THE SYSTEMATICS OF THE STINGRAY GENUS UROTRYGON WITH COMMENTS ON THE INTERRELATIONSHIPS WITHIN UROLOPHIDAE (CHONDRICHTHYES, MYLIOBATIFORMES)

Volume I

A Dissertation

by

TSUTOMU MIYAKE

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ABSTRACT

The Systematics of the Stingray Genus Urotrygon with Comments on the Interrelationships within Urolophidae (Chondrichthyes, Myliobatiformes). (August 1988).

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The species of the stingray genus Urotrygon were investigated to elucidate the species composition and to clarify the systematic status of the nomical genera Urotrygon and Urolophus (Urolophidae) within Myliobatiformes. Specimens of all nominal species were compared morphometrically by Principal Component Analysis, meristically by univariate analysis and according to their pattern of squamation. These analyses suggested that there are ten valid species of Urotrygon: Urotrygon daviesi, U. microphthalmum, U. venezuelae, U. munda, U. sp (1), U. sp (2), U. rogersi, U. chilensis, U. sp (3) and U. aspidura. Urotrygon binghami is considered a junior synonym of U. rogersi. Urotrygon asterias, U. serrula, U. peruana, U. caudispinosa and U. goodei are considered synonyms of U. chilensis.

The anatomical comparisons of morphological characters, i.e., cranial and visceral skeleton, cranial and visceral musculature, cranial nervous and vascular systems, pectoral and pelvic girdles and clasper skeleton, were made among most of the nominal genera of batoid fishes (sawfishes, guitarfishes, skates, electric rays and stingrays) to elucidate the systematic status of Urotrygon and Urolophus within

Myliobatiformes. The following conclusions can be drawn from the present study:

1) Urotrygon daviesi should be removed from the genus Urotrygon and regarded as incertae sedis within Myliobatiformes. The characters which distinguish U. daviesi from the remaining species of Urotrygon represent either primitive character states, homoplastic character states or character states of unknown polarity.

2) Urotrygon excluding U. daviesi is defined by one synapomorphy, the presence of the γ-cartilage closely associated with the β-cartilage.

3) Amphi-American Urolophus are provisionally considered monophyletic, distinct from the Australian-western Pacific Urolophus, and the genus Urobatis is resurrected for them. Urobatis and Urotrygon except U. daviesi possess one putative synapomorphy, an embryonic spiracular fold.

4) Australian-western Pacific Urolophus possess one putative synapomorphy, the presence of a large foramen for the n. opticus.

5). There are no known synapomorphies shared by the three nominal genera of Urolophidae, Urobatis, Urolophus and Urotrygon, and thus the systematic status of Urolophidae remains uncertain. The phylogenetic hypothesis of Brooks et al (1981), which consider Urolophus the sister group of the freshwater stingrays, is not supported by shared derived character states.

DEDICATION

This work is dedicated to my parents and two sisters and Drs. John D. McEachran, Teruya Uyeno and Katsuzo Kuronuma, for their patience, support and encouragement throughout the course of this endeavor.

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INTRODUCTION

Myliobatiformes (stingrays) are generally considered the most derived of the Batoidea (sawfishes, guitarfishes, skates, electric rays and stingrays). The order is composed of seven families and 145 to 149 species (Compagno, 1973; McEachran, 1982a). They occur worldwide in temperate to tropical waters. Most species are benthic and confined to the continental shelf waters, but others are epipelagic, or enter brackish, or are permanent residents in freshwater (Bigelow and Schroeder, 1953; Thorson et al., 1983). Freshwater stingrays are known from the deposits of the Late Cretaceous Lauce Formation, Paleocene Tongue River Formation and Middle Eocene Fossil Lake in North America (Grande, 1984; Cavender, 1986).

Urolophidae, the second largest taxon within Myliobatiformes, have long been placed in Dasyatididae (Garman, 1913; White, 1937; Beebe and Tee-Van, 1941). However, Whitley (1940) erected Urolophidae for the species with a caudal fin supported by cartilaginous radials. Bigelow and Schroeder (1953) added another character, weak indentation of the antero-medial margin of the neurocranium. Compagno (1973) followed Bigelow and Schroeder in recognizing this family and placed it within the superfamily Dasyatoidea as the most primitive of the stingrays.

Presently, Urolophidae include two recognized genera, Urolophus Müller and Henle (1841) and Urotrygon Gill (1863) although distinction

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between two genera is equivocal. The genus Trygonoptera Müller and Henle (1841) are generally placed in synonymy with Urolophus (McKay, 1966; Scott et al., 1974; Chirichigno and McEachran, 1979).

