nc
Pr
Soc
Ef
Af
Pf
Pt
A
B
10mm
20 mm

FIG. 94

Paratrygon aiereba, A.- Dorsal view of ischiopubic bar, female, 160 mm DL, INPA (uncatalogued embryonic specimen). B.- Ventral view of ventral portion of branchial skeleton, INPA (same uncatalogued specimen).

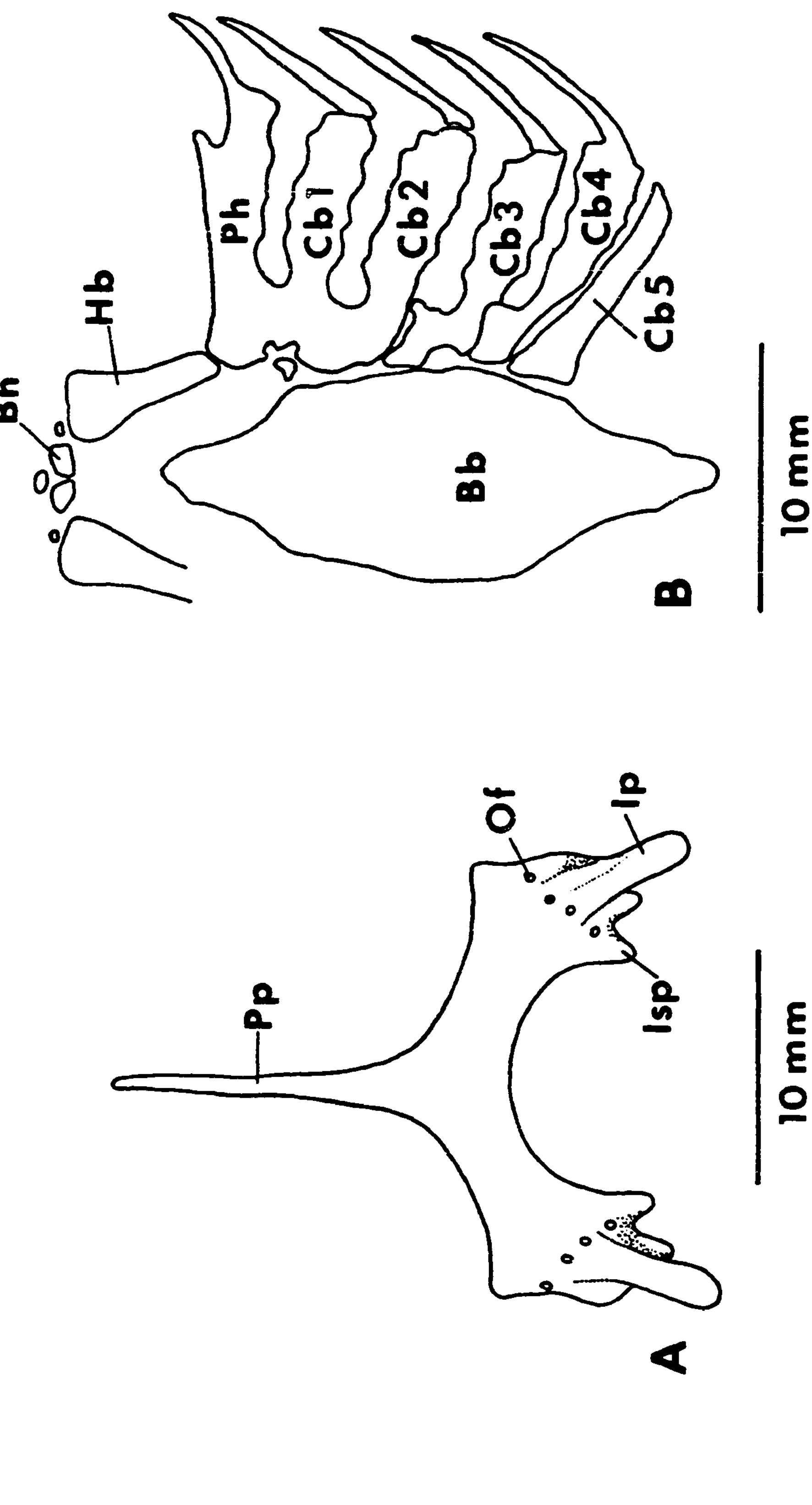

A
Pp
Of
Ip
Isp
10 mm
B
Bh
Hb
Ph
Cb1
Cb2
Cb3
Cb4
Cb5
Bb
10 mm

FIG. 95

<u>Paratrygon</u> <u>aiereba</u>, A - C.- Lateral, ventral, and dorsal views of intact left clasper, adult male, 920 mm DL, INPA (uncatalogued specimen).

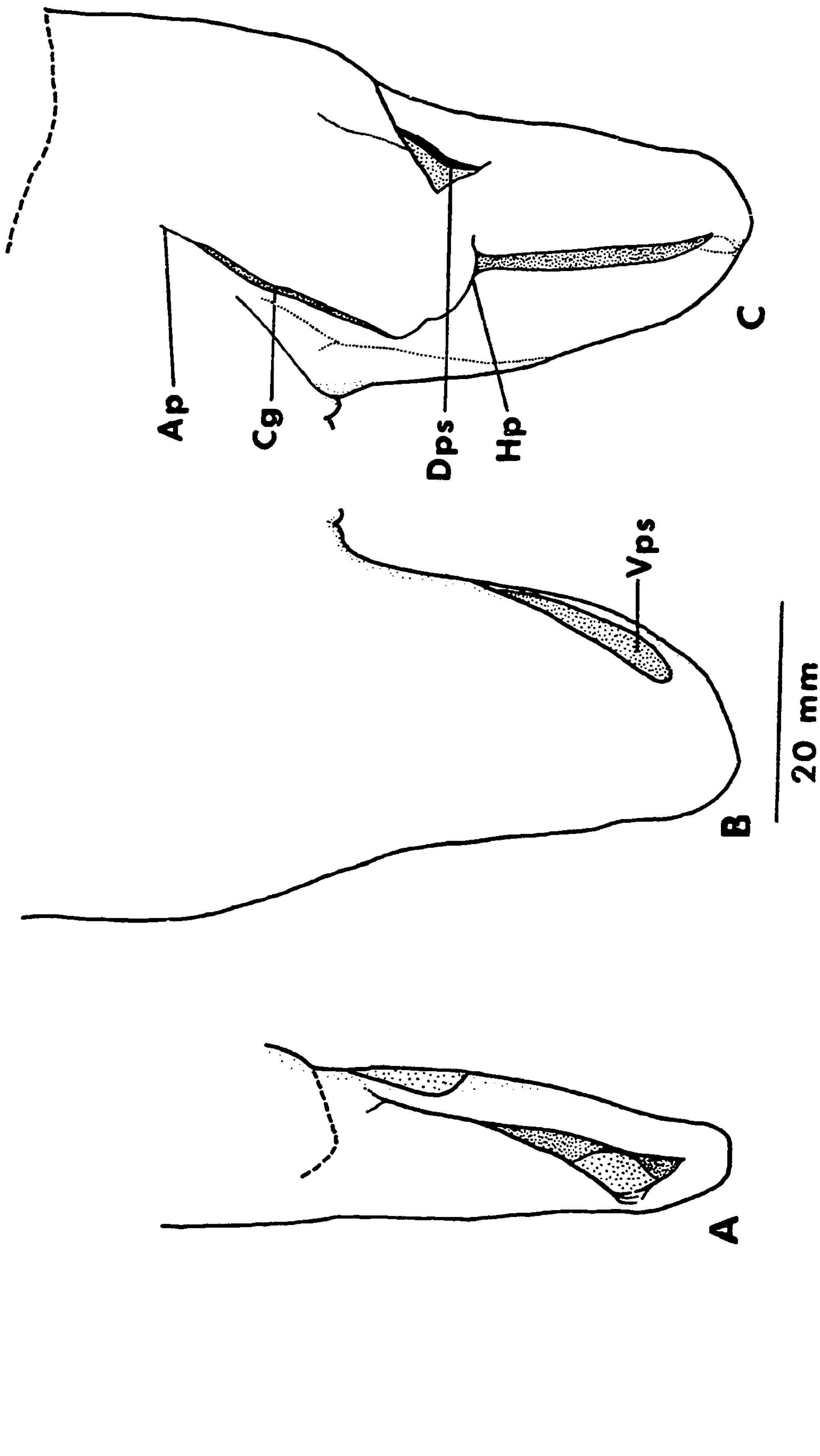
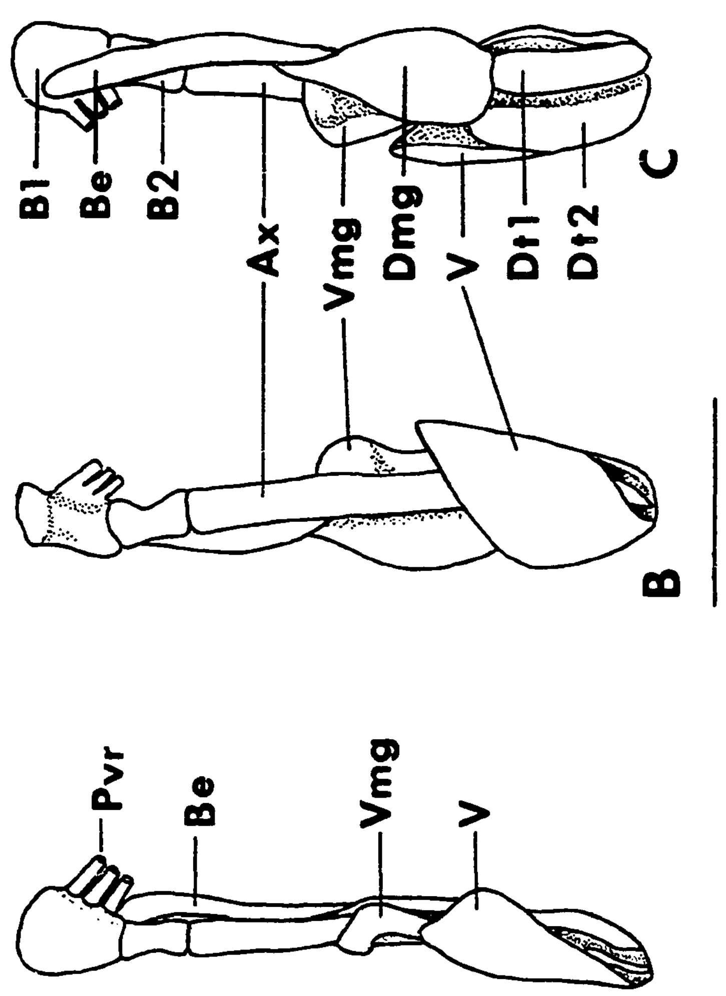

Ap
Cg
Dps
Hp
C
Vps
20 mm
B
A

FIG. 96

<u>Paratrygon</u> <u>aiereba</u>, A - C.- Lateral, ventral, and dorsal views of dissected left clasper, adult male, 920 mm DL, INPA (uncatalogued specimen).



A
Pvr
Be
Vmg
V
B
30 mm
Ax
Vmg
V
B1
Be
B2
Dmg
Dt1
Dt2
C

COMMENTS ON DOUBTFUL SPECIES

Raja ajereba Walbaum, 1792

Walbaum (1792) established this binomen only with a brief repetition of Marcgrave's (1648) account on Aiereba. No type specimen is known. Marcgrave's explorations of South America were limited to the northeastern coast of Brazil, from where the Potamotrygonidae are absent. For this reason, the Aiereba of Marcgrave is most probably a marine or estuarine dasyatid stingray, although its specific identifications is nearly impossible due to the innacuracy of the original description. Therefore, *Raja ajereba* should not be included in the family of neotropical freshwater stingrays, as done by Fowler (1948, 1970) and Castex (1968), but instead, should preferably be treated as a doubtful species (see section on the genera of Potamotrygonidae and Appendix C of this paper for further discussion on *Raja ajereba*).

The eventual rejection of *Raja ajereba* as a *nomen dubium* will not affect the status of *Trygon aiereba* Müller & Henle, even if the two specific names are interpreted as homonyms according to the new edition of the ICZN in preparation, because the two names have different generic placements.

Raja orbicularis Schneider, 1801

This is another binomen established for the Aiereba of Marcgrave, with a short repetition of the original description. No type material was mentioned by Schneider, although the dimensions cited by him were larger than those of Marcgrave's specimen. Ribeiro (1907) and Ihering (1940) denoted the marine origin of *Raja orbicularis* (and consequently of Aiereba) by placing it in the genus *Dasyatis*. *Raja orbicularis* should be considered a *nomen dubium* due to the impossibility of the specific diagnosis from the original description, and the lack of type material.

Elipesurus spinicauda Schomburgk, 1843

This species was described from Rio Branco, Brazil, and founded the monotypic genus *Elipesurus*. The description was probably based on a single, mutilated specimen, with a cut-off tail. The mutilation of the tail is the probable cause for the lack of the caudal sting and for the abnormal growth of the spines on the base of the tail. No type specimen is known. One application for the rejection of the binomen was made to the International Commission on Zoological Nomenclature by Castex (1968), subsequently criticized by Bailey (1969), and again reasserted by Castex (1969b). The decision is still pending, but I prefer to follow the majority of the authors who have dealt with the family Potamotrygonidae, and treat *Elipesurus* and *E. spinicauda* as *nomina dubia*. Further discussion on this subject can be found in Appendix B of this dissertation, which is a complete transcription of a paper separately submitted for publication.

Trygon garrapa Schomburgk, 1843

This species was described from Rio Branco, Brazil. It has been placed in the synonymy of *Potamotrygon motoro* by several authors (Eigenmann and Eigenmann, 1891; Garman, 1877, 1913; Berg, 1895; Eigenmann, 1910; Fowler, 1948; Castex, 1964b), but its original illustration differs from the latter species in showing the yellow ocelli continuing distally on the tail. In this character it resembles *Potamotrygon henlei* and *P. leopoldi*. The brief description of the teeth also resembles *P. henlei* (see remarks under *P. henlei* in the taxonomic section), but *P. henlei* is presently unknown from Rio Branco. The description and illustration of *T. garrapa* are poor in other diagnostic characters, and due to the lack of type specimen, I prefer to treat it for the moment as a doubtful species. Further collection in Rio Branco might eventually prove the validity of this species, placed in the genus *Potamotrygon*.

Pastinachus humboldtii Roulin in Duméril, 1865

This stingray was originally described from Río Meta in Colombia by Roulin (1829), under the vernacular name (without status in nomenclature) Pastenague de Humboldt. The name was first made available by Duméril (1865), who latinized the specific name to _humboldtii_ in binominal combination with _Pastinachus_. The brief repetition and reference to Roulin's description given by Duméril provided an indication to the name. Duméril (1865) mentioned that _P. humboldtii_ would probaly belong to the genus _Taeniura_ (which by that time was also used for potamotrygonids), and that the species was unknown at the Paris museum.

Garman (1877) redescribed the species and placed it in the genus _Potamotrygon_. Eigenmann and Bean (1907) and Ribeiro (1920) respectively cited the species for the Amazon and Rio Paraguay. Garman's (1877) redescription was not based on the original specimen, but on specimens collected in Brazil by the Thayer Expedition. Garman included _Trygon histrix_, _T. orbignyi_, and _Taeniura magdalenae_ as synonyms of _P. humboldtii_. Eigenmann (1910) and Lahille (1921) treated _P. humboldtii_ as the senior synonym of _P. histrix_. Among these proposed synomyms, only _P. orbignyi_ is plausible, because this species is also found in Río Meta. Garman's redescription possibly corresponded in part with _P. orbignyi_, especially for the account on the coloration. The material used in his redescription was probably heterogenous, because there were not as many specimens (fourteen as mentioned by Garman) identifiable as _P. orbignyi_ among the specimens collected by the Thayer Expedition.

Roulin's original description, on the other hand, cannot clearly be associated with _P. orbignyi_, even with its descriptive information content being relatively high for that time. The questionable aspects are the account on the coloration, which does not mention the typical reticulations of P. orbignyi, and all the cited morphometrics, which fall out of the corresponding ranges of P. orbignyi, with exception of the interocular distance. The cited preoral distance and eye diameter are much smaller than in P. orbignyi, while the precloacal distance and the branchial basket width are much larger. The original illustration also does not permit the identification with P. orbignyi. The eyes and nostrils are represented much closer to the snout, and the caudal stings much further from the tail base than in P. orbignyi. The relative size and shape of the caudal spines are also distinct from those of P. orbignyi.

Roulin apparently did not take his specimen of P. humboldtii to France, but only one caudal sting of unknown origin, as mentioned in the original description. No type of P. humboldtii exists in the MNHN (M. L. Bauchot, pers. comm.).

For the reasons above, I reject Garman's (1877) synonymy of P. humboldtii, as well as the inclusion of this species in the synonymies of P. histrix and P. orbignyi. The name P. humboldtii preferably should be treated as a nomen dubium.

Potamotrygon africana Arambourg, 1947

This is a fossil species, described from the upper Tertiary of Nanoropus, north of Lake Rudolph in Africa, based on caudal stings. Arambourg (1947) provisionally assigned this species to the genus Potamotrygon, based on his stratigraphic observations and the rest of the fossil assemblage, which indicated a freshwater paleoenvironment.

Dasyatid stingrays are known to enter and inhabit rivers. One extant African species, originally described as Potamotrygon garouaensis by Stauch and Blanc (1962), is now placed in the genus Dasyatis (see Castello, 1973; Thorson and Watson, 1975). Arambourg did not compare the fossil stings with potamotrygonid or dasyatid stings, therefore the original placement of the fossils in the genus Potamotrygon is based on uncertain evidence (Thorson and Watson, 1975). The illustrations of the stings suggest that they should be assigned to the genus Dasyatis (Brooks, Thorson and Mayes, 1981).

Potamotrygon alba Castex, 1963

This species was described from three specimens collected in Asunción, Paraguay. The original description is very poor, lacking a diagnosis, illustration, morphometric data, and type designation. Castex (1964b) placed P. alba in the synonymy of Potamotrygon motoro, stating that the former was an albino form of the latter. No similar specimens have been collected since, and the identity of the species remains doubtful. The present location of the original specimens is unknown, therefore P. alba preferably should be treated as a nomen dubium.

COMMENTS ON INVALID SPECIES (*NOMINA NUDA*)

Potamotrygon labratoris Castex, 1963

This specific name was first published as *Potamotrygon Labratoris* (sic) by indication only, as the legend of a figure (Castex, 1963b). No description or definition were included, therefore the name became unavailable. The description of the figured specimen was published in the same year (Castex, Maciel and Achenbach, 1963), with emendation of the specific name to *P. labradori*. The type, collected in Santa Fe, Argentina, is currently housed in MFA. Examination of the type revealed that it is a specimen of *Potamotrygon motoro*, and that the differential diagnostic characters given for *P. labratoris* (color pattern and development of dermal denticles) probably represent intraspecific variations of *P. motoro*. *Potamotrygon labratoris* is herein considered a *nomen nudum*.

Potamotrygon pauckei Castex, 1963

This specific name was first published by indication only, as the legend of a figure (Castex, 1963b), thus lacking availability. Castex (1963d) used this *nomen nudum* to describe a new species, based on six specimens from Santa Fe, Argentina, including the one previously figured. No holotype was designated at that time. Castex and Yagolkowski (1970) mistakenly designated as paratypes of *P. pauckei* two specimens which did not belong to the original type series. One "holotype" (sic), belonging to the original syntypes, was designated in the same publication. Examination of these specimens revealed that the species was based on heterogenous material, the lectotype being equal to *Potamotrygon motoro*, and the paralectotypes belonging to *Potamotrygon histrix* and *P. motoro*. All the diagnostic characters mentioned in the original description (color pattern, toxicity, sinuose disc margins, and asymmetry) are of questionable validity, and can be regarded as natural variations or mutilations of specimens of *P. histrix* and *P. motoro*. *Potamotrygon pauckei*, being a *nomen nudum*, should not be recorded in the synonymies of *P. histrix* and *P. motoro*.