Garman (1913) established the genus Urobatis for the amphi-American species of Urolophus which are distict from the Australian-western Pacific Urolophus in having a more circular disc and longer blunt tail. Most recent authors, however, synonymized Urobatis with Urolophus (Bigelow and Schroeder, 1953; Chirichigno and McEachran, 1979).

Much confusion exsits as to the validity of the nominal species of Urotrygon because of the paucity of material on which the original descriptions were based and of brevity and inconsistencies of the descriptions. To date no one has attempted a thorough revision of the genus.

Gill (1863) described Urotrygon munda from Panama Bay and established the new genus Urotrygon distinct from Urolophus. Urolophus chilensis was described from one adolescent specimen from Chile and characterized by the presence of three thorns on midline of the disc (Günther, 1871). Jordan and Gilbert (1881) reported a new species, Urolophus aspidurus, from the Bay of Panama along with several specimens identified as Urolophus mundus. The latter specimens along with some taken from Mazatlan, Mexico, were later described as Urolophus asterias (Jordan and Gilbert, 1882). Jordan and Bollman (1889) described Urolophus goodei based on one juvenile specimen from Panama. Jordan and Starks (1895) described Urolophus rogersi from Mazatlan and distinguished it from U. asterias by its

shape and denticle pattern of the disc. Jordan and Evermann (1896) listed the above described species under the genus Urolophus.

In the first decade of the twentieth century, a number of faunal studies reported on the species of Urotrygon from the eastern Pacific Ocean. In 1904, Gilbert and Starks recorded Urolophus aspidurus, U. mundus and U. goodei from Panama Bay. They synonymized Urolophus asterias with U. mundus because of differences in the position of tail spine and pattern of denticles on the disc. Kendall and Radcliffe (1912) reported Urolophus aspidurus and U. rogersi from Panama and noted that the specimen of the latter species has five thorns on the midline of the disc and three smaller ones on the tail. Osburn and Nichols (1916) reported Urolophus mundus in the Lower California.

Garman (1913) was the first to reaffirm the distinctness of Urotrygon Gill from Urolophus Müller and Henle, stating that Urotrygon has a more circular disc, longer tail and more pointed caudal fin than Urolophus. He included Urotrygon munda, U. chilensis, U. aspidura and U. goodei in the former genus. However, he treated Urotrygon asterias and U. rogersi as synonymies of U. munda. Most subsequent studies neither referred to type material nor examined the variation of characters such as patterns of denticles and thorns within and among these species.

Meek and Hildebrand (1923) reported Urotrygon asterias and U. aspidura from Panama. They resurrected U. asterias from U. munda based on the differences of denticles on the disc. Breder (1926) described Urotrygon binghami from one juvenile specimen from the Gulf of California. Kumada and Hiyama (1937) reported two species of Urotrygon as Urolophus asterias and U. sp. from Mexico.

Several check lists of the fishes of the eastern Pacific Ocean that treated the species of Urotrygon were published around the 1930s. Ulrey (1929) included only Urotrygon munda in his list of the fishes of the Southern and Lower Baja California. Jordan et al. (1930) listed Urotrygon munda, U. goodei and U. aspidura, and followed Garman (1913) in synonymizing U. asterias and U. rogersi with U. munda. Fowler (1930) listed all of the nominal species of Urotrygon except for U. chilensis and U. asterias in his check list of the elasmobranch fishes of the Pacific Ocean. Urotrygon binghami was the only species that Terron (1930) included in his list of the fishes in the Gulf of California.

Beebe and Tee-Van (1941) summarized the knowledge of the species of Urotrygon largely through a review of the literature. They recognized all the described species except for Urotrygon rogersi which they synonymized with U. asterias. Their lists of synonymies clarified some of the taxonomic confusion within Urotrygon, but the lack of adequate specimens precluded them from evaluating the validity of the species.

Delsman (1941) described the first species of Urotrygon (U. microphthalmum) from the Atlantic Ocean, from off the mouth of Amazon River. The species was distinguished from all the known species in having slender tail and relatively small eyes. Schultz (1949) described another Atlantic species, Urotrygon venezuelae, from the Gulf of Venezuela. The species was characterized by having enlarged denticles on the midline of disc and tail. Hildebrand (1946) described three species, U. serrula, U. peruana and U. caudispinosa from off the coast of Peru based on one juvenile or adolescent

specimen each. Urotrygon serrula was described from Tierra Bays and was distinguished by lacking denticles. Urotrygon caudispinosa, from Independecia Bay, was considered to resemble U. goodei in having a few denticles on the snout and midline of dorsal disc. Urotrygon peruana, from Paita Bay, was characterized by having a tail shorter than disc length, pointed caudal fin and a few denticles on the snout. Hildebrand's descriptions caused further taxonomic instability because he did not compare his specimens with comparable material of the other nominal species.

Bigelow and Schroeder (1953) reaffirmed the generic differences between Urotrygon and Urolophus and gave detailed descriptions of Urotrygon microphthalmum and U. venezuelae. However, because their study was limited to the western North Atlantic, taxonomic problems within Urotrygon in the eastern Pacific remained to be solved. Urotrygon microphthalmum was further reported from off the east coast of Venezuela and the mouth of Amazon River (Bigelow and Schroeder, 1962). Boeseman (1963) and Cervigon (1966) recorded Urotrygon microphthalmum from off the outlets of Surinam River and off the coast of Venezuela, respectively.

Koepcke (1959) reported Urotrygon peruana and U. caudispinosa from off Peru. In 1962, he listed these species from Peru and treated Urotrygon goodei as the subspecies of U. caudispinosus. Chirichigno (1963) reported the capture of Urotrygon munda, U. asterias, U. aspidura and U. goodei from off Peru. In 1974, Chirichigno confirmed the occurrence of all the described species of Urotrygon from the eastern Pacific Ocean except for Urotrygon binghami and U. rogersi.

Ricker (1959) recorded Urotrygon rogersi and U. caudispinosa as U. goodei caudispinosa from Acapulco to Cape San Lucas, Mexico. Castro Aguirre (1965a) reported Urotrygon chilensis from off the coast of Chiapas, Mexico. Subsequently, Castro Aguirre (1965b) reported U. munda, U. goodei, U. asterias, U. chilensis, U. binghami, U. nebulosa and U. aspidura from Mexican waters. Urotrygon nebulosa (Garman) is presently considered as a synonym of Urolophus halleri Cooper (Bigelow and Schroeder, 1953). Castro Aguirre et al. (1970) recorded U. asterias, U. aspidura and U. binghami from the Gulf of California. Ramirez Hernandez and and Gonzalez Pages (1976) included Urotrygon chilensis, U. goodei, U. munda and U. asterias in the catalogue of the fishes of Mexico.

Urotrygon daviesi, which is the only representative of Urotrygon in the Indo-western Pacific Ocean, was described from the mouth of Limpopo River, eastern South Africa (Wallace, 1967). This species not only is the largest species of Urotrygon, reaching at least 2.6 meters in total length, but also occurs at the greatest depths (300 to 400 meters). It has subsequently been recorded from the Gulf of Mannar, India (Nair and Soundararajan, 1973), Indonesia (Stehmann, pers. comm.), Japanese waters (Nakaya, 1982,1984) and Hawaii (Tinker, 1978). These specimens were also caught at great depths and were juvenile or immature specimens (481 to 590 mm in total length).

Chen and Chung (1971) recorded Urotrygon munda from Tungkong, Taiwan. Because their specimen is 437 mm in total length, far beyond the maximum size of U. munda in the eastern Pacific Ocean, and possesses a long snout, it probably represents Urotrygon daviesi or an undescribed species. Chu et al. (1981) described a new species,

Urolophus marmoratus, from the South China Sea. This specific name is, however, preoccupied by Urolophus marmoratus Philippi (1892) and the description and figure of the species indicate that it is Urotrygon daviesi or a closely related undescribed species.

Miyake and McEachran (1986) examined available material for all the nominal species of Urotrygon except for U. daviesi and their uni- and multivariate analysis supported the recognition of the following nominal species:

Urotrygon Gill, 1863

Indo-western Pacific Ocean

Urotrygon daviesi Wallace, 1967

Tropical western Atlantic Ocean

Urotrygon microphthalmum Delsman, 1941

Urotrygon venezuelae Schultz, 1949

Temperate and tropical eastern Pacific Ocean

Urotrygon munda Gill, 1863

Urotrygon rogersi (Jordan and Starks, 1895)

Urotrygon asterias (Jordan and Gilbert, 1882)

Urotrygon aspidura (Jordan and Gilbert, 1881)

Urotrygon binghami Breder, 1926

Urotrygon serrula Hildebrand, 1946

Urotrygon peruana Hildebrand, 1946

Urotrygon caudispinosa Hildebrand, 1946

Urotrygon goodei (Jordan and Bollman, 1889)

Urotrygon chilensis (Günther, 1871)

Urotrygon sp (1)

Urotrygon sp (2)

Urotrygon sp (3)

The purpose of this study is, therefore, to:

1) determine the species composition of *Urotrygon* based on the morphometric, meristic and external characters,
2) test the monophyly of two genera *Urotrygon* and *Urolophus* by comparing the internal morphology of selected species of five subgroups of batoid fishes (sawfishes, guitarfishes, skates, electric rays and stingrays) and
3) elucidate the interrelationships of *Urotrygon* and *Urolophus* within Myliobatiformes.