ANALYSIS OF CHARACTERS AND PHYLOGENETIC RELATIONSHIPS

Analysis of characters and phylogeny reconstruction followed the methodology of phylogenetic systematics (Hennig, 1966), with the modifications, additions, and philosophical justifications introduced in the more recent literature (Brudin, 1968; Rieppel, 1980; Arnold, 1981; Nelson and Platnick, 1981; Wiley, 1981). Polarity of character states was determined by the out-group comparison method (Arnold, 1981; Watrous and Wheeler, 1981; Maddison et al., 1984). Out-group study material included for the most part, specimens and/or published descriptive accounts of stingrays of the families Dasyatididae (genera *Dasyatis*, *Himantura*, and *Taeniura*), Urolophidae (genera *Urolophus* and *Urotrygon*), and Hexatrygonidae (genus *Hexatrygon*).

The Potamotrygonidae have been treated as close relatives of the Dasyatididae by Garman (1913) and Bigelow and Schroeder (1953). This hypothetical relationship possibly stemmed from the older classifications which placed the dasyatids and potamotrygonids in the family Trygonidae. It was most probably based on the external similarity of these stingrays, and has never been substantiated with an analysis of characters.

The concept of close relationships between dasyatids and potamotrygonids has been recently questioned by L. J. Compagno (pers. comm.), who mentioned that based on morphological grounds the Potamotrygonidae are closer to the Urolophidae than to the Dasyatididae, and by Brooks, Thorson and Mayes (1981), who treated the parasitic helminths of stingrays as cladistic characters, and found more parasite taxa shared between potamotrygonids and urolophids, than between potamotrygonids and dasyatids. Although few species of urolophids were examined in the present study, this more recent hypothesis of relationship is favored, and the Urolophidae along with Hexatrygon are considered the sister group of the Potamotrygonidae, based on synapomorphies discussed below.

The internal relationships of the Urolophidae are not resolved yet, and the grouping of the urolophid genera is based mainly on the presence of cartilaginous supporting elements (radials) in the tail finfolds. The use of this character as an exclusive synapomorphy of the Urolophidae is subject to question, because Hexatrygon (described in the new family Hexatrygonidae) has radials in the tail finfolds (fide Heemstra and Smith, 1980). The relatively more primitive genus Rhinobatos also shows similar radials, but due to its great phylogenetic distance from the stingrays, the radials are considered to have appeared independently in the two groups. The monophyly of the Urolophidae could possibly be attained with the inclusion of Hexatrygon in addition to the recognized genera of the family. The presence of the distally continuous dorsal and ventral finfolds, the reduction of tail length, and the presence of cartilaginous radials in the finfolds of adults are synapomorphies which indicate this rela-

FIG. 97

A.- Cladogram depicting the hypothetical familial out-group relationships of the Potamotrygonidae. Derived from the classification of Compagno (1973) with modifications.

B.- Cladogram depicting the hypothetical generic out-group relationships of the Potamotrygonidae. Discussion on the distribution of character states is found in the text. In-group synapomorphies are indicated on the subsequent cladogram. Other Myliobatiformes of the cladogram include the genera of Myliobatididae, Rhinopteridae, and Mobulidae. Dark bars across two branches indicate synapomorphies; dark bars on single branch indicate autapomorphies; hatched bars indicate homoplasies. ON = out-group node.

1. Presence of caudal sting (secondarily lost in some taxa). 2. Reduction of the rostral appendix cartilage. 3. Loss of the dorsal fin. 4. Pectoral fins laterally expanded. 5 and 6. Extreme reduction of tail (homoplasous in Gymnura and Paratrygon). 7. Loss of the buccal papillae. 8. Presence of caudal finfolds (secondarily lost in some taxa). 9 and 10. High modal number of pectoral-fin radials (homoplasous in dasyatids and Potamotrygon plus Paratrygon). 11 and 12. Loss

FIG. 97
(continued)

of the caudal finfolds (homoplasous in Himantura and Paratrygon). 13 and 14. Presence of internal spiracular papilla (homoplasous in Taeniura plus Dasyatis, and Potamotrygon). 15. Caudal finfolds supported by cartilaginous radials (ontogenetically lost in some taxa). 16. Radials of caudal finfolds retained in adults. 17. Reduction of tail length (homoplasous in urolophids and Potamotrygon plus Paratrygon). 18. Segmentation of basihyal cartilage. 19. Loss of the sixth gill arch. 20. Ontogenetic loss of the caudal finfold radials (other synapomorphies for this level and lower taxonomic levels within the Potamotrygonidae are indicated on the subsequent cladogram). 21. Loss of the dorsal caudal finfold (homoplasous in dasyatids, Plesiotrygon, and Paratrygon). 22. Beta cartilage of clasper continuous with dorsal marginal cartilage (homoplasous in Myliobatis, Himantura, and Paratrygon). 23. Short preorbital processes (homoplasous in Plesiotrygon. 24. Short postorbital processes (homoplasous in Plesiotrygon and Paratrygon). 25. Minute eyes (homoplasous in Urotrygon, Plesiotrygon, and Paratrygon).

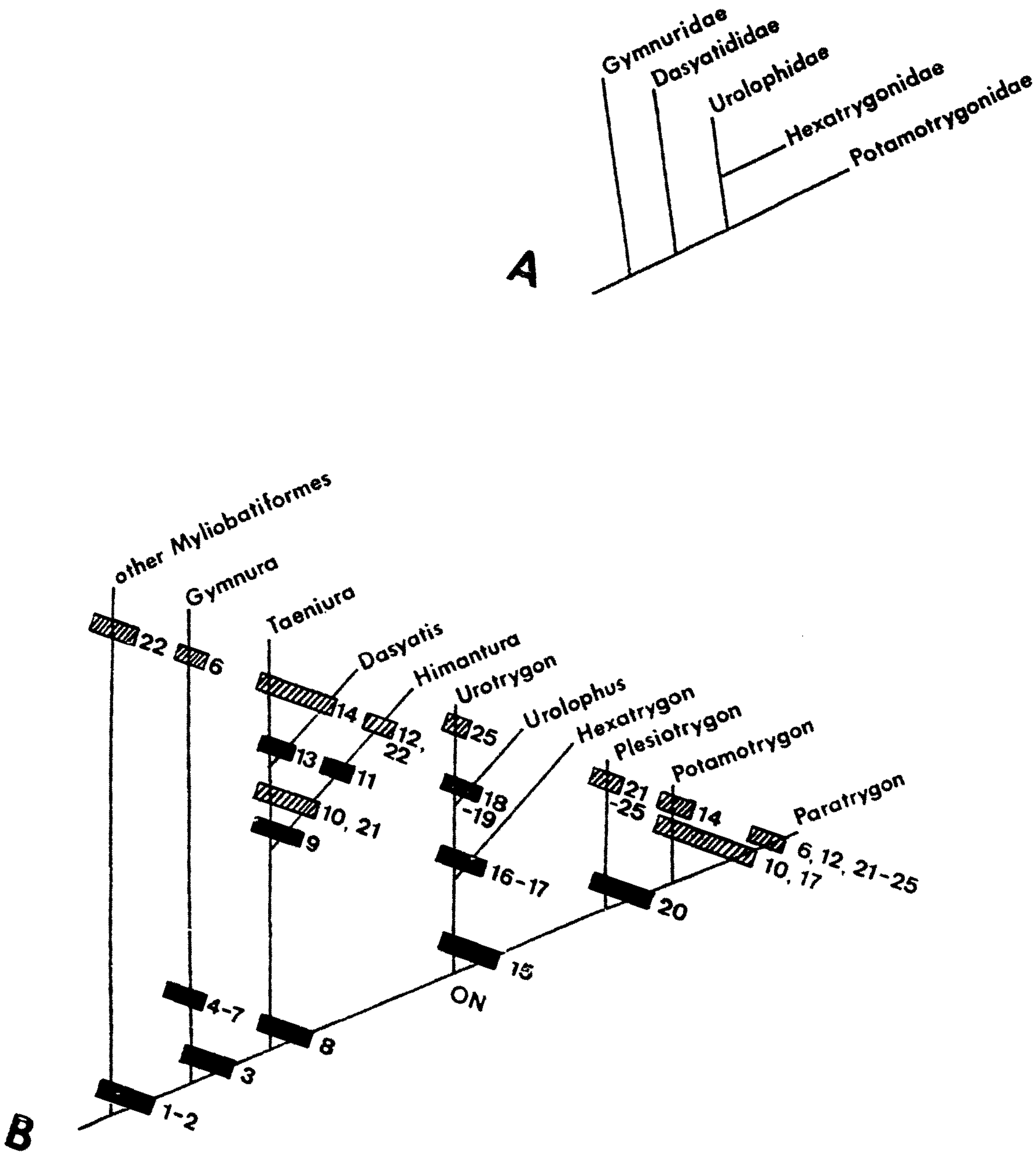
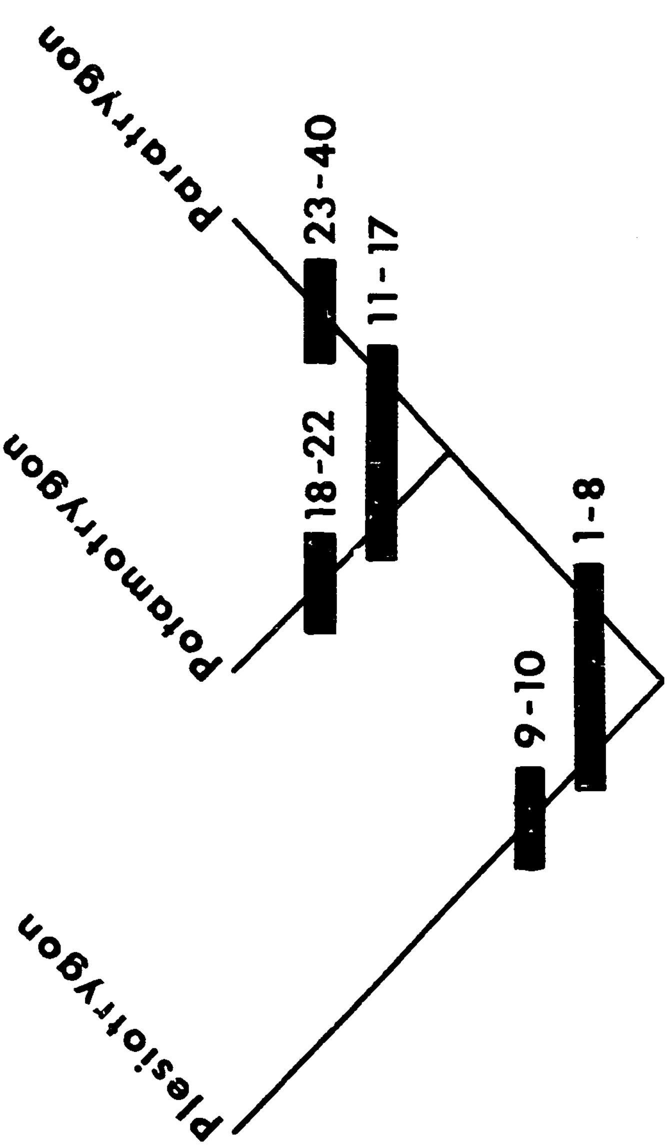

A
Gymnuridae
Dasyatididae
Urolophidae
Hexatrygonidae
Potamotrygonidae
B
other Myliobatiformes
Gymnura
Taeniura
Dasyatis
Himantura
Urotrygon
Urolophus
Hexatrygon
Plesiotrygon
Potamotrygon
Paratrygon
22
6
14
12, 22
13
11
10, 21
9
25
18 -19
16-17
21 -25
14
6, 12, 21-25
10, 17
20
15
ON
4-7
8
3
1-2

FIG. 98

Cladogram based on the distribution of derived character states in Potamotrygonidae. Polarity assessments are discussed in the text.

1. Presence of prepubic process on ischiopubic bar. 2. Ontogenetic loss of the rostral appendix cartilage. 3. Reduction of caudal fin skeletal support. 4. Complete adaptation to fresh water, and reduced tolerance to salt water. 5. Suppression of urea retention. 6. Reduction of rectal gland. 7. Reduction in number of diplospondylous caudal vertebrae. 8. Reduction of ampullae of Lorenzini and associated canals to a microampullary system. 9. Presence of spines distally on tail. 10. Innermost pelvic-fin radial attached to ventral marginal cartilage of clasper in mature males. 11. High modal number of pectoral-fin radials. 12. Low modal number of pelvic-fin radials. 13. Pelvic fins dorsally covered by disc. 14. Reduction of tail length. 15. High number of branchial rays on ventral pseudohyoid. 16. Fusion of inner margins of ceratobranchials one and two. 17. Reduction of the postventral fenestra of scapulocoracoid. 18. Increase in number of radials on anteriormost basal element of propterygium. 19. Presence of tegumentary ridges in buc-

cal cavity. 20. Buccal papillae elongated. 21. Presence of internal spiracular papilla. 22. Fusion of inner margins of ceratobranchials two, three, and four. 23. Anterior pectoral-fin radials greatly elongated. 24. Pectoral-fin basalia greatly enlarged. 25. Nostrils small. 26. Tranversely enlarged synarcual plates. 27. Presence of external spiracular prominence. 28. Postspiracular cartilages enlarged (fide Garman, 1913). 29. Presence of opercular cartilages. 30. Scapulocoracoid enlarged. 31. Anastomosed subpleural network of lateral line system. 32. Embryonic rostral projection on cranium. 33. Reduction of transverse constriction of cranial fontanelle. 34. Reduction of antorbital cartilage. 35. Extreme reduction of tail. 36. Reduction of caudal sting. 37. Loss of anterior prominence of disc. 38. Loss of caudal finfolds. 39. Reduction of relative clasper length in mature males. 40. Beta cartilage of clasper continuous with dorsal marginal cartilage.


Paratrygon
Potamotrygon
Plesiotrygon
23-40
11-17
18-22
1-8
9-10

tionship.

The phylogenetic relationships of the Potamotrygonidae and the immediate out-group families are depicted in one hypothetical cladogram (Fig. 97A), derived from Compagno's (1973) classification, with modifications. These modifications are the inclusion of the Hexatrygonidae in the classification, and the removal of the Gymnuridae from the sister group relationship with the Urolophidae, as the sequence of the classification would indicate. No synapomorphy schemes were tested to support this cladogram, and the position of the Gymnuridae and the Hexatrygonidae is particularly subject to question. Some pertinent synapomorphies and autapomorphies are indicated on the next cladogram (Fig. 97B), which was obtained by superimposing the potamotrygonid and studied out-group genera on the family cladogram. Several genera possibly pertinent to the cladogram (Trygonoptera, Urolophoides, and Urogymnus) were not included, due to the lack of available specimens for study and of relevant published information.

No exhaustive attempt to support the generic cladogram with synapomorphies was made in the present study, and the relative positions of the out-group genera may be subject of change, particularly those of Gymnura and Hexatrygon. If the synapomorphies indicated for urolophids and Hexatrygon were operative at the next lower node of the cladogram, Hexatrygon could be removed from its position to indicate a sister-group relationship with the urolophids plus the potamotrygonids. This change in the position of Hexatrygon would imply two extra reversals of polarity in the potamotrygonids (for the increase of tail length, and for the reduction of the tail finfold radials), but even if this change could be treated as more parsimonious with further synapomorphies, the present out-group analysis of characters based on this generic cladogram would not be substantially altered.

The analysis of the distribution of character states in the following section resulted in the potamotrygonid phylogenetic reconstruction depicted in Fig. 98. This cladogram indicates the phylogenetic relationships of the three genera of Potamotrygonidae based on the distribution of apomorphies. Both the holomorphological synapomorphies of the family and the autapomorphies of each genus are indicated on the cladogram.

The examined characters and their polarities

Few external morphological characters of stingrays provide useful taxonomic and/or phylogenetic information, therefore the internal characters, especially those of skeletal anatomy, must also be used in any attempt of phylogeny reconstruction. Myological and other soft-anatomy characters possibly are also informative, but were not analysed in this paper.

The holomorphological synapomorphies of the family Potamotrygonidae indicated on the in-group cladogram (Fig. 98) are characters mainly taken from the literature, with exception of characters [2], [3] and [7], which resulted from the present anatomical studies. The present analytical contribution deals with external and skeletal characters at the generic level, which are herein reported in topographic sequence. The polarity of character states is discussed in relation to their distribution in the out-groups and in the three recognized genera of Potamotrygonidae. Numbers in bars refer to the character states indicated on the in-group cladogram (Fig. 98).

The disc (pectoral fin).- The shape of the disc does not vary substantially within the study group, being nearly oval and anteriorly prominent in all species excepting *Paratrygon aiereba*, which has a nearly circular disc with a concave anterior margin. The oval and anteriorly prominent disc shape is found in the most closely related out-groups (*Urolophus*, *Urotrygon*), the lozenge disc shape of many dasyatids, *Gymnura*, and *Hexatrygon* possibly representing independent aquisitions. The anteromedian disc prominence found in *Plesiotrygon* and *Potamotrygon* is a widely distributed character in the out-groups, possibly representing the external vestige of the primitive rostrum. Therefore, the prominence is regarded as a plesiomorphy, being phylogenetically uninformative. The lack of the prominence in *Paratrygon* is regarded as an autapomorphy [37].

Concerning the number of pectoral-fin radials, urolophids showed counts around 80 (68-92), while the more derived character state in dasyatids showed counts around 120 radials. Within the potamotrygonids, Plesiotrygon has counts around 80 (78-82), Potamotrygon has a mode of 95 (82-112), and Paratrygon a mode of 110 (101-118), this higher modal number being regarded as synapomorphic for these last two genera [11]. Although I have not relied on fossil information for assessments of polarity, examination of this character within fossil records of batoids always revealed low number of radials (e.g. 47-54 in Cyclobatis, 85-96 in Heliobatis). The transformation series of this character along the phylogeny of stingrays is possibly towards an increase of the number of radials, allowing a more efficient locomotory action by undulation of the pectoral fins. The actively swimming myliobatid and mobulid stingrays, which have a different locomotory strategy (flapping of the pectoral fins), retained low number of pectoral-fin radials.

The phylogenetic increase in the number of pectoral-fin radials occurred mainly in the propterygium and metapterygium, and to a lesser extent in the mesopterygium. This transformation series was accompanied by the forward extension of the propterygium, its tip reaching the level of the nasal capsules on cranium, with a consequent reduction of the antorbital cartilages which link the two structures. The anterior basal element of the propterygium also showed a transformation series towards its forward extension, so that in Paratrygon the anterior right and left radials have merged together in front of the cranium [23], thus reducing the space primitively occupied by the rostrum. This anterior basal element also showed an out-group/in-group transformation series towards the increase in number of radials, although Paratrygon retained the primitive condition.

The eyes.- Two different character states are found in the out-groups: small, non-pedunculate eyes (e.g. Urotrygon), and normally developed and pedunculate eyes (Urolophus, Dasyatis, Himantura, and Taeniura). No out-group polarity assessment could be made for this character. The two states are also present in the potamotrygonids, where the correlation of characters indicated the reduced eyes as the primitive condition. The occurrence of reduced eyes in different stingray taxa possibly represent convergent adaptations to turbid environments, while their occurrence in Plesiotrygon and Paratrygon may represent closer parallelism (homoiology sensu Plate, 1920 cited in Hennig, 1966), or most probably, the retention of the plesiomorphic condition in Paratrygon.

The spiracles.- The position and relative size of the spiracles are nearly the same in the three genera of Potamotrygonidae. Their external aspects differ by the presence of the knob-shaped projection in Paratrygon, by a slight prominence on the medial spiracle margin of Potamotrygon, and by the lack of prominences on the nearly elliptical spiracle margins of Plesiotrygon. Internally, on the floor of the spiracular cavity, Potamotrygon has a papilla [21] which is lacking in the two other genera. No synapomorphies were found in these structures, and both the external projection in *Paratrygon* [27] and the internal papilla in *Potamotrygon* are regarded as autapomorphies. In the out-groups, a spiracular projection similar to that of *Paratrygon* is seen in the more primitive genus *Rhinobatus*, but their homology is uncertain due to their great phylogenetic distance. The internal papilla similar to that of *Potamotrygon* is found in *Dasyatis* and *Taeniura*.

The nostrils.- *Paratrygon* differs from *Potamotrygon* and *Plesiotrygon* in having relatively smaller nostrils. Both short (*Hexatrygon*, *Urotrygon*) and elongated nostrils (*Taeniura*, *Dasyatis*, *Urolophus*) are found in the out-groups, the latter state being possibly primitive. The character state in *Paratrygon* is regarded as autapomorphic [25].

The mouth.- The relative distance from the mouth to the snout is greater in *Paratrygon* than in *Potamotrygon* and *Plesiotrygon*. All the examined batoid out-groups, except those with long rostral projections, have relatively shorter preoral distances than *Paratrygon*. The character state of the latter genus is regarded as autapomorphic, and directly related to character [23].

Polarity assessments for the size, shape, and number of teeth, as well as for the occurrence of monognathic heterodonty, were difficult to establish due to the extreme variability (both inter and intraspecific) of these characters in the out-groups. The in-group transformation series by character correlation are towards the reduction in number of tooth rows, and the increase of the relative size of individual teeth. Monognathic heterodonty was observed in Paratrygon and Potamotrygon, but not in Plesiotrygon. This character was not used as a synapomorphy due to its general occurrence in batoids and sharks.

The papillae on the floor of the buccal cavity are found in the out-groups (Dasyatis, Himantura, Taeniura, Urolophus), but usually in smaller size than in Potamotrygon. Plesiotrygon and Paratrygon lack or have small buccal papillae, and this is regarded as the primitive condition. The well-developed buccal papillae of Potamotrygon are considered autapomorphic [20].

The pelvic fins.- The out-groups show pelvic fins more or less dorsally covered by the disc (Dasyatis, Himantura, Taeniura), or pelvic fins broadly exposed behind the disc (Gymnura, Hexatrygon, Urotrygon, Urolophus), the latter state being regarded as plesiomorphic. Within the potamotrygonids, Potamotrygon and Paratrygon share the derived state [13]. The out-group polarity assessment for the number of pelvic-fin radials was questionable, Urolophus showing a range of 19 to 24 radials, similar to that of potamotrygonids. Dasyatid stingrays showed slightly higher counts (20-28 radials), and Urotrygon slightly lower counts (14-19 radials). The in-group polarity by character correlation indicated the reduction in the number of radials shared by Potamotrygon and Paratrygon as the derived state [12].

The claspers.- The external aspect of potamotrygonid claspers is similar to those of most myliobatoids, and considerably different from most rajoids. The internal structure of potamotrygonid claspers is also essentially similar to those of the studied myliobatoids, the shape and position of the cartilages being generally the same, the major differences being their relative size and articulations. Compared with rajoids, potamotrygonid claspers show a general decrease in length (relative to disc width) and in the number of cartilages (although the homologies of these cartilages are not clearly established yet), and the lack of spiny projections.

Within potamotrygonids, Plesiotrygon and Potamotrygon have relatively long mature claspers, as in the myliobatoid out-groups (Himantura, Dasyatis, Myliobatis, Urolophus), while Paratrygon has relatively short mature claspers, an unique derived (autapomorphic) condition [39]. Another autapomorphy in Paratrygon claspers is the distal expansion of the Beta cartilage, which becomes continuous with the dorsal marginal cartilage [40]. The opposite state (separated Beta and dorsal marginal cartilages) is found in Plesiotrygon, Potamotrygon, and in the most closely related out-groups (Urolophus). The presence of continuous Beta and dorsal marginal cartilages in myliobatids and dasyatids is regarded as homoplasous with Paratrygon. Mature males of Plesiotrygon show the innermost pelvic-fin radial attached to the ventral marginal cartilage of clasper, a condition which is not found in the other potamotrygonid genera nor in the studied out-groups, therefore being regarded as an autapomorphy [10].

The tail.- The relative size of the tail varies considerably in the out-groups and within the potamotrygonids. Other tail characters that show a considerable amount of variation in stingrays are: the position and relative size of the tail finfolds (occasionally absent); the position and relative size of the caudal sting; the presence or absence of tail spines, their shape, position, and relative size; and the shape of the distal portion of the tail. Dasyatid stingrays usually have elongate tails, more or less distally whip-like, with well-developed ventral finfold (Dasyatis, Taeniura), or entirely lacking finfolds (Himantura). Urolophids have relatively shorter tails, lacking a distal filiform portion. The small size of the tail is probably associated with the presence of well-developed dorsal and ventral finfolds, internally supported by cartilaginous radials, and possibly functional in locomotion by lateral displacement of the tail. The out-group analysis revealed an equivocal polarity assessment for tail size. The in-group correlation of characters indicated the most generalized state of elongate, whip-like tails (as in Plesiotrygon) as the primitive condition. The reduction of tail length in Potamotrygon and Paratrygon is regarded as synapomorphic, while possibly independent reductions occurred in urolophids and in *Gymnura*.

The presence of cartilaginous radials in embryonic finfolds of Potamotrygon may indicate that the urolophid-potamotrygonid common ancestor already had the potential to form well-developed caudal finfolds. The out-group polarity assessment indicated the presence of dorsal and ventral finfolds as the primitive state. Within the study group, *Plesiotrygon* and *Potamotrygon* share the plesiomorphic ventral finfold, *Plesiotrygon* and *Paratrygon* respectively lost the dorsal finfold and both finfolds. The loss of the dorsal finfold could be regarded as synapomorphic for these two genera, but most possibly occurred independently (homoplasous). The in-group distribution of these character states is regarded as phylogenetically uninformative in expressing relationships of the potamotrygonid genera, and shows a reversal of polarity in *Potamotrygon*.

The relative size of the tail also varies ontogenetically in potamotrygonids, being larger in embryos, and progressively decreasing after birth. The post-natal shortening of the tail was observed in *Potamotrygon constellata* (as *P. circularis*) and in *P. motoro* by Thorson, Langhammer and Oetinger (1983), who suggested that the distal portion of the tail was gradually nipped off by carnivorous fishes. They supported this view with observation of captive stingrays which kept their tails intact in the absence of carnivorous fishes. The data of Thorson et al. indicated that the progressive reduction of the relative tail size is also due to the negative allometric growth of this structure, starting in the late embryonic phases of development. This fact is also corroborated by my observation that adult specimens of *Paratrygon* and *Potamotrygon* (*P. magdalenae*, *P. motoro*, and *P. yepezi*) with intact tails always have relatively shorter tails than the embryos from the same populations.

The caudal sting varies considerably in size among myliobatoids, being occasionally absent in *Gymnura*, *Myliobatis*, and *Aetobatus*, among other genera. The size of the sting in different species may be generally related to the position of its insertion: long stings are usually inserted more distally on the tail, while short stings are inserted much closer to the base of the tail, where they are obviously less functional. Both dasyatids and urolophids have relatively long and distally positioned stings. Within potamotrygonids, *Plesiotrygon* has a condition similar to these out-groups, *Paratrygon* has reduced sting [36] inserted much closer to the disc, and *Potamotrygon* has an intermediate condition. The in-group transformation series clearly shows a phylogenetic decrease in sting size, accompanied by the shortening of the tail and of the distance from the insertion of the sting to the base of the tail.

The number of caudal stings varies among the out-groups and within the study group. *Plesiotrygon* and *Potamotrygon* have one, two, or more rarely three stings, while *Paratrygon* has one, or more rarely two stings. The presence of more than one sting is possibly related to the process of shedding, observed in captive specimens of Potamotrygon by J. K. Langhammer (Belle Isle Aquarium, pers. comm.). The distribution of relative sting size in potamotrygonids with two stings is clearly bimodal, suggesting that the large sting is shed and substituted by the growing one. The relative position of the two stings is variable, the growing one being found in front of or behind the large sting.

The neurocranium.- Within the batoid level of universality, the lateral expansion of the neurocranium at the orbital and otic regions represent derived conditions, synapomorphic to the Myliobatiformes (see Heemstra and Smith, 1980). This lateral expansion of the cranium is represented by the enlargement of the preorbital and postorbital processes and of the supraotic crest (sensu El-Toubi and Hamdy, 1969a; = postorbital process of Haswell, 1884, Compagno, 1977, and Compagno and Roberts, 1982). The term supraotic crest is preferred for the latter structure, which possibly is not homologous to the postorbital processes of sharks, but a secondary aquisition of batoids related to the dorsal position of the spiracles. Among the out-groups, Dasyatis, Himantura, Taeniura, Hexatrygon, and Urolophus have well-developed processes, while Urotrygon has very short processes. Among potamotrygonids, Plesiotrygon and Paratrygon have relatively short preorbital and postorbital processes, while Potamotrygon has more or less developed processes. The preorbital cranium width in the latter genus is usually greater than the cranium width at the nasal capsules. The out-group polarity assessment showed the well-developed processes as the primitive state at the potamotrygonid level. The small processes of Plesiotrygon and Paratrygon and interpreted as homoplasous rather than synapomorphic, and possibly related to the small eye size in these genera, or representing the retention of a more distant plesiomorphy. The supraotic crests show a similar relative size in the three potamotrygonid genera.

The cranial fontanelle is more or less transversely constricted at the orbital level in Hexatrygon and Urolophus; Himantura and Urotrygon lack this constriction, while the species of dasyatis present both states. This constriction possibly represents a relict of the complete separation of the anterior and frontoparietal fontanelles, as found in rajiforms. Among myliobatiforms, the transverse constriction represents the primitive state, while a broad and more or less continuous transition between the anterior and frontoparietal fontanelles represent the derived state (see Heemstra and Smith, 1980). Among potamotrygonids, the embryos show relatively more constricted fontanelles, the adult Plesiotrygon and Potamotrygon have more or less constricted fontanelles, while adult Paratrygon has a less pronounced constriction, a condition regarded as autapomorphic [33].

A small dagger-shaped cartilage is found medially in the anterior prominence of the disc, between the first pair of pectoral-fin radials, in all examined embryonic specimens of

Potamotrygon (P. magdalenae, P. motoro, P. yepezi, Potamotrygon sp. B). This cartilage is not found in any adult potamotrygonids, nor in embryos of Paratrygon. Embryos of Plesiotrygon are not yet available for study. Among the examined out-groups, this cartilage is found in embryonic Dasyatis sayi, and in adult Urotrygon microphthalmum. The position and shape of this cartilage suggest that it is a relict of the primitive rostral appendix cartilage of rajoids. The reduction of this cartilage may be regarded as a synapomorphy of the Myliobatiformes, while its complete absence in Paratrygon could represent an autapomorphy. Embryos of Paratrygon show a median projection on the anterior margin of the neurocranium, a character which is lacking both in embryos and adults of the other potamotrygonid and out-group genera. This projection is regarded as autapomorphic in Paratrygon [32].

Other cranial characters, such as the cranial foramina, could not be comparatively studied in the three potamotrygonid genera, due to the insufficiency of specimens available for dissection. Further anatomical study of neurocrania may provide additional information regarding the phylogenetic relationships of these genera.

The vertebral column.- The anterior portion of the vertebral column of potamotrygonids is represented by two synarcual plates, as in all Myliobatiformes. The first (cervicothoracic) synarcual shows all the vertebrae fused to each other, and few or none distinct vertebral centra remain at its distal portion. The second (thoracolumbar) synarcual shows all the vertebral centra radiographically distinct. The position of the synarcual plates, relative to the branchial skeleton and to the coracoid bar, is essentially the same in the three genera of Potamotrygonidae. Their shapes are modified in Paratrygon, which shows both synarcuals relatively broader than the the two other potamotrygonid genera and the out-groups. The transverse enlargement of the synarcuals is regarded as autapomorphic in Paratrygon [26].

The number of distinct vertebral centra in the first synarcual varies from zero to eight in potamotrygonids, and from two to six in the examined out-groups (Urolophus, Urotrygon, Dasyatis, Taeniura). The out-group polarity assessment indicated the low number of centra found in Plesiotrygon (zero to three) as the primitive state, but the counts of the two other potamotrygonid genera broadly overlap with this range. Therefore, the distribution of this character state is uninformative in the study group, even when only modal numbers are taken into consideration.

The total number of distinct vertebrae in potamotrygonids (111-138) is slightly lower than in the examined out-groups, excepting freshwater species of Himantura (108-116 vertebrae fide Compagno and Roberts, 1982). Potamotrygon shows the greatest range (115-134), while Plesiotrygon (114-121) and Paratrygon (114-126) have narrower ranges. This distribution of states is uninformative, and even if modal numbers are considered, Potamotrygon and Paratrygon would share the primitive condition.

The distal portion of the vertebral column of potamotrygonids usually shows diplospondylous vertebrae, although adult specimens may lack them. The number of these vertebrae varied from zero to 24 in potamotrygonids. Among the studied out-groups, Urolophus, Urotrygon, and Taeniura show considerably higher counts (around 50), possibly related to the great development and mobility of the caudal finfolds in these genera. Freshwater species of Himantura also show high counts of diplospondylous vertebrae (62-76 fide Compagno and Roberts, 1982). Hexatrygon apparently lacks diplospondily, by having the distal vetrebral centra fused to each other (fide Heemstra and Smith, 1980). Within potamotrygonids, the maximum number of diplospondylous vertebrae is similar in the three genera. The lack of these vertebrae occurred only in adult specimens of Potamotrygon and Plesiotrygon, but adult specimens of Paratrygon with intact tails were not available for radiographic study. The out-group polarity assessment revealed the high number of diplospondylous vertebrae as the primitive state at the out-group node, therefore the reduction in their numbers is regarded as synapomorphic to the potamotrygonids [7].

The branchial skeleton.- The anteriormost element of the batoid branchial skeleton is the basihyal cartilage, a transverse bar lying between the hypobranchial cartilages. The basihyal is entire (Hexatrygon) or segmented (Urotrygon, Urolophus, Dasyatis, Taeniura) in the studied out-groups. The potamotrygonids always have segmented basihyals, the number of segments ranging from two to eight in Potamotrygon, four to five in Paratrygon, and nine in Plesiotrygon (only one specimen dissected). Although few out-group specimens were studied, the transformation series seems to be towards the reduction in size of the basihyal, by its subdivision in smaller pieces, with subsequent phylogenetic loss of segments. In this sense, the basihyal represents a multi-state character, where an entire or two-segmented broad cartilage would be the primitive condition, a large number of smaller segments an intermediate condition, and few reduced pieces the most derived state. Further study of these character states in potamotrygonids and out-groups is necessary to evaluate their information content at different levels of universality.

The hypobranchial cartilages link the basihyal to the ventral portion of the pseudohyoid cartilages. The hypobranchials are entire (Urotrygon, Urolophus, Dasyatis, Taeniura) or segmented (in Hexatrygon fide Heemstra and Smith, 1980, fig. 10) in the out-groups, and always entire in potamotrygonids. Potamotrygon has an anterior expansion on the outer margin of the hypobranchials, similar to those found in Urotrygon and Dasyatis. The hypobranchials are uninformative regarding the phylogenetic relationships of the potamotrygonid genera.

The anterior ray-bearing element in the batoid branchial skeleton is the pseudohyoid cartilage (sensu El-Toubi and Hamdy, 1969b). The ventral portion of the pseudohyoid is fused to the first ceratobranchial in potamotrygonids and in the studied out-groups (Urotrygon, Urolophus, Dasyatis, Taeniura) with exception of Hexatrygon (fide Heemstra and Smith, 1980, fig. 10). Ceratobranchials one to four show various degrees of fusion of their inner margins in potamotrygonids and in the out-groups. Urotrygon aspidurus and Taeniura lymma (fide Garman, 1913, plates 69, 71), and one specimen of Urolophus jamaicensis examined by the author have all ceratobranchials free from each other. Urotrygon microphthalmum has the single fusion of ceratobranchials one and two. Dasyatis uarnak has ceratobranchials one to four all fused to each other (El-Toubi and Hamdy, 1969b). One embryonic specimen of Dasyatis sayi examined by the author shows only ceratobranchial three and four fused to each other. Hexatrygon bickelli apparently has all ceratobranchials free from each other, as illustrated by Heemstra and Smith (1980, fig. 10).

Among potamotrygonids, Plesiotrygon has all ceratobranchials separated, Potamotrygon (P. magdalenae, P. motoro, P. yepezi, Potamotrygon sp. B) has the fusion of ceratobranchials one to four, while Paratrygon has the single fusion of ceratobranchials one and two. An out-group polarity assessment for these fusions is presently questionable, due to the scarcity of material studied so far. The in-group correlation of derived states indicated that the fusion of ceratobranchials one and two is synapomorphic to Potamotrygon and Paratrygon [16]. Therefore, the complete separation of the ceratobranchials is regarded as the primitive condition, a polarity which is in agreement with an ontogenetic criterium, due to the separate embryonic origin of these cartilages.

The number of rays in the ventral portion of the branchial arches (ventral pseudohyoid and ceratobranchials one to four) varies from one to eight in the examined out-groups (Urotrygon and Dasyatis). The maximum number is found in the pseudohyoid, and the minumum in the fourth ceratobranchial. Within potamotrygonids, Plesiotrygon has four to six ventral rays on each arch, the studied species of Potamotrygon have four to ten, and Paratrygon has seven to ten ventral radials. The relatively larger number of rays (7-10) in the ventral pseudohyoid is considered synapomorphic to Potamotrygon and Paratrygon [15].

The most distal branchial ray of the ventral pseudohyoid and of ceratobranchials one to four is attached to the inner margin of the propterygium, both in potamotrygonids and in the out-groups. The fifth ceratobranchial lacks branchial rays, and makes the connection of the basibranchial plate with the scapulocoracoid in all batoids. Urotrygon microphthalmum has a basal segment on the inner margin of fifth ceratobranchial, with two small branching rays. One embryonic specimen of Potamotrygon magdalenae similarly shows four basal segments on the fifth ceratobranchial. These cartilages may represent the relict of a primitive sixth gill arch, as found in Hexatrygon.

Paratrygon has five opercular cartilages (fide Garman, 1913, plate 70), ventrally associated with the outer margins of the ray-bearing arches (ventral pseudohyoid and ceratobranchials one to four). One fully formed Paratrygon embryo (INPA uncatalogued, 160 mm DL) lacks entire opercular cartilages, but shows them as five distinct chondrification centers which picked up alcian blue stain. The opercular cartilages are absent from the examined out-groups and from the two other potamotrygonid genera, therefore they are regarded as an autapomorphy of Paratrygon [29].