LITERATURE REVIEW

Phylogenetic interrelationships

Although a great number of anatomical investigations of sharks and batoid fishes were conducted in the late nineteeth and early twentieth centuries, little effort was made to use this information to elucidate their phylogenetic interrelationships. Most workers expressed the view that sharks and batoid fishes were derived from a common ancestor. Müller and Henle (1841) divided recent elasmobranchs into the sharks (Squali) and batoids (Rajea). Regan (1906) treated sharks and batoids as suborders (Pleurotremata and Hypotremata, respectively), urging that the taxon Tectospondyli (including batoids and squaloid sharks without anal fins) should be dismissed, because of the morphological differences between sharks and batoids. Garman (1913) gave equal rank to sharks (Antacea) and batoids (Platosomia). Despite the fact that he failed to justify his interrelationships of recent elasmobranchs, his study greatly contributed to the comparative anatomy of these groups.

Goodrich (1909) classified batoids as an equivalent taxon to squaloid sharks which together consitituted one or two major subdivisions of recent elasmobranchs. Edgeworth (1935), based on a comparative study of musculature of vertebrates, considered batoids to be derived from sharks. Batoids possess homologous muscles to those of sharks, but in some cases they are modified or there are newly innovated muscles to meet unique demands of their radical changes in body plan. Based on external and internal characters of recent sharks

and batoids, White (1937) concluded that batoids originated from a Squatina-Rhina like ancestor during the Jurassic.

Holmgren (1940,1941,1942) proposed a diphyletic origin of sharks and batoids from placoderm-like ancestor. His view was based on detailed examination of morphology of embryos and adults of sharks and batoids. His paper in 1940 dealt with morphogenesis of neurocranial and visceral cartilages of several sharks and batoids, and interpreted the homology of characters in light of development of embryonic tissues. He then listed the embyronic characters that were uniquely possessed by either sharks and batoids. In 1941 and 1942 he examined the neurocranium and associated structures of adult chondrichthyans (holocephalans and elasmobranchs) and extinct acanthodian fishes. These comparisons convinced him that, although batoids shared many characters with sharks, their unique characters indicate an indepedent origin from a placoderm ancestor. Jarvik (1977,1980) also thought that sharks and batoids are diphyletic with sharks more closely related to extinct acanthodian fishes than to batoids.

Schaeffer (1967a) recognized three levels of organization (grades) within recent elasmobranchs: cladodont, hybodont and modern level, each uniquely defined in their morphological organization. He stated that even though recent sharks and batoids clearly belong to the same organization level and arose from the hybodont level, the distinctive characters of each group obscured their interrelationships. He also pointed out that the phylogenetic position of pristiophorids (sawsharks) and squatinoids (angel sharks) was problematical. Compagno (1973) gave a comprehensive review of the evolution of modern sharks and batoids along with new data on the

morphological characters. He stated that batoids are derived from a common ancestor with recent sharks. They form one of the four major taxa of neoselachians, the others being Squalomorphii, Squatinomorphii and Galeomorphii. Sawsharks in the Squalomorphii was considered to be closest to batoids. In 1977 Compagno supported his previous views. However, in both studies Compagno apparently confounded plesiomorphic and apomorphic character states, so that, as indicated by Maisey (1984a), further scrutiny of character distribution and polarity is needed to determine which characters are synapomorphies within batoids. Unlike Compagno (1973,1977), Thies (1982) suggested a close affinity between batoids with orectolobiform-like sharks.

Interrelationships within batoids are uncertain partly because of a lack of a broadly based comparison of their morphological characters. Garman (1913) may have conducted the broadest anatomical survey within batoids but he did not integrate his observations into a phylogenetic hypothesis. However, he briefly outlined the affinity of several groups. Batoids were derived into six suborders in which sawfishes were included in the Rhinobatoidei (guitarfishes). Stingrays were subdivided to three suborders Dasybatoidei, Myloidei and Mobuloidei. Sawfishes were considered to be closely allied to skates although Garman pointed out that they resemble sharks in several respects such as their elongate form and absence of connection between pectoral fins and head.

White (1937) was the first to propose a hypothesis of batoid interrelationships based on the morphology of both sharks and batoids. She proposed that batoids were composed of two major groups, stingrays and the rest of batoid fishes. Within the stingrays, the Dasyatididae

were thought to be the most primitive and in turn gave rise to the pelagic stingray groups (eagle rays, cow-nose and devil rays). The electric rays were derived from the most primitive group guitarfishes, through sawfishes and skates.