The scapulocoracoid (pectoral girdle).- The examination of potamotrygonid scapulocoracoids in the present study was limited to the dissection of their ventral aspects, and their radiographic comparison in the three recognized genera. No specimens of Plesiotrygon and Paratrygon were available for complete dissection required for the study of the lateral faces of scapulocoracoids, which implies the disarticulation of the whole skeleton. Out-group information on scapulocoracoids is available in Garman (1913), Heemstra and Smith (1980) and Compagno and Roberts (1982), especially in their illustrations, and from specimens of Dasyatis and Urotrygon dissected by the present author. All the examined out-groups have relatively thin coracoid bars, and more or less developed postventral fenestra on the lateral face of the scapulocoracoid. Hexatrygon apparently lacks this fenestra. Within potamotrygonids, Plesiotrygon has a large postventral fenestra, while Potamotrygon and Paratrygon have reduced fenestrae, a state which is regarded as synapomorphic to these latter genera [17]. Paratrygon has a broad and stout coracoid bar, not seen in other stingrays, and considered as an autapomorphy [30].

The ischiopubic bar (pelvic girdle).- The pelvic girdle of potamotrygonids is characterized by a long median prepubic process, which is absent (Urotrygon, Urolophus, Dasyatis, Himantura, Taeniura) or moderately developed (Myliobatis, Aetobatus, Rhinoptera, Mobula fide Garman, 1913, plate 54) in the out-groups. The long prepubic process is regarded as a synapomorphy of the family Potamotrygonidae [1].

The number of obturator foramina in the pelvic girdle varies from two (Urotrygon) to five (Himantura, fide Compagno and Roberts, 1982) in the out-groups. The potamotrygonids commonly show three, or rarely four foramina. The distribution of this character state was uniformative at the in-group generic level.

The coloration.- The batoids have on their dorsal surface either uniform dull colors (usually gray or brown), or more vivid and elaborate color patterns (variously spotted, reticulated, or ocellated). The former condition prevails among dasyatid stingrays, while the latter is more common in Urolophus and potamotrygonids. The more elaborate color patterns possibly represent derived states related to the adaptation to benthic mode of life, but no out-group polarity assessment could be made for this transformation series. Even the more primitive out-groups, like rajoids and rhinobatoids, show both kinds of coloration. There is a considerable amount of intraspecific variation and of temporal changes of individual color patterns in several batoid species. One specimen of _Rhinobatos percellens_ kept in a tank by the present author continually changed its coloration back and forth from a reticulate to an ocellated pattern. Intraspecific variation of color in species of _Urolophus_ was described and illustrated by Bigelow and Schroeder (1953), Babel (1967), and Böhlke and Chaplin (1968). Periodic changes of coloration were observed in aquarium specimens of _Potamotrygon motoro_ (J. K. Langhammer, pers. comm.) where the characteristic ocelli of this species nearly faded and subsequently returned to their bright condition.

Despite the intraspecific variation, color characters were taxonomically useful in keying the species of Potamotrygonidae, because most species have more or less distinct color patterns. On the other hand, very little phylogenetic information could be obtained from color characters, especially at the potamotrygonid generic level. The exceptions occur at the specific level, where some unique color characters may be shared by two or more species. For instance, the caudal ocelli of _Potamotrygon henlei_ and _P. leopoldi_ seem to indicate a sister-group relationship between these two species. Other ocellated and reticulate patterns of several species of _Potamotrygon_ possibly represent parallelisms, and therefore are not true indicators of relationship.

Phylogenetic relationships

The preceding analysis of characters suggested that <u>Potamotrygon</u> and <u>Paratrygon</u> are sister-groups, and that <u>Plesiotrygon</u> is the primitive potamotrygonid genus. Referring to the numbers on the in-group cladogram (Fig. 98), <u>Plesiotrygon</u> is characterized by apomorphies [9] and [10]; <u>Potamotrygon</u> and <u>Paratrygon</u> share the apomorphies [11] through [17]; the character states [18] through [22] are unique apomorphies of <u>Potamotrygon</u>, and [23] through [40] are unique apomorphies of <u>Paratrygon</u>.

The monotypic genus <u>Paratrygon</u> shows the highest degree of anagenetic changes among potamotrygonids, as revealed by its great number of autapomorphies, and by its morphological divergence from the basic oval and anteriorly prominent disc form, found both in the other potamotrygonid genera and in the immediate out-groups. <u>Paratrygon</u> would possibly receive a higher taxonomic ranking in an evolutionary (gradist) classification (see Mayr, 1981), justified by this great divergence, while <u>Plesiotrygon</u> and <u>Potamotrygon</u> possibly would be combined as sister-groups, due to their greater morphological resemblance.

The genus <u>Potamotrygon</u> has speciated in most of tropical South America, with little departure from the hypothetical ancestral form, excepting <u>P. brachyura</u>, which paralleled <u>Paratrygon</u> in attaining large body sizes, in the reduction of the tail, and in the increase in the number of pectoral-fin radials. If *P. brachyura* or other species of *Potamotrygon* is shown to be the sister-species of *Paratrygon aiereba*, their separate generic status would lack a phylogenetic basis, and the latter species should be included in *Potamotrygon* in a phylogenetic classification, despite its great morphological divergence.

One alternative hypothesis for the ancestry of potamotrygonids has been proposed by G. Dingerkus (AMNH, pers. comm.), where he considered *Taeniura* as the sister-group of *Potamotrygon*. This hypothesis was based on his observation of a short prepubic process in *Taeniura*, and possibly on the study of branchial skeletal characters. Dingerkus apparently did not examine the two other potamotrygonid genera. The specimen of *Taeniura lymma* examined by the present author had the pelvic girdle slightly pointed anteriorly, but failed to show the prepubic process. Its branchial skeleton was not studied, but I cannot support this hypothesis, because it would imply more reversals of polarity (e.g. for the number of pectoral and pelvic-fin radials), and a *de novo* appearence of several characters like the dorsal tail finfold. A thorough study of *Taeniura* and other out-groups is necessary to establish more firmly the sister-group relationships of the Potamotrygonidae.

In terms of phylogenetic classifications, the Potamotrygonidae should not be treated as a subfamily of Dasyatididae, with the exclusion of urolophids and possibly of *Hexatrygon* from the family, in order to avoid paraphyly. Further study is necessary to establish the position of Hexatrygonidae, which possibly would fit better in the superfamily Dasyatoidea (*sensu* Compagno, 1973), instead of having a sister-group relationship with all the Myliobatoidei, as originally proposed by Heemstra and Smith (1980). The usage of sequenced classifications (Nelson, 1972; Wiley, 1981) to express new hypotheses of relationship among the batoid families would avoid the creation of unnecessary new suprafamilial names, especially at this time when this relationships are far from being resolved.

BIOGEOGRAPHY

General distribution

The potamotrygonids are endemic to South America, occurring in all South American countries except Chile, which lies entirely on the western side of the Andes (Castello, 1975, 1976). They occur in most river systems of tropical and subtropical South America, except those draining into the Pacific Ocean, and all the Atlantic coastal drainages from Rio Parnaíba in Brazil to Río de la Plata in Uruguay. The potamotrygonids are possibly absent from the Rio São Francisco drainage in eastern Brazil (Brooks, Thorson and Mayes, 1981), since there are no records in the literature, nor specimens from this drainage in recent collections. Three specimens of *Potamotrygon* (MCZ 1445-S, MCZ 1446-S, MCZ 1447-S) were supposedly collected in Rio das Velhas, a tributary of the upper São Francisco in Minas Gerais. There is no mention of stingrays from Rio São Francisco and Rio das Velhas in Halfeld (1860) and in Lütken (1875). There is a remote possibility that the potamotrygonids have gone undiscovered in Rio São Francisco drainage, or that they disappeared from there due to man-caused environmental impact.

In terms of the South American zoogeographic regions de-

FIG. 99

Distribution of the Potamotrygonidae based on material examined. Doubtful localities not plotted. Circles = species of *Potamotrygon*; squares = *Paratrygon*; triangles = *Plesiotrygon*. Each symbol may represent more than one specimen or sample.

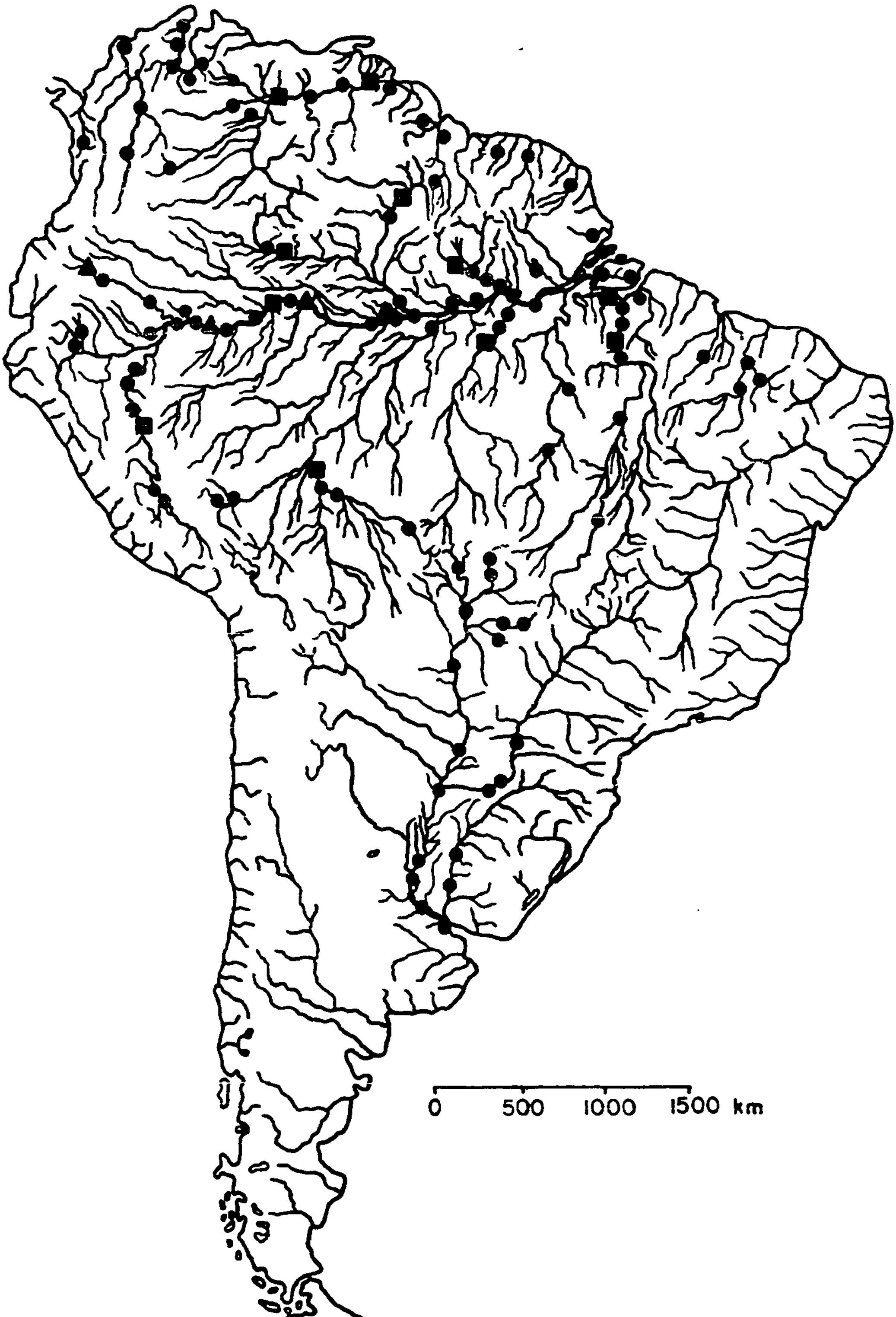

0
500
1000
1500 km

FIG. 100

Geographic distribution of species of *Potamotrygon* based on material examined. *Potamotrygon brachyura* (black squares), *P. castexi* (black circles), *P. constellata* (black stars), *P. dumerilii* (open stars), *P. falkneri* (open circles), and *P. henlei* (open squares).

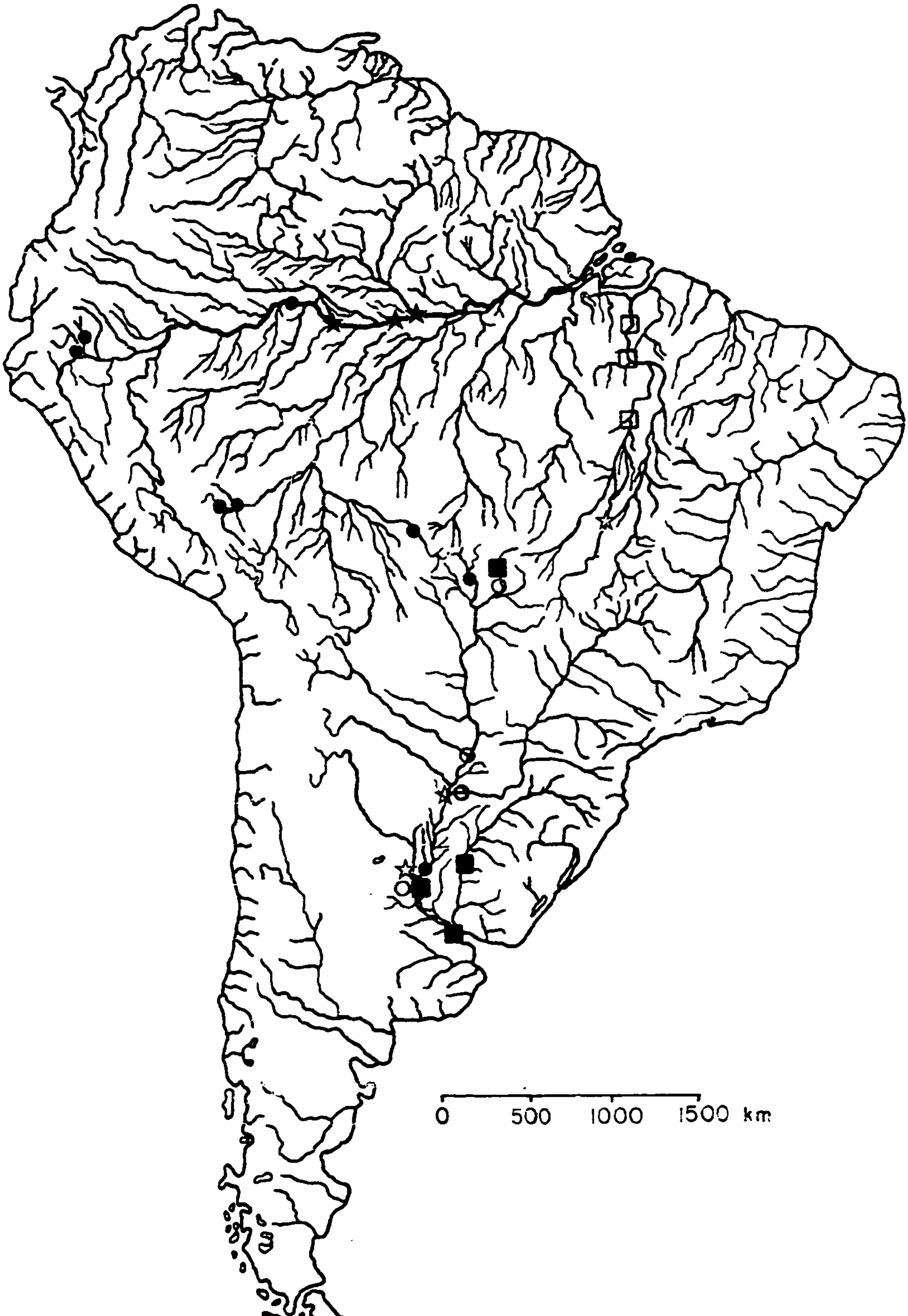

0 500 1000 1500 km

FIG. 101

Geographic distribution of species of *Potamotrygon* based on material examined. *Potamotrygon histrix* (open circles), *P. humerosa* (black stars), *P. leopoldi* (open squares), *P. magdalenae* (black squares), *P. motoro* (black circles), and *P. ocellata* (open star)

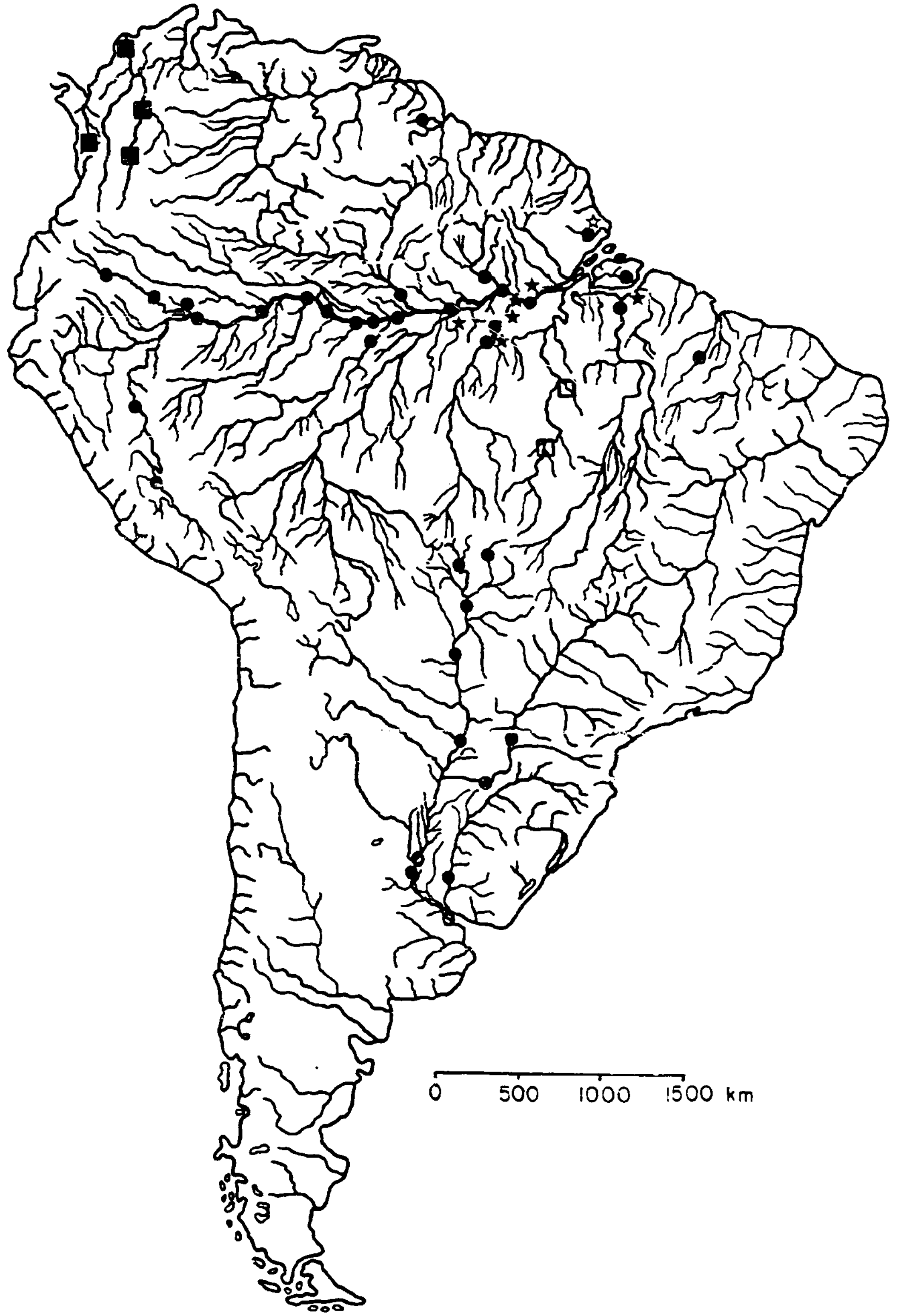
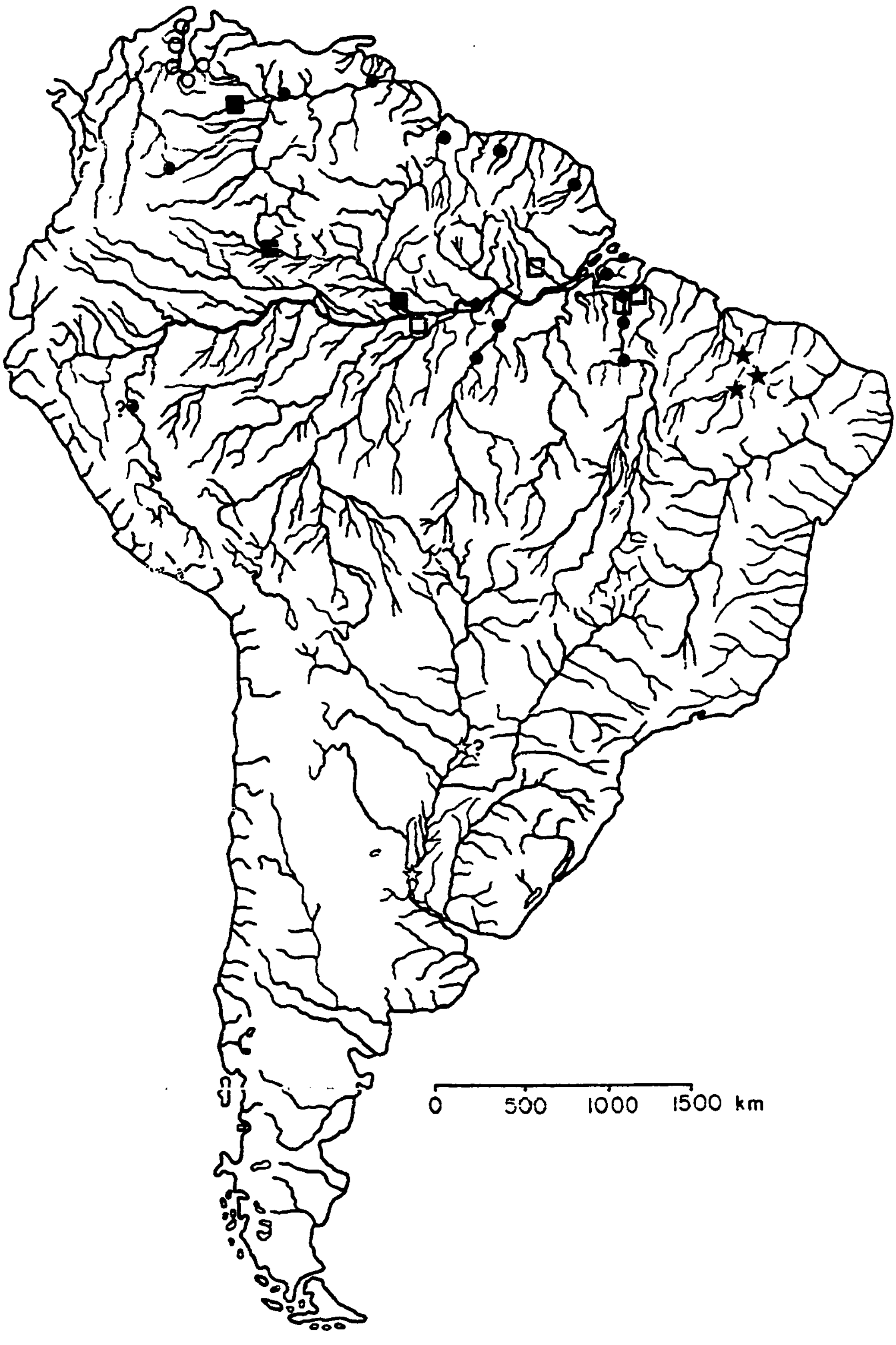

0 500 1000 1500 km

FIG. 102

Geographic distribution of species of *Potamotrygon* based on material examined and verified literature records. *Potamotrygon orbignyi* (black circles), *P. schroederi* (black squares), *P. schuemacheri* (open stars), *P. scobina* (open squares), *P. signata* (black stars), and *P. yepezi* (open circles). Question marks refer to tentatively identified specimens.


?
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fined by Eigenmann (1910), and modified by Géry (1969) and Lowe McConnell (1975), the potamotrygonids are present in the Orinoco-Venezuelan, Magdalenean, Trans-Andean (Río Atrato in Colombia), Paranean (lower Rio Paraná), and Guianean-Amazonean regions, and are absent from the Andean, Patagonian, and East-Brazilian regions, and from the Trans-Andean Region to the south of Colombia.

The distribution of the Potamotrygonidae based on the material examined is shown in Fig. 99. Localities of the Thayer Expedition specimens were mapped according to Dick (1977).

Historical biogeography and the origin of the Potamotrygonidae

Several hypotheses have been forwarded to explain the origin and distribution of the Potamotrygonidae, ranging from an entirely freshwater origin of the group, to multiple invasions of continental South America by marine ancestors (Thorson and Watson, 1975; Brooks, Thorson and Mayes, 1981). It has been suggested (see Thorson et al., 1967; Thorson and Watson, 1975; Thorson, Brooks and Mayes, 1983) that the potamotrygonids evolved from freshwater ancestors that never retained urea, instead of having secondarily lost the ability to concentrate urea. Thorson and Watson (1975) mentioned that convincing evidence was lacking for both alternatives, but considered unlikely that the potamotrygonid ancestors had no urea retention, due to the late appearance of stingrays in geological time, relative to other elasmobranchs which were essentially marine. An implication of the hypothesis of freshwater origin would be that the potamotrygonids possibly were one of the most primitive batoid groups, since all the marine relatives would represent secondary invasions of the sea derived from freshwater ancestors. It would also imply in a de novo appearance of the urea retention, since the early marine elasmobranchs presumably had the ability to retain urea (Thorson and Watson, 1975). The present knowledge of phylogenetic relationships within the elasmobranchs (see Compagno, 1977) does not support a diphyletic origin of batoids and other elasmobranchs, nor the freshwater origin of potamotrygonids, because the stingrays occupy a relatively derived position among the batoids. Also there are no primitive sister groups of the stingrays known to occur in freshwater.

Brooks, Thorson and Mayes (1981) formulated four different hypotheses concerning the origin and evolution of the Potamotrygonidae, and discussed their testability and viability according to biogeographic evidence and parasitological data. Hypothesis One was based on the freshwater origin of potamotrygonids, and implied the presence of a relatively primitive parasitic fauna in the group. Hypothesis Two consisted of multiple invasions of the continent by marine ancestors through different river systems. It implied the polyphyly of potamotrygonids and their parasitic fauna, and closest phylogenetic relationships of potamotrygonid parasites from one river system to those found in marine stingrays at the mouth of that river, instead of those from other river systems. The Atlantic origin of the Potamotrygonidae and a dasyatid sister-group were two questionable assertions linked to Hypothesis Two, and they will be discussed below.

Hypothesis Three consisted of the marine origin from a single species of Dasyatididae, which invaded one river system (possibly the Amazon) and dispersed from there into other parts of South America. Hypothesis Three implied a monophyletic origin of the potamotrygonids and their parasites, and also that the closest relatives of potamotrygonid parasites inhabit Atlantic dasyatids. Again, as with Hypothesis Two, the Atlantic origin was inadequately indicated as a premise.

Hypothesis Four, the one most corroborated by Brooks et al. parasitological data, stated that the "potamotrygonids represent a monophyletic group whose ancestor was a non-dasyatid marine stingray trapped in South America by Andean orogeny" (Brooks, Thorson and Mayes, 1981). It implied the monophyly of the parasitic fauna, that the closest relatives of parasites of potamotrygonids from one river system occur in potamotrygonids of adjacent river systems, that the closest relatives of potamotrygonid parasites inhabit Pacific non-dasyatid stingrays, and finally it implied the Pacific origin of the Potamotrygonidae.

Hypotheses Two and Three were labelled as dispersalist, and Hypothesis Four as vicariant.

Brooks, Thorson and Mayes (1981) probably based their mutually exclusive criteria of Atlantic-dasyatid versus Pacific-urolophid ancestry on the present distribution of these groups. Present-day distributions do not necessarily reflect paleodistributions, i. e., the present low species diversity of urolophids in the Atlantic does not imply that they were not abundant there in the past. The same may be true for dasyatids in the Pacific coast of South America. The two groups could even have had a cosmopolitan distribution around the South American continent. In this sense Brooks et al. did not generate all possible hypotheses concerning the origin of potamotrygonids, because there could be an Atlantic-urolophid ancestor, or a Pacific-dasyatid one. The question about the center of origin (Atlantic versus Pacific) seems to be irrelevant, since the Panamanian Isthmus was open until the early-mid Pliocene (Berggren and Hollister, 1974), and because several marine transgressions on South America, from Cretaceous to Oligicene, provided shallow marine connections between the Atlantic and Pacific (Harrington, 1962). Both conditions permitted the faunal interchange between the two oceans, as evidenced by the distribution of fossil and extant marine animals.

In order to explain the circum-Pacific distribution of urolophid stingrays, and possibly to avoid a trans-Pacific dispersal track, Brooks, Thorson and Mayes (1981, figs. 26 and 27) established a priori an Antartic track, which is not supported by the present-day distribution, nor by the fossil records of urolophids. Their map depicting the ancestral distribution of these stingrays ignored fossil records of Urolophus from southern Europe (Woodward, 1889), which suggest a Tethyan distribution of the group. Some other Tethyan and North American fossil genera described under the Trygonidae (Heliobatis, Leiobatis, Hypolophus) may be more closely related to urolophids than to dasyatids. Norman (1975) suggested that the extant Dasyatididae do not include the fossil genera from the Cretaceous. The contemporary track of urolophids by Brooks et al. neglected the presence of the group in the Atlantic, for Urolophus is present in the Caribbean region as mentioned by them, and Urotrygon occurs as far as northeastern Brazil. The presence of Urotrygon in the Western Atlantic was also overlooked by Springer (1982).

Straney (1982) commented on Brooks, Thorson and Mayes (1981) paper, and mentioned that many other conclusions were possible from their set of data. According to Straney, the southeastern Pacific and freshwater South American track was not supported by the parasite data, but instead, there was a component uniting South America with the northeastern Pacific-Caribbean area. Therefore, the southeastern Pacific ancestry of the potamotrygonids was not well supported, but their association with north Pacific-Caribbean ancestors was more likely.

The Caribbean-Tethyan track for the ancestral stingray fauna does not invalidate the possibility of the Antarctic track, but the former is a more attractive and parsimonious hypothesis, due to the presence of urolophid-like fossils around the Mediterranean and in eastern North America. The Tethyan track also conforms with a Mesozoic generalized track for tropical marine organisms (Croizat, 1964). Although Tethys is usually restricted to the Eurasian seaway in the geological literature, the name has been used in paleobiogeography to denote a faunal province (Tethyan), which extended to the Caribbean region and North America (Ekman, 1953; Hallam, 1972; Berggren and Hollister, 1974). Tethys connection with the proto-Atlantic was formed by Middle-Permian (Kamen-Kaye, 1972, 1976); by the late Cretaceous, western Thethys was widely opened and connected with the Atlantic, a connection which persisted until the Miocene (Hsü, 1971; Smith, 1971; Berggren and Hollister, 1974). The direct connection of Tethys with southeast Asia and Australia, present since the early Paleozoic, persisted until the mid Tertiary, as shown by the distribution of fossil fish faunas (Arambourg, 1943). The connection of the western part of the Tethyan seaway (Caribbean region) with the Eastern Pacific was through the Panamanian region. The effectiveness of this past communication for coastal marine fauna is revealed by many shared genera and species pairs of invertebrates and fishes, on both sides of the Panamanian isthmus (Ekman, 1953). This trans-isthmian track could be part of a larger quasi-circumtropical track linking the Atlantic and Pacific basins (Briggs, 1974; Croizat et al., 1974).

Since the urolophids are absent from the Pacific and

Antarctic tectonic plates, except for Urotrygon daviesi, a relatively deep-water species reported from off Hawaii (Springer, 1982), and since no urolophid fossils are known from these areas, the most parsimonious hypothesis to explain their distribution, is that they have never been present on these plates. Springer (1982) proposed and favored this reasoning (his "Reality Hypothesis") against an alternative "Extinction Hypothesis", to explain the distribution of many fish and invertebrate taxa around the Pacific plate.

A quasi-circumtropical ancestral track could be drawn for the urolophids. The urolophid-like ancestor of the potamotrygonids possibly was distributed marginally on the Pacific plate, reaching the Eastern Pacific, and on the Caribbean and Atlantic coasts of South America.

Potamotrygonidae and South American biogeography

> "It is not coastal life which has "immigrated" by casual means to the bottom of certain Andean and Central American valleys, foothills, etc. It is on the contrary the coast itself which has "emigrated" away because of geological reasons, leaving behind stranded life that once grew by the shore" (Croizat, 1964, pp. 116-117).

Accepting the marine origin of the Potamotrygonidae from a marine urolophid-like ancestor, and favoring a vicariant (instead of dispersalist) reasoning (Brooks, Thorson and

Mayes, 1981), an explanation similar to that in Croizat's statement cited above, would be the most plausible to account for the presence of these stingrays in South American fresh waters. Such explanation would also conform with recently acquired data on the paleogeography and geological history of South America.

The main "geological reason" for stranding marine organisms, including the urolophid-like ancestors of potamotrygonids as proposed by Brooks, Thorson and Mayes (1981) and Thorson, Brooks and Mayes (1983), is the orogeny of the Andes during the Tertiary, caused by the westward relative movement of the South American tectonic plate, and its collision with the Nazca plate. This orogeny isolated inland seas, formed by the Pacific arms which previously extended eastward on the Brazilian Shield (Grabert, 1983). These basins evolved into sub-Andean freshwater lakes ("molasses"), along with the stranded marine fauna. Therefore, we may expect that several freshwater groups with marine origin, from invertebrates to aquatic mammals, show similar biogeographic patterns in South America. Similar explanation for the origin of secondary freshwater fishes of South America was forwarded by Eigenmann (1906), although this author relied on a dispersalist reasoning (from sea, through brackish water into fresh water) to account for the cis-Andean distribution of these fishes. Other authors (e.g. Marlier, 1973) explained the presence of marine-related animals in the upper Amazon by migration from the Atlantic.

Beurlen (1970) and Grabert (1983) treated the geology and paleogeography of the Amazon region. Both authors agreed that during the Tertiary the Amazon was a westward flowing river, draining into the Pacific Ocean at the region of Guayaquil, Ecuador. The reversal in the direction of flow started in the Lower Miocene (Grabert, 1983) or in the Pliocene (Beurlen, 1970) as a consequence of Andean orogeny. The erosion at the watershed caused the sub-Andean lakes to empty to the east into the Amazon basin, forming new tributaries and the modern Amazon drainage system.

The critical period in the early differentiation of the South American secondary freshwater groups possibly occurred in the sub-Andean lakes. The formation of these basins occurred so rapidly that the marine fauna had either to adapt to the new conditions or disappear (Grabert, 1983). The biogeographic pattern of distribution of the potamotrygonid genera suggest that their early differentiation occurred in a sub-Andean basin in eastern Ecuador and northern Peru. Grabert (1983) presented a similar example for the differentiation of the freshwater dolphins (genus _Inia_), based on the phylogenetic relationships of the species and subspecies of _Inia_. _Inia_ _boliviensis_, restricted to sub-Andean waters of Bolivia, is considered the primitive form. This species has minute eyes, which may indicate that it initially inhabited turbid environments (such as the white-water rivers), and that the regressive evolution of the eyes occurred prior to speciation and subspeciation (Grabert, 1983).

The hypothetical primitive genus of Potamotrygonidae (Plesiotrygon) similarly shows minute eyes, and possibly was subject of identical selection pressure.

The phylogenetic spliting into the derived genera (Potamotrygon and Paratrygon) may have occurred by fragmentation of the original environment by further orogeny or erosion. The three genera subsequently gained access to the modern Amazon drainage, Potamotrygon and Paratrygon reaching also the clear-water and black-water rivers (see Sioli, 1967, and Marlier, 1973, for a classification of Amazonian water types). Paratrygon seems to be more abundant in the white-water rivers of the upper Amazon and Madeira drainages, and members of this genus retained the primitive small eyes. The distribution of the genus Potamotrygon could be explained by dispersal through the Amazon drainage, with invasions of interconnected basins to the north and south, and by subsequent localized vicariant events which resulted in speciation.

Connections of the Amazon river system with the northern drainages are known between the rivers Negro and Orinoco (through the Canal de Cassiquiare), Japurá and Magdalena, Vaupés and Guaviare, Guainía and Inírida, and Mapuera and Essequibo (Sioli, 1967; Roberts, 1972; Soares, 1977; Lowe-McConnell and Howes, 1981).

Connections of the Amazon river system with the Rio Paraguay drainage possibly occurred and are periodically re-established through the upper reaches of rivers Xingu, Tapajós, Araguaia, and Guaporé (Pearson, 1937; Sioli, 1967; Roberts, 1972; Lowe-McConnell, 1975; Soares, 1977; Innocêncio, 1977; Lowe-McConnell and Howes, 1981). Haseman (1912) denied the connection of Rio Paraguay and Rio Guaporé, and although he admitted that some other restricted connections might have occurred between the Amazon and Rio Paraguay, he considered that those connections could not be operative for the exchange of fishes from the two basins, with the possible exception of some highland forms. Haseman (1912) tried to explain the similarity of the fish faunas of the Amazon and Paraguay, including two shared species of Potamotrygon (which he did not name), by parallel evolution in the two basins.

Pearson (1937) criticized Haseman's explanation, and analyzing the composition of the fish faunas of the Beni-Mamoré and Paraguay drainages, he stated that the origin of the latter could be explained by "migration" (=dispersal) from the north. He considered the highlands of Mato Grosso as barriers of recent origin, which presently preclude fish dispersal. Ihering (1897) mentioned that the absence of potamotrygonids from southern Brazil, and their presence in Río de la Plata could be explained by a dispersal way from the Amazon through Rio Paraguay. He supported this view by stating that all species of Potamotrygon excepting P. brachyura were identical to Amazonian species. Pearson (1937) cited two species of Potamotrygon as occurring both in the Amazon and Paraguay basins (P. histrix and P. dumerilii). Potamotrygon histrix is yet unknown from the Amazon, but P. dumerilii occurs in the lower Rio Paraná and in Rio Araguaia. In addition, _P. motoro_, and the more recently described species _P. castexi_, occur in both basins. Although their phylogenetic relationships are yet unknown, the species of _Potamotrygon_ endemic to the Paraguay-Plata river system might have originated locally, in tributaries isolated during the interglacial marine transgressions of the lower Paraná.

Other speciation patterns might have similarly occurred in the tributaries of the lower Amazon, for instance of _Potamotrygon leopoldi_ and _P. henlei_, which seem to form a species pair in the Xingu and Tocantins-Araguaia rivers. The eustatic sea level rise (nearly 50 m) which preceeded the Würm-Wisconsin glaciation drowned a large part of the Amazon basin, including Rio Solimões (Haffer, 1969; Vuilleumier, 1971). This transgression formed a marine embayment which isolated the tributaries of the mid and lower Amazon from each other, with saline water at their mouths. This process could account for the fragmentation of previously widely distributed species, and their differentiation in isolated rivers, resulting in speciation patterns.

Other speciation events in the genus _Potamotrygon_ possibly occurred in the late Tertiary, still associated with Andean orogeny. The origin of _P. magdalenae_ in Colombia possibly occurred before the final rise of the Cordillera Ocidental, which presently separates the Magdalena and Atrato river drainages. The speciation of _P. yepezi_ possibly occurred along with the uplift of the Cordillera de Merida, which isolated the Maracaibo basin from the inland drainages.