Holmgren (1941) proposed that the stingrays and electric rays were most primitive batoid groups. These taxa gave rise to skates, sawfishes and guitarfishes.

Bigelow and Schroeder (1953), on the basis of the hypothesis that batoids were derived from sharks, assumed sawfishes to be most primitive because they possess a shark-like body form and aplesodic fin rays (radials not reaching the fin edge and with ceratotrichia supporting the fin periphery). Guitarfishes were the next most primitive group and in turn gave rise to electric rays and skates. They stated that extremely specialized stingrays were derived from skate-like ancestor. Chu and Meng (1979) reached similar conclusions based on the lateral-line canal and ampullae of Lorenzini of the chondrichthyan fishes from off China. However, they proposed that electric rays are derived from skates.

Compagno (1973) provided a comprehensive character analysis of batoid groups, in which each subgroup of batoids was characterized by a minimum of thirty morphological attributes. His study offered, for the first time, data to support monophyly of five major subgroups of batoids. His lack of rigorously distinguishing between plesiomorphic and apomorphic characters for each group, however, weakened his analysis of phylogenetic interrelationships within batoid groups. Skates and guitarfishes were assumed to form a stem group which gave rise to the rest of batoid taxa. Since sawfishes has a short

synarcuum, unsegmented propterygia and no connection of propterygia with neurocranium, they were proposed to be derived from fossil guitarfish Spathobatis-like ancestor which also exhibited similar character states. Electric rays were treated as an enigmatic group because of their mosaic distribution of primitive and derived character states. Like Bigelow and Schroeder (1953), Compagno favored a derivation of stingrays from skates because of the latter's synarcual structures and scapular articulation with vertebral column. Subsequently, Compagno (1977) placed electric rays as the most primitive group because one taxon (Narke) retains a plesiomorphic character (conncetion of ceratohyal cartilage with hyomandibular cartilage by means of ligamentous tissue).

Maisey (1984a) reached similar conclusions to those of Compagno (1977) in a cladistic analysis which included two fossil batoid taxa, Spathobatis and Belemnobatis. He allied sawfishes with fossil groups because of similar organization of the basibranchial complex. Guitarfishes, skates and stingrays were placed in an unsolved trichotomy. He also agreed with Compagno (1977) that electric rays were the most primitive of the five taxa because of their retention of primitive character, i.e., connection of the ceratohyal with hyomandibular cartilage by means of ligamentous tissue.

Heemstra and Smith (1980) re-examined the characters given by Compagno (1973,1977) and proposed sawfishes as the sister group of the rest of batoid fishes and electric rays as the sister group of the remaining batoid fishes. Dingerkus (2nd International Conference on Indo-Pacific Fishes, Tokyo, Japan, 1985) agreed with Heemstra and Smith's placement of sawfishes and proposed sequential apomorphic

groups from the most primitive form: sawfishes, electric rays, skates and stingrays. The differences in the assignment of plesiomorphic groups in the above studies result from different interpretation of the hypobranchial skeleton in batoids. These incongruencies in turn may, in large part, be due to a lack of understanding of the morphology and evolution of gill arches in recent elasmobranchs as suggested by Nelson (1969).

Brooks et al (1981) proposed that Urolophus and Potamotrygonidae (freshwater South American stingrays) form a monophyletic group because of their closely related helmith parasites. Dingerkus (ASIH Auunal Meeting, DeKalb, 1982) reported that the genus Urolophus is the most primitive taxa within Myliobatiformes and forms the sister group of the rest of the stingrays. Urotrygon and seven-gilled stingrays Hexatrygon form a sister group and in turn form the sister group of the remaining stingrays. Nishida (1985) described the anatomical structures of Japanese stingrays and questioned the relationships of Urolophus, Dasyatis and Gymnura because of lack of synapomorphies. Later in 1985, he suggested that Potamotrygonidae are the most primitive stingrays (2nd International Conference on Indo-Pacific Fishes, Tokyo, Japan, 1985).

Rosa (1985) divided stingrays into two monophyletic groups, one of which include Gymnuridae, Dasyatididae, Urolophidae, Hexatrygonidae and Potamotrygonidae. Potamotrygonidae are considered to be the most advanced and the sister group of Urolophidae and Hexatrygonidae. Three taxa share one synapomorphy: caudal fin supported by radial cartilages. The presence of segmentation of basihyal cartilage and loss of the sixth gill arch defined the monophyly of Urolophidae.