Discussion

The apparent gap in distribution of potamotrygonids in the southern tributaries of the Amazon (see Fig. 99) possibly is an artifact, due to the lack of collections from these rivers. Similar apparent gaps are observed in the distribution of other fish groups (e.g. genus Cichlasoma, see Kullander, 1983). There is no obvious reason for the absence of stingrays, at least of some species of the most widely distributed genus Potamotrygon, in the southern tributaries of the Amazon. Further collection may prove that the stingrays are abundant in these rivers, especially in their lower portions. Due to the same lack of collections, it is not known to what extent the potamotrygonids occur in the upper reaches of these rivers which drain the Brazilian Shield. There is evidence that in rivers Xingu and Araguaia they occur above rapids and falls.

The absence of potamotrygonids from Africa, and from the main rivers (Rio São Francisco and upper Rio Paraná) which drain the oldest Brazilian terrains (Brazilian Shield), suggests that the early differentiation of these stingrays in fresh water possibly occurred in the Tertiary, after the separation of Africa and South America.

The restricted distribution of the hypothesized primitive genus (Plesiotrygon) in the upper Amazon suggests that the early differentiation of the group occurred in the western portion of the primitive Amazon basin, possibly in freshwater lakes and white-water rivers formed along with the uplift of the Andes. The south to north pattern of phylogenetic derivation of the Potamotrygonidae, starting in the Paraná-Paraguay system and proceeding to the Amazon (Brooks, Thorson and Mayes, 1981; Thorson, Brooks and Mayes, 1983) cannot be supported by the present phylogenetic and biogeographic data. The pattern probably was based in part on the false notion that the Paraná-Paraguay had been formed as a freshwater system before the Amazon, and that it remained as such throughout its history. The south to north pattern of derivation may eventually prove true for the drainages to the north of the Amazon (Orinoco, Maracaibo, and Magdalena), but its confirmation depends on further phylogenetic studies of the organisms concerned. In other words, the presence of apparently related species in different drainages does not tell anything about their evolutionary history, unless their characters are phylogenetically analysed. The model of Brooks et al. could only be corroborated if the transformation series of most of the analyzed stingray characters conform to a certain linear south-north pattern, i.e. increasing apomorphy towards northern South America.

The biogeographer should keep in mind that vicariance does not always occur in continental geographic scales, but may be the result of more localized processes. Several small-scale phenomena in tropical drainages, such as meandering, lake isolation, and stream capture, may result in vicariance or secondary contacts of populations. Furthermore, the present biogeographic patterns may be the results not only of vicariant events, but could also be affected by subsequent dispersal involving interconnected drainages. Therefore, the strict application of the chrorological method (*sensu* Hennig, 1966) in establishing linear phylogenetic/biogeographic progressions for tropical freshwater organisms should be regarded with caution.

CONCLUSIONS

The present systematic revision recognizes nineteen valid species (see Table 25) from the thirty-seven names previously assigned to the Potamotrygonidae. One new species, placed in the new genus *Plesiotrygon* is added to the family. Two possibly new species of the genus *Potamotrygon* are commented upon, but are not named due to the lack of adequate series of specimens for comparisons or descriptions.

The remaining eighteen names include eight junior synonyms (see Table 25), five doubtful names (*Elipesurus spinicauda*, *Pastinachus humboldtii*, *Potamotrygon africana*, *P. alba*, and *Trygon garrapa*), two nomina nuda (*Potamotrygon labratoris* and *P. pauckei*), two doubtful names corresponding to one unidentified species of Dasyatididae (*Raja ajereba* and *R. orbicularis*), and one freshwater species of *Dasyatis* (*D. garouaensis*) originally described in the genus *Potamotrygon*.

Two previously established generic names (*Paratrygon* and *Potamotrygon*) are recognized as valid, the two other generic names used exclusively for freshwater stingrays, *Elipesurus* and *Disceus*, being respectively considered doubtful and a junior synonym of *Paratrygon*. *Potamotrygon* is the type genus because the family name Potamotrygonidae Garman has priority over Paratrygonidae Gill. Potamotrygon is a polytypic genus, and both Paratrygon and Plesiotrygon are monotypic, as far as known.

Potamotrygon and Paratrygon are regarded as sister-groups, and Plesiotrygon as the primitive potamotrygonid genus, based on a cladistic analysis of characters. Limitations of the data base, in terms of number of specimens available for dissection, precluded the anatomical study of several species, and the phylogenetic analysis at the specific level of Potamotrygon.

A considerable amount of intraspecific variation regarding external characters such as coloration, dentition, and spines, was found in all species of the family. Several nominal species that had been based exclusively on external characters proved to be synonyms of previously described species. For these reasons, the examination of large series of specimens is recommended before the establishment of new additional taxonomic names.

TABLE 25

VALID SPECIES OF THE POTAMOTRYGONIDAE, AND THEIR JUNIOR SYNONYMS

VALID SPECIES	JUNIOR SYNONYMS
Paratrygon aiereba	Trygon strogylopterus
	Disceus thayeri
Potamotrygon brachyura	Potamotrygon brumi
Potamotrygon castexi	
Potamotrygon constellata	Potamotrygon circularis
Potamotrygon dumerilii	
Potamotrygon falkneri	Potamotrygon menchacai
Potamotrygon henlei	
Potamotrygon histrix	
Potamotrygon humerosa	
Potamotrygon magdalenae	
Potamotrygon motoro	
Potamotrygon ocellata	
Potamotrygon orbignyi	Trygon reticulatus
Potamotrygon schroederi	
Potamotrygon schuemacheri	
Potamotrygon scobina	
Potamotrygon signata	
Potamotrygon yepezi	
Plesiotrygon iwamae n.gen., n. sp.	

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APPENDIX A

MATERIAL EXAMINED

<u>Paratrygon</u> <u>aiereba</u>.- AMNH (one uncatalogued female specimen, currently housed at UMMZ), Departamento Beni, Bolivia; AMNH (one uncatalogued male specimen, currently housed at UMMZ), idem; FMNH 84092, Río San Alejandro, near Puerto Nuevo, Peru; INPA TOC-409, Itupiranga, Rio Tocantins, PA, Brasil; INPA (one uncatalogued male specimen), upper Rio Negro, AM, Brasil; INPA (one uncatalogued female specimen), idem; INPA (two uncatalogued female specimens), Rio Branco, RB, Brasil; IRSNB 1788, Ilha Verício, Boa Vista, Rio Branco, RB, Brasil; MCZ 297-S (syntype of <u>Disceus</u> <u>thayeri</u> by original indication), Manaus, AM, Brasil; MCZ 563-S (syntype of <u>Disceus</u> <u>thayeri</u> by original indication), Rio Pará, PA, Brasil; MZUSP 530 (one taxidermal female specimen), Rio Juruá, AM, Brasil; MZUSP 8286, Lago Parú, Oriximiná, PA, Brasil; MZUSP 8287, idem; MZUSP 10288, São Luís, Rio Tapajós, PA, Brasil; MZUSP 14772, Bagazan, Río Ucayali, Peru; MZUSP 14773, idem; MZUSP 14774, Ilha Xibeco, Rio Solimões, above mouth of Rio Jutaí, AM, Brasil; SOSC (one uncatalogued male specimen, currently housed at UMMZ), Isla San Rafael near Tucupita, Delta Amacuro, Venezuela; UFPB 1453, Souzel, Rio Xingú, PA, Brasil; UMMZ 204320 (one partially preserved female specimen), Río Itenez, 1 km above Costa Marques, RO, Brasil; UMMZ 204584, no locality data; UMMZ 204840 (two embryos and jaws of one adult female specimen), Río Baurer, Departamento Beni, Bolivia; UMMZ 204942-S (jaws of one male specimen), Río Itenez, 10 km SE of Costa Marques, Bolivia.

<u>Plesiotrygon</u> <u>iwamae</u> new genus, new species.- FMNH 94500 (paratype), Anaga, Río Napo, napo, Ecuador; MNRJ 573 (paratype), no locality data; MZUSP 10153 (holotype), Ilha Mari-Mari, Rio Solimões above Tefé, AM, Brasil; MZUSP 14789 (paratype), Lago Januacá, Rio Solimões, AM, Brasil; USNM 258289 (paratype), Tabatinga, Rio Solimões, AM, Brasil; ZMH 10343 (paratype), Rio Solimões, AM, Brasil.

<u>Potamotrygon</u> <u>brachyura</u>.- BMNH 1879.2.12.4 (neotype), Buenos Aires, Argentina; MACN (one uncatalogued female specimen), Río Paraná, Argentina; MFA 233, Río Paraná, Argentina; MFA 237, Río Colastiné Sur, Provincia de Santa Fe, Argentina; MFA 238, idem; MFA 239, idem; MFA 243, idem; MFA 244, idem; MFA 352, no locality data; MFA (one uncatalogued female specimen), no locality data; MZUSP 14819, Rio Cuiabá, Municípío de Poconé, MT, Brasil; ZVC 3108, Isla de Zapallo, Río Uruguay, Departamento Artigas, Uruguay.

<u>Potamotrygon</u> <u>castexi</u>.- ANSP 142482, Gomero, Río Manu below Boca Pinquen, Peru (12°11'S, 70°58'W); ANSP 142483, idem; ANSP 142484, tributary on SW bank of Río Manu, 7 km below Boca Pinquen, Peru (12°12'S, 70°59'W); ANSP 142486, Gomero, Río Manu below Boca Pinquen, Peru; ANSP 142487, tributary on SW bank of Río Manu, 7 km below Boca Pinquen, Peru; FMNH 84091, Río San Alejandro, near Puerto Nuevo, Río Pachitea drainage, Peru; FMNH 94289, Maciel, Río Guaporé, Bolivia; FMNH 94291, Huanaco, Quebrada San Alejandro, Río Pachitea drainage, Peru; LACM 39895-1 (tentatively identified), Río Yutupis, Shiringa, 1.8-2.0 km W-SW of La Poza, Amazonas, Peru; LACM 39934-1, idem; LACM 39935-2, Río Yutupis, headwaters, Amazonas, Peru. LACM 39942-1, Shiringa, Río Yutupis, Amazonas, Peru; LACM 41772-2, Río Santiago, small "quebrada" across from La Poza, Amazonas, Peru; MFA 288 (paratype), Río Colastiné Sur, Provincia de Santa Fe, Argentina; MZUSP 10151, Fonte Boa, Rio Solimões,

AM, Brasil; MZUSP 10152, idem; MZUSP 14848, Reserva de Taiamã (SEMA), Rio Paraguai, MT, Brasil; UFPB 1473 (formerly ZUEC 179), Rio Moa, Serra do Moa, AC, Brasil; UMMZ 204551, Río Itenez, 9 km SE of Costa Marques, RO, Brasil ($12^{\circ}32.4$'S, $64^{\circ}16.6$'W).

Potamotrygon constellata.- MCZ 291-S (syntype of Potamotrygon circularis by original indication), Tefé, Rio Solimões, AM, Brasil; MNHN A. 1005 (paralectotype), Calderão, AM, Brasil; MNHN A.1006 (paralectotype), idem; MNHN A.1010 (lectotype), idem; MNRJ 586, Manaus, AM, Brasil; MZUSP 14810, Lago Januacá, Rio Solimões, AM, Brasil.

Potamotrygon dumerilii.- MFA 267 (radiograph and jaws only), Río de Oro, near the confluence of Río Paraguay and Río Paraná, Provincia del Chaco, Argentina; MFA 268, Río Colastiné Sur, Provincia de Santa Fe, Argentina; MFA 328, Puerto de Santa Fe, Río Paraná, Provincia de Santa Fe, Argentina; MNHN 2367 (holotype), Rio Araguaia, Goiás or Pará, Brasil.

Potamotrygon falkneri.- BMNH 1895.5.11.276, Río Paraguay, Paraguay; BMNH 1895.5.11.277, idem; MACN 6475, Río Paraná, Provincia de Santa Fe, Argentina; MFA 235 (paratype), Paraná, Rio Paraná, Entre Ríos, Argentina; MFA 236 (holotype), idem; MFA 279, Río Colastiné Sur, Provincia de Santa Fe, Argentina; MFA 292, idem; MFA 342, idem; MFA 347, idem; MZUSP 14578, Fazenda Santo Antonio do Paraíso, Rio Piquiri, Itiquira, MT, Brasil; MZUSP 14812, Rio Cuiabá, Município Barão de Melgaço, MT, Brasil; UMMZ 206379 (three specimens), Río Paraná, S of Hohenau, Departamento Itapúa, Paraguay ($27^{\circ}12$'S, $55^{\circ}37$'W); ZMH 10339, Río Paraffia, Itapitapunta (questionable locality names), Paraguay.

Potamotrygon henlei.- INPA TOC-614, Rio Tocantins, PA, Brasil; INPA

TOC-725 (three specimens), Igarapé Canoal, Breu Branco, Rio Tocantins, PA, Brasil; MNHN 2353 (holotype), Rio Tocantins, PA, Brasil; MZUSP 14768, Marabá, Rio Itacaiúnas, PA, Brasil; UFPB 1454, Pedral, Rio Itacaiúnas, PA, Brasil; UFPB 1455 (two specimens), Tucuruí, Rio Tocantins, PA, Brasil.

Potamotrygon histrix.- BMNH 1872.6.8.1, Paraná, Río Paraná, Argentina; MACN 6141, Río Paraná, Provincia de Santa Fe, Argentina; MFA 300, Puerto de Santa Fe, Río Paraná, Provincia de Santa Fe, Argentina; MFA 312, idem; MFA 315, idem; MFA 317, Río Colastiné Sur, Provincia de Santa Fe, Argentina; MNHN 2443 (holotype), Buenos Aires, Argentina.

Potamotrygon humerosa.- CAS 48554 (five specimens), Santarém, Rio Tapajós, PA, Brasil; FMNH 94287 (two specimens), idem; MCZ 299-S (holotype), Monte Alegre, Rio Amazonas, PA, Brasil; MZUSP 3729, Belém, Rio Pará, PA, Brasil; MZUSP 5737, Santarém, Rio Tapajós, PA, Brasil; MZUSP 8472, Alter do Chão, Santarém, Rio Tapajós, PA, Brasil; MZUSP 14793, Rio Canumã, AM, Brasil; MZUSP 14794, idem; MZUSP 14795, idem; MZUSP 19198, Monte Cristo, Rio Tapajós, PA, Brasil; MZUSP 19199, idem; MZUSP 19200, idem; MZUSP 21824, Cachoeira Lombo de Anta, near São Luís, Rio Tapajós, PA, Brasil.

Potamotrygon leopoldi.- IRSNB 23936 (holotype), upper Rio Xingú, below the confluence of Rio Auaia-Missú, MT, Brasil; MZUSP (one uncatalogued female specimen), Rio Fresco, tributary of Rio Xingú, PA, Brasil.

Potamotrygon magdalenae.- ANSP 86871. Honda, Río Magdalena, Colombia; CAS 11560 (two specimens), Puerto del Río, Cienaga, Colombia; FMNH 59517, Río Sucio, Colombia, FMNH 75160 (radiograph only), Río Truando, Colombia; FSM (two uncatalogued specimens, currently housed at USNM), Río Salado, near Teresita, Choco, Colombia; MACN 5438 (formerly ILAFIR 119, five specimens), Río Magdalena, Colombia; MNHN 2368 (holotype), idem; SU 36844 (six embrionic specimens), Río Apulo and Río Truandó, Colombia; TBT 76-36, Río Magdalena, near San Cristobal, Colombia; TBT 76-37, idem; TBT 76-38, idem; TBT 76-39, idem; TBT 76-40, idem; TBT 76-41, idem; TBT 76-42, idem; TBT 76-51, idem; TBT 76-52, idem; TBT 76-53, idem; TBT 76-54, idem; TBT 76-56, idem; TBT 76-57, idem; TBT 76-59, idem; TBT 76-60, idem; TBT 76-61, idem; TBT 76-62, idem; TBT 76-63, idem; TBT 76-64, idem; TBT 76-65, idem; TBT 76-66, idem; TBT 76-67, idem; TBT 76-82, idem; TBT 76-83, idem; TBT 76-84, idem; TBT 76-85, idem; TBT 76-86, idem; TBT 76-91, idem; TBT 76-95, idem; USNM 1674, Turbo, Colombia.

Potamotrygon motoro.- AMNH (one uncatalogued male specimen, currently housed at UMMZ), no locality data; ANSP 119894, Leticia, Rio Amazonas, Colombia; ANSP 130565, Río Napo, Ecuador; BMNH 1892.12.29.2, Río Paraguay, Paraguay; BMNH 1934.9.12.1, Cuyuni River, Guyana; BMNH 1935. 6.4.4, Asunción, Paraguay; CAS 40400, Rio Amazonas, no further data; CAS 48551, idem; FMNH 93054, Descalvados, Rio Paraguai, MT, Brasil; FMNH 94288, Corumbá, Rio Paraguai, MS, Brasil; IUM 16139 (two specimens), Yarinacocha, Peru; LACM 42359-1, Lago Anacurucu, AM, Brasil; MACN 6124, Río Paraná, Provincia de Santa Fe, Argentina; MACN 7272, mouth of Río Paranay-Guazu, tributary of Río Paraná, Provincia de Misiones, Argentina; MACN (one uncatalogued male specimen, formerly ILAFIR 11), no locality data; MCZ 287-S, Codajás, AM, Brasil; MCZ 288-S, idem; MCZ 290-S (two specimens, syntypes of Potamotrygon laticeps by original indication), Tefé, AM, Brasil; MCZ 294-S, Rio Tocantins, PA, Brasil; MCZ 295-S (two specimens, syntypes of Potamotrygon circularis by original indication), Coari, Rio Solimões, AM, Brasil; MCZ 298-S, Lagoa do Máximo, Rio Amazonas, AM, Brasil; MCZ 604-S (two specimens), Lago Saraçá, Silves, Am, Brasil; MCZ 605-S (syntype of Potamotrygon laticeps by original indication), Óbidos, PA, Brasil; MCZ 607-S, Rio Içá, AM, Brasil; MCZ 608-S, Óbidos, PA, Brasil; MCZ 609-S, Rio Trombetas, PA, Brasil; MCZ 612-S (two specimens), Villa Bella (currently Parintins), AM, Brasil; MCZ 613-S, Lago Hyanuary, Rio Negro, AM, Brasil; MCZ 1446-S, Sete Lagoas, Rio das Velhas, MG, Brasil (questionable locality data); MCZ 46019, Cachoeira do Arari, Rio Arari, Ilha de Marajó, PA, Brasil; MCZ 52597, Paraná de Januacá, AM, Brasil; MCZ 52598, idem; MFA 232, Río Colastiné, Santa Fe, Argentina; MFA 245, idem; MFA 270, idem; MFA 276, idem; MFA 346, idem; MFA (one uncatalogued female specimen), no locality data; MNHN A-1003, Calderão, AM, Brasil; MNHN A-1004, idem; MNM 434, Paysandu, Río Uruguay, Uruguay; MNRJ 592, no locality data; MNRJ, Calderão, AM, Brasil; MNRJ 595, São Luis de Cáceres, Rio Paraguai, MT, Brasil; MNRJ 599, Estado do Amazonas, Brasil; MNRJ 10619, Fazenda Modelo do Aporema, Rio Aporema, AP, Brasil; MZUSP 6397, Lago Beruri, Rio Purus, AM, Brasil; MZUSP 13361, Porto Mendes, Rio Paraná, PR, Brasil; MZUSP 14767, Cametá, Rio Tocantins, PA, Brasil; MZUSP 14771, Río Ucayali, Peru; MZUSP 14776, São João, near Tupurucuara, AM, Brasil; MZUSP 14779, Monte Cristo, Rio Tapajós, PA, Brasil; MZUSP 14780, idem; MZUSP 14781, idem; MZUSP 14782, idem; MZUSP 14783, idem; MZUSP 14784, idem; MZUSP 14785, idem; MZUSP 14786, idem; MZUSP 14787, Jacaré, Rio Trombetas, PA, Brasil; MZUSP 14799, Igarapé Uruazinho, Vila Mariauatá, PA, Brasil; MZUSP 14801, Lago Januacá, Rio Solimões, AM, Brasil; MZUSP 14803, idem; MZUSP 14804, idem; MZUSP 14805, idem; MZUSP 14806, idem; MZUSP 14807, idem; MZUSP 14808, idem; MZUSP 14809, idem; MZUSP 19190, Fonte Boa, Rio Solimões, AM, Brasil; MZUSP 19191, idem; MZUSP 19196, Lago Grande, Rio Curuá de Alenquer, PA, Brasil; MZUSP (one uncatalogued female specimen), Rio Mearin, MA, Brasil; MZUSP (one uncatalogued female specimen), Rio Tapajós at mouth of Igarapé Boa Vista, ca. km 62 of BR-230, Parque Nacional da Amazonia, PA, Brasil; SU 64195, Yahnas Yacu, near Pebas, Peru; SU 68801, Sansho Caño, near Pebas, Peru; UFPB 1474 (formerly ZUEC 545), Volta Grande, Santo Antônio do Leverger, MT, Brasil; UMMZ 207766, Paso Horqueta, Río Aquidabanat, ca. 24 km NW of Loreto, Colombia; USNM 181696, Lago Ypacaray, near San Bernardino, Paraguay; USNM 153588 (formerly MCZ 301-S), Óbidos, PA, Brasil; USNM 167713, Yarinacocha, Río Ucayali, Pacaya, Loreto, Peru; ZMB 4662 (lectotype, only photograph examined), Cuiabá, MT, Brasil.

Potamotrygon cf. ocellata.- MNRJ 10620, Rio Pedreira, Macapá, AP, Brasil.

Potamotrygon orbignyi.- AMNH 20913, Belém, PA, Brasil; AMNH 20914, Kartabo, ca. 40 mi. SW of Georgetown, Guyana; AMNH 20915, idem; ANSP 103998, Caño Emma, Finca El Viento, 33.5 km NE of Puerto López, Río Meta, Meta, Colombia (04°08-9'N, 72°39'W); ANSP 134006, Caño Rico at Brasilia, Meta, Colombia (03°59'N, 73°08'W); ANSP 135812, Lago Mozambique, Meta, Colombia (03°58'N, 73°04'W); ANSP 135813, idem; ANSP 135814, idem; ANSP 135815, idem; ANSP 135816, Venturosa, near Puerto López, Meta, Colombia (04°05'N, 72°58'W); ANSP 135817, Lago Mozambique, Meta, Colombia (03°58'N, 73°04'W); BMNH 1870.3.10.1 (type of Trygon reticulatus), Surinam; BMNH 1926.3.2.1, Approuague River, French Guiana; BMNH 1926.3.2.2, idem; BMNH 1926.3.2.3, idem; CAS 42264, Playa Tama, Río Orinoco, Tama, Venezuela; FMNH 53271, Rockstone, Guyana; FMNH 69931 (five specimens), Río Cinaruco, Apure, Venezuela; FMNH 93506, Pará, Brasil; FMNH 94286, idem; IRSNB 17894, Vila Amazonia, Igarapé Murutaba, tributary of Rio Amazonas at Paraná Ramos, below Parintins, AM, Brasil; IUM 12101, Rockstone, Guyana; MCZ 304-S, Pará, Brasil; MNHN 2333 (holotype), Rio Tocantins, PA, Brasil; MZUSP 10281, Jatobal, Rio Tocantins, PA, Brasil; MZUSP 10282, Cachoeira Lombo de

Anta, near São Luís, Rio Tapajós, PA, Brasil; MZUSP 10283, Cachoeira do Maranhão, near São Luís, Rio Tapajós, PA, Brasil; MZUSP 10289, São Luís, Rio Tapajós, PA, Brasil; MZUSP 14769, Marabá, Rio Itacaiúnas, PA, Brasil; MZUSP 14770 (tentatively identified), Río Ucayali, Peru; MZUSP 14775, Jatobal, Rio Tocantins, PA, Brasil; MZUSP 14791, Rio Tocantins, marginal lake near Baião, PA, Brasil; MZUSP 19192, Rio Tocantins, marginal lake near Jatobal, PA, Brasil; MZUSP 25582, Rio Tapajós, at mouth of Igarapé Boa Vista, ca. km 62 of BR-230, Parque Nacional da Amazonia, PA, Brasil; RMNH 4258, Surinam; RMNH 26177 (three specimens), Tapoeripa Creek, N of Brokopondo, Surinam; RMNH 26181, Brokopondo Reserve, Surinam; RMNH 26182, Brokopondo, Surinam; SOSC (one uncatalogued female specimen, currently housed at UMMZ), Río Orinoco, near Curiapo, Delta Amacuro, Venezuela; SOSC (idem, idem), Río Orinoco, near Caño Paloma, Delta Amacuro, Venezuela; SSC (one uncatalogued male specimen), Río Tucupido, Portuguesa, Venezuela; SU 22062 (six specimens), Pará, Brasil; UMMZ 146244, El Sombrero, Río Guárico, Guárico, Venezuela; UMMZ (one uncatalogued female specimen), Essequibo River, Guyana; USNM 52557, Pará, Brasil; USNM 124925 (tentatively identified), Sansho Caño, near Pebas, Peru; USNM 257090, Río Orituco, Guárico, Venezuela; ZMH 11175, Rio Souve, Ilha de Marajó, PA, Brasil.

Potamotrygon schroederi.- BMNH 1893.4.24.42, Manaus, AM, Brasil; INPA (one uncatalogued male specimen), upper Rio Negro, AM, Brasil; MNRJ 3532 (three specimens), Uipiranga, Rio Negro, AM, Brasil; MZUSP 10290, vicinity of Manaus, Rio Negro, AM, Brasil; MZUSP 19209, Rio Negro, at mouth of Rio Cuieiras, above Manaus, AM, Brasil.

Potamotrygon schuemacheri.- MFA 269 (holotype), Río Colastiné Sur, Provincia de Santa Fe, Argentina; USNM 181767 (tentatively identified), Asunción, Río Paraguay, Paraguay.

Potamotrygon scobina.- AMNH 3883, Belém (at fish market), PA, Brasil; MCZ 602-S (holotype), Cametá, PA, Brasil; MZUSP 6607, Lago Manacapuru, AM, Brasil; MZUSP 14792, Reserva Biológica de Trombetas, Rio Trombetas, PA, Brasil.

Potamotrygon signata.- ANSP 69344, Ceará, Brasil (questionable locality data); MCZ 600-S (lectotype), São Gonçalo, Rio Parnaíba, PI, Brasil; MZUSP 19233 (tentatively identified), Rio Sambito, between São Felix and Santa Cruz dos Milagres, PI, Brasil; MZUSP 19234, Teresina, Rio Poti, PI, Brasil; USNM 153589 (paralectotype, formerly MCZ 560-S), Rio Poti, PI, Brasil.

Potamotrygon yepezi.- MCNG 775-1, Represa de Tulé, Maracaibo drainage, Zulia, Venezuela; MCNG 775-2, idem; MCNG 775-3, idem; MCNG 775-8, idem; MCNG 775-10, idem; MCNG 775-11, idem; MCNG 775-12, idem; MCNG 775-18, idem; MCNG 775-19, idem; MCNG 795-1, El Congo, mouth of Río Bravo, Lago de Maracaibo, Venezuela; MCNG 795-2, idem; TBT 77-70, Lago de Maracaibo, Venezuela; TBT 77-90, idem; TBT 78-44 (radiograph only), idem; TBT 78-94 (idem), idem; TBT 78-97 (idem), idem; TBT 78-98 (idem), idem; UFPB 1427 (two specimens, formerly TBT 77-7 and TBT 77-8), Lago de Maracaibo, Venezuela; UFPB 1428 (two specimens, formerly MBUCV V-14150), Ciénaga Gran Eneal, NW of Sinamaica, Zulia, Venezuela; USNM 121661, Río Agua Caliente, 2-3 km above Lago de Maracaibo, Venezuela; USNM 121662 (holotype), Río Palmar, at bridge 70 km SW of Maracaibo, Venezuela; USNM 121664 (paratype, currently housed at MACN), Lago Maracaibo, near the mouth of Río Concha, Venezuela; USNM 121666 (two specimens), Ciénaga del Guanavana, 10 km N of Sinamaica, Zulia, Venezuela; USNM 121668 (currently housed at MACN), Río Apon, 35 km S of Rosario, Zulia, Venezuela; USNM 205274 (two specimens), Río Palmar, at bridge 70 km SW of Maracaibo, Venezuela; USNM 205276 (three specimens), Río Mechango, at bridge S of Lagunillas, Maracaibo drainage, Venezuela; VIMS 06064 (two specimens), Lago de Maracaibo, Venezuela.

Potamotrygon sp. A.- ANSP 88601, Contamana, Rio Ucayali, Peru; ANSP 142481. Lago Tupuhumaro, NW of Puerto Maldonado, Madre de Dios, Peru (12°33'S, 69°13'W); ANSP 142488, idem; CAS 48552 (two specimens), Río Morona, Gosalina Cocha, Peru; CAS 48553, Iquitos, Río Amazonas, Loreto, Peru; MCZ 601-S, Óbidos, Rio Amazonas, PA, Brasil; MNHN A-1008 (two specimens), Calderão, AM, Brasil; SU 36844 (two specimens), vicinity of Pebas, Rio Amazonas, Loreto, Peru; UFPB 1475, Rio Juruá, Cruzeiro do Sul, Acre, Brasil.

Potamotrygon sp. B.- RMNH 26179, Brokopondo Reserve, Sipaliwini, Surinam; USNM 225216, stream about 0.5 km inland of Camp Mataway, Nickerie District, Surinam; USNM 225574 (three specimens), Matapi Creek, ca. 1 km from Corantijn River, Nickerie District, Surinam; USNM 225575, Corantijn River at km 180, Nickerie District, Surinam; USNM 226191, idem; USNM 226192 (three embryonic specimens), Matapi Creek, ca. 1 km from Corantijn River, Nickerie District, Surinam; USNM 226193 (two specimens), stream on south bank of Lucie River, ca. 6 km upstream of ferry crossing Amotopo-Camp Geol. Rd., Corantijn drainage, Nickerie District, Surinam.

Out-group Specimens

Dasyatis garouaensis.- TBT (one uncatalogued specimen), Benoue River, Nigeria.

Dasyatis guttata.- UFPB 0194, Cabedelo, PB, Brasil; UFPB 0578, Praia de Tibau, RN, Brasil.

Dasyatis sayi.- VIMS (two uncatalogued specimens), York River, VA, USA.

Gymnura micrura.- UFPB 1112, João Pessoa, PB, Brasil; UFPB 1466, idem.

Rhinobatus percellens.- UFPB 1469, João Pessoa, PB, Brasil; UFPB 1470, idem.

Taeniura lymma.- AMNH 44078, Cebu Island, Philippines.

Urolophus halleri.- TBT (two uncatalogued specimens), Coast Of California, USA.

Urolophus jamaicensis.- VIMS (one uncatalogued specimen), Coast of Florida, USA.

Urolophus maculatus.- CAS 36591, Baja California, S of Los Frailes, Mexico.

Urotrygon microphthalmum.- RMNH 24707, Surinam, NW of Piektschin; TBT 75-2, Coast of Venezuela; TBT 80-3, idem; UFPB 1230 (two specimens), João Pessoa, PB, Brasil; UFPB 1231 (two specimens), idem.

APPENDIX B

Further comment on the nomenclature of the freshwater stingray *Elipesurus spinicauda* Schomburgk, 1843 (Chondrichthyes: Potamotrygonidae)

Ricardo S. Rosa

Abstract

The monotypic genus *Elipesurus* of neotropical freshwater stingrays, and its type species *E. spinicauda*, are known from a single specimen which lacked a developed tail and caudal sting. No type or similar specimens exist. The original description and illustration are inaccurate, without diagnostic measurements or characters, excepting those mentioned above. Therefore, a precise identification of *E. spinicauda* remains impossible, and both names are considered doubtful. Since all other potamotrygonid stingrays have more or less developed tails and stings, the *Elipesurus* condition is regarded as a mutilation.

Introduction

The monotypic genus *Elipesurus* of South American freshwater stingrays was established by Schomburgk (1843). The type species, *E. spinicauda*, was based on a single and probably mutilated specimen from Rio Branco, Brazil (Garman, 1877, 1913; Vaillant, 1880; Eigenmann &

Eigenmann, 1891; Castex, 1964, 1968, 1969; Bailey, 1969). The generic and specific diagnoses were based on the presence of a very short tail, and the lack of the caudal sting normally found in other species of the family. Numerous spines were present at the base of the tail.

The specimen of E. spinicauda apparently was never sent to European museums, nor was found elsewhere. No type is known, and no similar specimens have been collected since the original description. Therefore, the generic and specific identities have remained uncertain (Castex, 1964, 1968). As explained below, Elipesurus and E. spinicauda are nomina dubia, and should be accordingly rejected.

Taxonomic history

Duméril (1865) emended Elipesurus to Ellipesurus, and was followed by Günther (1870), Eigenmann & Eigenmann (1891), and Ribeiro (1907). Garman (1913) improperly included Trygon strogylopterus Schomburgk, 1843 in the genus Elipesurus. Castex (1966) mistakenly considered E. spinicauda as a nomen oblitum. Castex (1968) proposed the suppression of the binomen for the purposes of the Law of Priority (relative to Potamotrygon Garman, 1877), and its placement in the Official Index of Rejected and Invalid Names in Zoology. Bailey (1969) reviewed these proposals and other items in Castex's paper, and concluded that E. spinicauda was a senior synonym of Disceus thayeri Garman, 1913. Two wrong statements by Castex (1968, statements 2 and 4) escaped Bailey's criticism: Paratrygon Duméril, 1865 was not a redescription of Elipesurus nor was based on Raja ajereba Walbaum, 1792; Elipesurus was firstly emended to Ellipesurus by Duméril (1865), and not by Günther (1870). Most of Bailey's arguments against the rejection of Elipesurus were effectively criticized in a reply by Castex (1969), but they deserve further comment.

1. Elipesurus spinicauda was not well illustrated and described. The short descriptive accounts of the genus and species were not sufficiently diagnostic, and disc length and width were the only measurements given. Schomburgk's illustrations were made in Europe from field sketches, and probably had errors in proportions and coloration (Eigenmann, 1912; Böhlke et al., 1978).

2. Elipesurus spinicauda is not equal to Disceus thayeri. Proportional measurements and other observations made by the present author on twenty-three specimens of D. thayeri, including the syntypes, differ substantially from the description of E. spinicauda. The crucial relative morphometrics are the preocular length and the eye diameter, which in Disceus are respectively larger and smaller than in Elipesurus. Small eyes, far removed from the snout, are not seen in the illustration of E. spinicauda, nor mentioned in its description. The color patterns of the two nominal species are also different from each other. All D. thayeri observed in this study, including freshly preserved specimens, were brown and not yellow, and lacked the reticulation seen in E. spinicauda. The presence of strong spines at the base of the tail is not decisive for synonymizing the two species, because specimens of D. thayeri may lack them, and because several species of the genus Potamotrygon may have these spines. The absence of an anterior median prominence on the disc, and the coverage of the pelvic fins by the disc, are similarly irrelevant. The former character is never greatly developed in any species of the family. Sometimes the prominence is missing or folded downward, and could be easily overlooked. Covered pelvic fins occur also in other species of the family, and vary depending on sex and conditions of fixation.

3. Discceus thayeri does not undergo notable changes in morphometrics and color with age. The tail and eyes are the only structures that show considerable allometry, the major diagnostic morphometrics being stable with growth. Slight variations of color are found in all ontogenetic stages, due to differences in pigment distribution.

4. The placement of T. strogylopterus in the synonymy of E. spinicauda is implausible, because the respective descriptions and illustrations do not correspond with respect to diagnostic characters, proportional measurements, and coloration.

5. I agree with Bailey in that T. strogylopterus is a synonym of D. thayeri. Some of the diagnostic characters of the latter species are represented in Schomburgk's illustration of T. strogylopterus. A spiracular prominence is present, the tail tapers abruptly behind the sting, and the coloration resembles that of D. thayeri. The synonymy of these two species was supported by Castex & Castello (1969), who rediscovered the type specimen of T. strogylopterus in Berlin, and concluded that it was identical with D. thayeri. Examination of a radiograph and photographs of this type specimen by the present author, corroborated this synonymy.

6. Potamotrygon brachyura (Günther, 1880) is presently unknown from the Amazon basin as Bailey (1969) remarked, therefore its synonymy with E. spinicauda, suggested by Castex (1968, 1969), is uncertain. Castex's (1966) statement that P. brachyura is found in the Amazon is doubtful, and probably based on misidentified specimens. Furthermore, the reticulations in the color pattern of P. brachyura are larger than those seen in the illustration of E. spinicauda. The Amazonian species Potamotrygon orbignyi (Castelnau, 1855) and P. humerosa (Garman, 1913) have reticulate

patterns similar to E. spinicauda, but this character alone is insufficient for their synonymization.

Referring to Castex's (1969) reply, I agree with objections (1) to (6), and partially with (9) and (10). The difference in the color patterns (9) of E. spinicauda and P. brachyura was already mentioned. From the position of the eyes (10) seen in Schomburgk's illustrations, E. spinicauda is clearly different from D. thayeri, but T. strogylopterus has an intermediate condition between Disceus and Potamotrygon. Comment (7) is false because a cut-off tail normally assumes a blunt end, and not the pointed condition seen in the illustration of E. spinicauda, where it was probably misrepresented. Tail denticles and spines usually tend to increased development in cut-off tails.

Discussion

Garman's (1913) placement of T. strogylopterus in the genus Elipesurus was inadequate, because that species had the caudal sting and spiracular process, contradicting the diagnostic characters of Elipesurus (see Garman's key to the genera). Garman himself considered questionable his identification of T. strogylopterus, and added that the species could even belong to the genus Disceus, as he originally had proposed in 1877. When Garman (1913) redescribed D. strogylopterus, presumably as the new species D. thayeri, he needed a new generic placement for T. strogylopterus. The latter species was clearly distinct from all Potamotrygon, therefore the only possible combination was with Elipesurus, since Garman did not recognize Paratrygon as a valid genus. Regarding E. spinicauda, Garman (1913) pointed that it had large eyes anteriorly positioned, and therefore differed from Disceus, where the opposite states of these characters are found, and represent important diagnostic features.

Several authors (Vaillant, 1880; Eigenmann & Eigenmann, 1891; Garman, 1913; Devicenzi & Teague, 1942; Castex, 1964, 1968, 1969) regarded E. spinicauda as a doubtful or provisional name. Among recent authors, only Ribeiro (1907), Fowler (1948, 1970), and Bailey (1969) considered Elipesurus valid, each one with a different taxonomic connotation. The tentative identifications of E. spinicauda from the original description (Ribeiro, 1907; Garman, 1913; Castex, 1964, 1968, 1969) resulted in a confusing synonymy, including Potamotrygon dumerilii, P. motoro, P. brachyura, and Disceus thayeri. The description and illustration of E. spinicauda do not contain enough diagnostic characters to permit its association with any of these species, nor with any other species of the family Potamotrygonidae. Therefore, the name should not be used to imply D. thayeri and its synonyms, nor any of the species of the genus Potamotrygon.