Anatomy

Jarvik (1980) provided a review of the general anatomy of vertebrates and gave comprehensive comparisons of homologous characters of recent elasmobranchs with those of other vertebrate groups. Daniel (1934) compiled early published data on the anatomy of recent elasmobranchs. Holmgren (1943) discussed the problems with the homology of the crania and related structures of chondrichthyan fishes on a developmental and comparative anatomical basis. Bjerring (1977) dealt with the anatomy and development of crania of fishes with reference to teleostean fish Amia, and discussed many problems in determining the homologies of associated structures in light of metameric organization of vertebrate crania.

Gegenbaur (1865,1872) and Parker (1879) were the first to systematically study the anatomy and ontogeny of cartilaginous skeletons. Garman (1913) presented well illustrated skeletal features and some soft anatomical features of batoid groups as well as of a few sharks. White (1937) summarized many morphological aspects of structures such as heart, denticles, claspers, radials of fins and neurocrania. Gans and Parsons (1964) and Gilbert (1973) provided a review of the anatomy of the shark Squalus acanthias, especially circulatory, nervous and muscular systems. Hoffmann (1913) described the developmental and anatomical structures of two rather superficially similar elasmobranch taxa Pristiophorus and Pristis. Compagno provided a comprehensive review of the anatomy pf recent sharks and batoids (Compagno, 1973,1977) and a summary of anatomical structures within carcharhinoid sharks (Compagno, 1979).

The fossil record of chondrichthyans has been little used but offers potential in clarifying the homology of morphological characters. Zangerl (1981) described the morphology of the Paleozoic elasmobranchs. Maisey (1984b) has conducted a number of very thorough anatomical studies of the Paleozoic and Mesozoic elasmobranchs and offered some new perspectives on skeletal homologies. Patterson (1965) described the morphology of fossil holocephalans in relation to recent forms. Lund (1977,1982) described the Paleozoic holocephalan Echinochimaera and holocephalan-like Harpagofututor and revealed several important morphologies: jaws, neurocranium, paired fins and claspers. Young (1982) described the denticles, spines and neurocrania of the Devonial sharks from Australia and Antarctica. Schaeffer (1981) gave a comprehensive review of the anatomy of the Paleozoic xenacanth fishes. Maisey described detailed anatomical features of the Mesozoic Hybodus sharks in 1982 and 1983 and cranial anatomy of the Mesozoic Synechodus shark in 1985. Oelofsen (1986) described the anatomical features of the neurocranium of Permo-Carboniferous Dwykaselachus from South Africa. Klausewitz (1986) redescribed a Permian xenacanth shark and revealed the morphology of the axial and fin skeletons. Saint-Seine (1949) compared morphological features of two guitarfish-like genera Spathobatis and Belemnobatis with those of recent groups. Maisey (1976) presented additional information on the morphology of Belemnobatis and synonymized Protospinax with Belemnobatis.

Until recently the vascular system of the head region has been largely ignored in phylogenetic analysis of recent elasmobranchs except for Schaeffer (1981) and Maisey (1982,1983) who described the

vasucular system of the Paleozoic fishes. Ridewood (1899) dealt with the afferent branchial aorta of teleostean fishes. Bertmar (1965) described the development of the jugular and cerebral veins of fishes. de Beer (1926,1931,1937) treated the developmental pattern of cephalic arterial and venous systems of various sharks and batiod fishes. Holmgren (1942,1943) gave the comprehensive treatment of the development and evolution of cephalic arterial and venous systems of fishes including those of Urolophus halleri. Jarvik (1980) described the pattern of cephalic arterial system of various lower vertebrate groups and discussed its origin and evolution in light of metamerism of vertebrate body. Daniel (1934) summarized and described earlier data on the vascular system of recent elasmobranchs. Hyrtl (1858), Corrington (1930) and Gohar and Mazhar (1964) studied the pattern of the vascular system of various groups of recent elasmobranchs. Allis (1923) gave a detailed description of cephalic vascular systems of chlamydoselachian shark and compared it with those of other sharks. Marples (1936) described the vascular system of Squatina squatina. O'Douoghue and Abotto (1927) and El-Toubi (1941) described the cephalic and other regions of vascular system of Squalus acanthias. Meurling (1967) described the vascularization of pituitary of recent elasmobranchs. Munoz-Chapuli and Garcia-Garrido (1986) described the pattern of cephalic arterial system of selected groups of recent elasmobranchs and discussed the evolution of the system within recent elasmobranchs.