Adult specimens of Potamotrygonidae usually lack the distal portions of their tails, and sometimes lack the caudal sting. The various explanations for this fact include serrasalmid fish bites and human action. Schomburgk himself mentioned that the indians used to cut off stingray tails, to obtain the stings which they used as arrow heads. An accidental or teratological loss of the tail and sting is the most plausible explanation for the absence of these structures in the specimen of E. spinicauda. Therefore, it is not reasonable to consider valid a genus and species established to include stingrays lacking developed tails and caudal stings.

Conclusions

Elipesurus was unwarrantably established for a teratologic or mutilated specimen, by a poor description and a probably inaccurate illustration, without type designation. Elipesurus, its emendation Ellipesurus, and the binomen E. spinicauda are herein considered nomina dubia. Therefore, the question of priority is moot, and these names do not require suppression, as requested by Castex (1968, request 1). The International Commission on Zoological Nomenclature should support all the other requests of Castex (1968, requests 2 to 6), with the correction of the gender of Potamotrygon in request (2) as suggested by Bailey (1969), the observation that the spelling Trygon histrix Müller & Henle in: d'Orbigny, 1834 has priority over Trygon hystrix Müller & Henle, 1841 in request (2), and the correction of the publication date of Potamotrygon and Potamotrygonidae (1877 instead of 1878) in request (6).

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APPENDIX C

Paratrygon aiereba (Müller & Henle, 1841): a senior synonym of the freshwater stingray *Disceus thayeri* Garman, 1913 (Chondrichthyes: Potamotrygonidae)

Ricardo S. Rosa

Abstract

A comparative review of the original descriptions and available types of the freshwater stingrays *Trygon aiereba* Müller & Henle, 1841, *Trygon strogylopterus* Schomburgk, 1843, and *Disceus thayeri* Garman, 1913 indicated that these three nominal species are synonyms. The senior name, placed in the monotypic genus *Paratrygon* Duméril, 1865, established for *T. aiereba*, is available and valid.

The description of *T. aiereba* clearly corresponds with a freshwater stingray, therefore this species is not a synonym of *Raja ajereba* Walbaum and *Raja orbicularis* Schneider, both names established for the marine "Aiereba" of Marcgrave, and herein considered *nomina dubia*.

Paratrygon does not replace *Potamotrygon* Garman, 1877 as the type genus, because the family name Potamotrygonidae Garman, 1877 has priority over Paratrygonidae Gill, 1893.

Introduction

The family Potamotrygonidae (Garman, 1877) has consisted of the monotypic genus Disceus Garman, 1877, and the polytypic Potamotrygon Garman, 1877. However, when Garman erected the family, two other nominal genera had already been used: Elipesurus Schomburgk, 1843, and Paratrygon Duméril, 1865. Elipesurus, known only from the poor original description of a mutilated specimen, was considered provisional or doubtful by several authors (Eigenmann and Eigenmann, 1891; Garman, 1913; Castex, 1964, 1968; Rosa, in press). Paratrygon, established for Trygon aiereba Müller & Henle, 1841, was synonymized with Disceus by Jordan (1887).

A review of the original description of Paratrygon aiereba (Müller & Henle), and its comparison with Trygon strogylopterus Schomburgk, and the more usually recognized junior synonym Disceus thayeri Garman, corroborates the generic synonymy proposed by Jordan (1887), and indicates that P. aiereba is the senior synonym of the other two nominal species. This paper is a contribution to revisionary studies on the taxonomy of Potamotrygonidae.

Methods and Materials

Measurements taken were limited to those cited by Müller and Henle (1841). Measurements under 150 mm were taken to the nearest tenth of millimeter, with dial calipers; measurements over 150 mm were taken to the nearest millimeter. The German "Zoll" used in Müller and Henle's measurements was converted to 26.15 mm. Measurements of the type of T. strogylopterus were taken on photographs and radiograph.

"Aiereba" is used in this paper to refer to vernacular citations (non-binominal) of the pre-Linnaean name Aiereba (or Ajereba) of Marcgrave. Institutional abbreviations are: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; FMNH, Field Museum of Natural History; INPA, Instituto Nacional de Pesquisas da Amazônia; IRSNB, Institut Royal des Sciences Naturelles de Belgique; LACM, Natural History Museum of Los Angeles County; MCZ, Museum of Comparative Zoology; MZUSP, Museu de Zoologia da Universidade de São Paulo; SOSC, Oceanographic Sorting Center, Smithsonian Institution; UMMZ, University of Michigan Museum of Zoology; USNM, U. S. National Museum of Natural History; ZMB, Zoologisches Museum der Hümboldt-Universität, Berlin.

Material examined.- _Paratrygon aiereba_, 22 specimens (121-738 mm in disc length, DL): AMNH (2 uncatalogued specimens housed in UMMZ); FMNH 84092; INPA TOC-409; INPA (4 uncatalogued specimens); IRSNB 17884; MCZ 297-S (syntype of _D. thayeri_); MCZ 563-S (idem); MZUSP 8286; MZUSP 8287; MZUSP 10288; MZUSP 14772; MZUSP 14773; MZUSP 14774; SOSC (1 uncatalogued specimen housed in UMMZ); UMMZ 204320; UMMZ 204584; UMMZ 204840; ZMB 4632 (type of _T. strogylopterus_, photographs and radiograph only). _Potamotrygon castexi_, 5 specimens (226-538 mm DL): ANSP 142484; ANSP 142486; LACM 39934-1; LACM 41722-2; MZUSP 10152. _Potamotrygon magdalenae_, 3 specimens (134-254 mm DL): USNM 1674; USNM (2 uncatalogued specimens). _Potamotrygon orbignyi_, 7 specimens (110-317 mm DL): ANSP 103998; ANSP 134006; FMNH 53271; MZUSP 14769; MZUSP 14775; MZUSP 14791; MZUSP 19192. _Potamotrygon schroederi_, 2 specimens (206-231 mm DL): MZUSP 10290; MZUSP 19209. _Potamotrygon yepezi_, 4 specimens (136-159 mm DL): USNM 121666;

USNM 205276 (3 specimens).

Paratrygon Duméril

Paratrygon.- Duméril, 1865: 594 [type species Trygon aiereba Müller & Henle, 1841 (non-Marcgrave) by monotypy. Not Trygon Cuvier, 1816 = Dasyatis Rafinesque, 1809].

Disceus.- Garman, 1877: 208 (type species Trygon strogylopterus Schomburgk, 1843 by monotypy).

Paratrygon aiereba (Müller & Henle)

Trygon aiereba.- Müller and Henle, 1841: 196 (not 160, non-Marcrave), (original description, Brasil; type lost, originally deposited in München Zoologisches Museum).

Trygon strogylopterus.- Scomburgk, 1843: 183, plate 22 (original description, Rio Branco, Brasil).

Disceus strongylopterus.- Garman, 1877: 208 (redescription of Trygon strogylopterus, with lapsus calami).

Disceus thayeri.- Garman, 1913: 426 (new name for Disceus strogylopterus; three syntypes, Thayer Expedition, Óbidos, Manaus, and Pará, Brasil).

Remarks.- Raja ajereba Walbaum, 1792, and Raja orbicularis Schneider, 1801 are nomina dubia for a marine taxon based on the original description of "Aiereba" Marcgrave, which cannot be properly identified.

Taxonomic History

"Aiereba" (Marcgrave, 1648) is the earliest name and description of a South American stingray. This name was considered doubtful (Walbaum, 1792; Müller and Henle, 1841; Garman, 1913; Castex, 1964), because the imprecise description precluded its identification even at the familial level (Castex and Castello, 1969). The original illustration probably did not correspond with Marcgrave's specimen, because it lacked the two caudal stings mentioned by the author, and because the illustration had previously been used by Laet (1640), the editor of Marcgrave's book, for a marine batoid that he called "Paraque" (Whitehead, 1979a). The same print, with modifications of the tail, appeared as a freshwater stingray from the Rio Paraná drainage (Dobrizhoffer, 1822). The original oil painting ("Ajereba" MSS in Theatri rerum naturalium Brasiliae, Vol. 1: 29), which served as a model for the published woodcut illustration, similarly lacked the caudal stings and diagnostic details. The "Aiereba" probably was a marine dasyatid stingray, because the freshwater Potamotrygonidae are absent from the area sampled by Marcgrave and other Dutch naturalists. Marcgrave visited Salvador, possibly in March 1638 (Whitehead, 1979b). He also visited Fort Maurits (Penedo) at the São Francisco River, possibly in May 1639 (see Marcgrave, 1648: 204). There is no exact reference to his travels to the north of Recife, but he probably went as far as Rio Grande do Norte, as shown by the map based on his topographical work (Barlaeus, 1647). Marcgrave's longest journey took one month and nine days, round trip from Recife, with a party of 415 men. It is almost certain that they never reached the lower Amazon drainage, the eastern limit of the distribution of _Paratrygon_. Furthermore, there is no mention in the Historia Naturalis Brasiliae that Marcgrave visited the Amazon River.

The marine origin of "Aiereba", though not cited by Marcgrave, was inferred by Schneider (1801), who based _Raja orbicularis_ on "Aiereba", and cited its habitat as the same for Raja guttata ("...Americae australis, maria..."). Ribeiro (1907), and Ihering (1940) considered R. orbicularis (and consequently "Aiereba") as a marine Dasyatis from the Brazilian Atlantic coast. Marcgrave's specimen of "Aiereba" was never found, and the tentative identifications based on the original description (Martius, 1867; Ribeiro, 1907; Garman, 1913; Carvalho and Sawaya, 1942; Fowler, 1948) resulted in an extensive synonymy, including Trygon aiereba Müller & Henle, Raja ajereba Walbaum, Raja orbicularis Schneider, and Disceus thayeri Garman.

Müller and Henle (1841) described Trygon aiereba, which was not merely a binomial repetition of "Aiereba" Marcgrave, as were Aiereba brasiliensibus Jonston, 1649 (also Willughby, 1686; Jonston, 1718), Raja ajereba Walbaum, 1792, and Raja orbicularis Schneider, 1801, but was based on a new specimen from Brazil. Müller and Henle's type was redescribed with slightly different measurements by Duméril (1865), who established the subgenus Paratrygon for the species. Günther (1870) used Paratrygon in the generic level, by including P. aiereba in the synonymy of Trygon orbicularis (Schneider). Müller and Henle's type was lost in Munich, probably destroyed in World War II (Castex and Castello, 1969; F. Terofal, pers. comm.).

Garman (1877) established the new genus Disceus for T. strogylopterus Schomburgk, 1843. The identity of T. aiereba and T. strogylopterus, previously suggested by Müller and Troschel (1848), was denoted by the inclusion of the former species in Garman's synonymy of D. strogylopterus. Garman (1913) redescribed D. strogylopterus, and changed the specific name to D. thayeri (Figs. 1 and 2). Trygon strogylopterus was removed from the synonymy, but T. aiereba was retained as a possible synonym.

Jordan (1887), Eigenmann and Eigenmann (1891), and Eigenmann (1910,

1912) considered Paratrygon as a senior synonym of Disceus. Eigenmann (1912) mistakenly named R. orbicularis as the type species of Paratrygon, due to nomenclatural confusion in previous synonymies. Paratrygon was originally established with the single species T. aiereba (type species by monotypy). The name D. thayeri was used commonly after 1913, until more synonyms were suggested. Bertin (1939) and Fowler (1948) mistakenly synonymized Paratrygon and Potamotrygon. Fowler (1948, 1970) and Castex (1968) mistakenly selected the marine R. ajereba as the type species of Paratrygon. Bailey (1969) stated that Elipesurus spinicauda and T. strogylopterus were senior synonyms of D. thayeri, and chose the former name as valid for the species. Castex and Castello (1969) stated that the original description of T. strogylopterus lacked differential characters and "systematical value", but considered this species as a senior synonym of D. thayeri, by identifying Schomburgk's type specimen (Figs. 3 and 4) with Garman's syntypes. They also synonymized T. strogylopterus with T. aiereba, but chose D. strogylopterus (Schomburgk) as the valid name for the species.

Discussion

The identity of T. strogylopterus and D. thayeri is irrelevant to the solution of the nomenclatural problem, because T. aiereba Müller & Henle, 1841, placed in the genus Paratrygon, is a senior synonym of both nominal species. The original description of T. aiereba contains most of the characters for the species usually known as D. thayeri, including the large knob-shaped appendix projecting into the posterior rim of the spiracles ("Am hintern Rande des Spritzlochs befindet sich ein ungemein grosser zapfenartiger Vorsprung, in das Spritzlochsragend"); teeth flat, few in number ("Zähne wenig zahlreich, plat"); very small eyes ("Augen ausserordentlich klein"); buccal papillae lacking ("Zapfen im Munde wurden nicht wahrgenommen") or minute. The measurements given for the type are similarly diagnostic, and when compared with morphometrics of *Potamotrygon* and *Disceus* (Table 1), are much closer to the latter. Diagnostic morphometrics are the relative distance from mouth to scapulocoracoid cartilage, and the relative preocular, preoral, and prenarial lengths (Fig. 5), which show the highest significant differences between these two genera. The agreement of diagnostic character states and morphometrics demonstrates the synonymy of *P. aiereba* and *D. thayeri*. Moreover, nothing in Müller and Henle's description precludes such a synonymy.

The pre-Linnaean name "Aiereba" of Marcgrave has no status in nomenclature, therefore its mention in the original synonymy of *P. aiereba*, as well as its other post-Linnaean vernacular citations (Walbaum, 1792; Cuvier, 1816) do not prevent the availability of the specific name *aiereba* in *Trygon aiereba* Müller & Henle, where it was first binominally used for a freshwater batoid. Variable spelling of "Aiereba" ("Ajereba" MSS in the Theatri; *Aereba* in Willughby, 1686, pl. 12) was found since Marcgrave's manuscripts. Walbaum (1792: 533-535) used both "Aiereba" and *R. ajereba*. When Müller and Henle described *T. aiereba*, its specific name was not in competition with *ajereba* (in *R. ajereba* Walbaum), because they had different generic placements. The former was used for a freshwater stingray, and the latter referred to a marine species, the "Aiereba" of Marcgrave. The selection of *R. ajereba* as the type species of *Paratrygon* (Fowler, 1948, 1970; Castex, 1968) is erroneous because this nominal species was not cited when the generic name was established.

The citations of *R. ajereba* in the genus *Paratrygon* should not be considered homonymous with *P. aiereba* under the provisions of the International Code of Zoological Nomenclature (ICZN, article 58), although they eventually will be treated as homonyms in the new code in preparation (P. J. P. Whitehead and R. V. Melville, pers. comm.). Even with the new rules in effect, the secondary homonym *Paratrygon ajereba* (Fowler, 1948, 1970), being a misidentification of a marine batoid as a freshwater species, could not be maintained in nomenclature (see ICZN, article 49).

Conclusions

The "Aiereba" Marcgrave (1648) and its vernacular repetitions (Marcgrave, 1658; Walbaum, 1792; Cuvier, 1816) have no taxonomic status. The taxa based on its original description (*Aiereba brasiliensibus*, *Raja ajereba*, and *Raja orbicularis*) are herein considered *nomina dubia*.

Paratrygon Duméril, 1865 is the senior synonym of *Disceus* Garman, 1877. *Paratrygon* was established for the freshwater stingray *Trygon* aiereba Müller & Henle, not for *Raja ajereba* Walbaum, as erroneously stated by Castex (1968), nor for "Aiereba" of Marcgrave, as misinterpreted by Bailey (1969).

The review of the original description of *Trygon aiereba* showed that it clearly applied to a freshwater stingray, but not to any known marine batoid species. *Trygon aiereba* is not a junior synonym nor a primary homonym of *Raja ajereba*, and the latter species, being a marine batoid, should not be cited in the genus *Paratrygon*. *Paratrygon aiereba* (Müller & Henle, 1841) is the senior synonym of *Trygon strogylopterus* Schomburgk, 1843 (= *T. strogyloptera* sensu Günther, 1870), of *Disceus strogylopterus* (Schomburgk, 1843), and of *Disceus thayeri* Garman, 1913.

Therefore, it is the valid name for the taxon associated with these nominal species.

Potamotrygon should be maintained as the type genus, because the family name Potamotrygonidae Garman, 1877 has priority over Paratrygonidae Gill, 1893.

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Resumo

A revisão comparativa das descrições originais e dos espécimes-tipo disponíveis para as raias de água doce *Trygon aiereba* Müller & Henle, 1841, *Trygon strogylopterus* Schomburgk, 1843, e *Disceus thayeri* Garman, 1913 indicou que estas três espécies nominais são sinônimas. O nome mais antigo, citado no gênero *Paratrygon* estabelecido por Duméril, 1865 para *Trygon aiereba*, é considerado disponível, e válido para a espécie pelo princípio de prioridade.

Dois fatores contribuiram para aumentar a complexidade relativa ao problema de nomenclatura. O primeiro deles foi o uso do nome específico *aiereba* por Müller e Henle, inicialmente referido por eles à "Aiereba" de Marcgrave, e assim interpretado pela maioria dos autores subsequentes. O segundo fator foi a utilização do binômio *Paratrygon ajereba* por Fowler, 1948 para a espécie *Raja ajereba* Walbaum, o que criou uma potencial homonímia com a espécie de Müller e Henle.

A "Aiereba" de Marcgrave era provavelmente uma raia marinha do gênero *Dasyatis*, já que este naturalista visitou apenas a costa nordeste do Brasil, de onde está ausente a família Potamotrygonidae. O nome "Aiereba", sendo pré-Linneano, não tem efeito na nomenclatura zoológica, mesmo quando citado em sinonímias. O primeiro binômio pós-Linneano estabelecido para a "Aiereba" foi *Raja ajereba* Walbaum. A utilização do nome específico *aiereba* em *Trygon aiereba* não constituíu homonímia primária com *Raja ajereba*, sendo portanto válida. A referência inicial à "Aiereba" feita por Müller e Henle também não invalida a espécie *Trygon aiereba*, uma vez que fica perfeitamente claro por sua descrição original, que não

se trata de um sinônimo de Raja ajereba, e sim de uma espécie de água doce. A citação de Fowler, 1948, de Raja ajereba no gênero Paratrygon não pode ser mantida na nomenclatura zoológica, pois trata-se da identificação errônea de uma espécie marinha como representante da família Potamotrygonidae. Os binômios Raja ajereba e Raja orbicularis Schneider, 1801, ambos baseados apenas na pobre descrição original da "Aiereba" de Marcgrave, são considerados nomina dubia.

O gênero Paratrygon não substitui Potamotrygon como gênero-tipo, pois o nome da família Potamotrygonidae Garman, 1877 é prioritário sobre Paratrygonidae Gill, 1893.

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VITA

<u>Ricardo de Souza Rosa</u>

Son of David de Souza Rosa and Refcá Canetti Rosa, born in Porto Alegre, Rio Grande do Sul, Brazil, April 21, 1954. Graduated from Instituto de Educação Ministro Costa Manso (high school), São Paulo, December 1971; from Instituto de Biociências, Universidade de São Paulo (B.A. in Zoology), June 1976. Visiting student at the Fish Division of Museu de Zoologia, Universidade de São Paulo, 1973 to 1977. Visiting scientist at Instituto de Pesquisas da Marinha, Cabo Frio, May to July 1977. Assistant professor at Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, from August 1977 to the present date.

Started graduate studies at the School of Marine Science, College of William and Mary, in August 1979. By-passed the Masters Degree in December 1981. The author is married to Ierecê de Lucena Rosa, and they have one daughter, Carolina.