The musculature of teleostean fishes has been intensively studied and used to infer the phylogenetic analysis, i.e., the treatment of synonymy of the striated muscles of teleost and lower vertebrates

(Winterbottom, 1974; Greenwood and Lauder, 1981; Wiley, 1979a,b; Jollie, 1982) and relationships of euteleostean groups (Kaufman and Liem, 1982; Winterbottom and Tyler, 1983; Yabe, 1985). However, it has been neglected in phylogenetic studies of chondrichthyans. Allis (1917) dealt with the homology of the musculature of lower vertebrates in conjunction with the description of the muscles of shark genera Scyliorhinus and Mustelus. Subsequently, he gave a comprehensive review of the development and homology of musculature throughout all vertebrate groups (Edgeworth, 1935). Marion (1905) described the mandibular and pharyngeal muscles of the shark Squalus vulgaris and skate Raja (Leucoraja) erinacea. Davidson (1918) described the musculature of the shark Heptranchias maculatus, including that of claspers. Howell (1933) treated the musculature of pectoral girdle of shark Squalus acanthias. Kesteven (1942) described the musculature of several sharks and batoids and discussed the homologies. Gottenbos (1956a,b,c) examined the correlation between the muscles and the neurocranial structure of occipital and otic regions in Raja (Dipturus) batis. Vasisht and Chawla (1969) described the muscles in several sharks and batoids including the stingray genus Himantura. However, their description and illustrations were not adequate to discern the detailed patterns of the muscles.

The neurocrania and associated structures have intensively been studied for the last hundred years. de Beer and Moy-Thomas (1935) studied the development of the neurocrania of holocephalans and proposed the homology of several structures, i.e., preorbital process and pharyngeal skeletons, with those of sharks and batoids. Gegenbaur (1872), Parker (1879) and Garman (1913) summarized the neurocranial

structures of various groups of recent elasmobranchs. Major papers dealing with the neurocrania of recent elasmobranchs are: for sharks, Chlamydoselachus anguineus (Allis, 1923); Japanese Scyliorhinidae (Nakaya, 1975); Hemiscyllidae (Dingerkus and DeFino, 1983); Megachasma pelagios (Taylor et al., 1983); carcharhinoid sharks (Compagno, 1979); Carcharhinus (Gohar and Mazhar, 1964); Isistius brasiliensis (Shirai, 1985); Pristiophorus (Hoffmann, 1913); and for batoid fishes, Pristis (Hoffmann, 1913); Rhinobatos and Rhynchobatus (El-Toubi and Hamdy, 1959; Nishida, 1985); Torpedo (Hamdy and Hassan, 1973a; Capape and Desoutter, 1979), Diplobatis (Fechhelm and McEachran, 1984) and Narke (Holmgren, 1941; Nishida, 1985); skates (Ishiyama, 1958; Hulley, 1972), Raja (Hamdy, 1971; Khalil and Hassan, 1973a; Nishida, 1985), Bathyraja (Ishihara and Ishiyama, 1985), Gurgesiella (McEachran and Compagno, 1979), Neoraja and Gurgesiella (McEachran and Compagno, 1982), Sympterygia (McEachran, 1982b) and Psammobatis (McEachran, 1983); Urolophus (Nishida, 1985), Dasyatis (El-Toubi and Hamdy, 1959; Capape, 1983; Nishida, 1985), Himantura (Compagno and Roberts, 1982), Gymnura (Hamdy, 1973a; Nishida, 1985), Hexatrygon (Heemstra and Smith, 1980), Paratrygon and Potamotrygon (Rosa, 1985), Myliobatis (Nishida, 1985), Aetomyleus (Hamdy and Khalil, 1964b,1972a), Rhinoptera (Hamdy, 1960b,c; Nishida, 1985) and Mobula (Nishida, 1985).

Holmgren (1941) and de Beer (1937) described the developmental aspects of neurocrania of sharks, batoid taxa (including Urolophus) and other vertebrates, and discussed in detail the problems with the homology of the structures in light of the embryonic tissues. Holmgren (1943) studied the evolution of the crania in fishes based on his series of investigations on the developmental and comparative

anatomy of fish skulls. El-Toubi (1949) and Jollie (1971) studied the development of the neurocranium and gill arches of the shark genus Squalus. de Beer (1926,1931) presented detailed description of the development of the neurocrania of electric ray Torpedo and shark Scyliorhinus, respectively.

Hamdy (1974) discussed the morphology and evolution of rostral cartilage. The spiracular cartilages were studied in several sharks and batoids (Holmgren, 1940,1942), Rhinobatos (Hamdy, 1956a) and Squalus acanthias (El-Toubi, 1947; Jollie, 1971). Bigelow and Schroeder (1953) mentioned the presence of the spiracular skin fold in the stingray genus Urolophus. La-Marca (1963) undertook the histological studies of this embryonic structure and suggested possible functional attributes. Hamdy described the development and evolution of several parts of neurocranium: nasal cartilages in recent elasmobranchs (Hamdy, 1959), dorsal fontanelle on the neurocrania of recent elasmobranchs (Hamdy, 1960a), mandibular arch of guitarfish genus Rhynchobatus (Hamdy, 1964a) and orbital area of neurocrania of recent elasmobranchs (Hamdy, 1964b). Holmgren (1941), Hamdy (1960c), Jollie (1971) and Maisey (1983) dealt with the morphology and evolution of labial cartilages. Maisey (1980) examined the articulation of the jaws with neurocrania in recent elasmobranchs and showed that there are more variable repertoires of jaw suspension than hyostylic, amphistylic and autostylic modes.

The structure and development of the visceral arches of recent elasmobranchs are poorly known (Nelson, 1969). However, there have been a number of the studies on the visceral arches of specific taxa or specific structure of the visceral arches in recent elasmobranchs.

Hamdy and Khalil (1973b) studied the cartilages in recent elasmobranchs, showing that recent elasmobranchs exhibit a great variety of different arrangements of skeleton of ventral gill arches. Holmgren (1940) described the development of visceral arches of several sharks and batoids. Subsequently, El-Toubi (1952) and Jollie (1971) presented a detailed description of the development of visceral arches of Squalus acanthias. The latter author expressed the view that histological studies of the developmental sequences of visceral arches should be extended to those of blastematic stages to clarify homologies. Hamdy (1957,1961b) examined the development of visceral arches of guitarfish genus Rhinobatos. The major studies dealing with the structure of the visceral arches are as follows: visceral arches and associated muscles of Chlamydoselachus anguineus (Allis, 1923), hyoid and branchial arches of Hemiscyllidae (Dingerkus and DeFindo, 1983), basibranchial cartilages of Echinorhinus (Ridewood, 1899), morphological changes in visceral arches in relation to the specialization of feeding mechanism in Isistius (Shirai, 1985), morphology of hyoid arches of several batoid fishes (Hamdy and Khalil, 1963), superb illustrations of visceral arches of major groups of batoid fishes (Garman, 1913), visceral arches of electric ray Torpedo (Hamdy and Hassan, 1973b), and Diplobatis (Fechhelm and McEachran, 1984), Raja (Khalil and Hassan, 1973b), Daysatis (Hamdy et al., 1974b) and Gymnura (Hamdy, 1973b), those of six-gilled stingray Hexatrygon (Heemstra and Smith, 1980), freshwater stingrays Paratrygon and Potamotrygon (Rosa, 1985) and eagle ray Aetomyleus (Hamdy and Khalil, 1972b).

Ridewood (1897) and Hamdy (1961a) examined the extra-visceral cartilages of recent elasmobranchs. Khalil (1979) described the extra-visceral cartilages in several batoid fishes. Hamdy (1956b) dealt with the extra-visceral cartilages of guitarfish Rhinobatos. Regan (1906), Daniel (1934) and Hamdy (1975) reported the extra-branchial arches in some sharks and batoid fishes.

There has been some controversy regarding the interpretation of the hyoid cartilages in batoid fishes. Based on histological sections, Edgeworth (1931) argued that batoid fishes lack special hyoid arches (pseudo-hyal) but have ceratohyal cartilages. However, de Beer (1932) showed that so-called pseudo-hyal cartilages as well as short ceratohyal cartilages are present in electric ray genus Torpedo. The existence of pseudo-hyal cartilage was later confirmed in several batoid fishes (Hamdy, 1952; Hamdy and Khalil, 1973a).

The vertebral column has been used to infer phylogenetic relationships of major vertebrate groups. Gadow (1933) described the development and evolution of the vertebral column of vertebrates. Gardiner (1983) gave a recent accout of the morphology and evolution of the vertebral column of vertebrates. White (1937) examined the cross-sectioned calcification pattern of vertebral centra of many shark groups and suggested their importance in phylogenetic analysis. Garman (1913) examined the synarcual structures of vertebral centra of batoid fishes with the fine illustrations. de Beer (1937) described the development of the anterior vertebral column of batoid fishes.

Studies of the structure and development of the paired fins and girdles of vertebrates have been important in elucidation of phylogenetic relationships of vertebrates. Jarvik (1980) presented

detailed description and discussed the evolution of the paired fins and girdles in fishes. Rosen et al. (1981) gave a comprehensive review of the morphology and evolution of paired fins in lower vertebrates, suggesting the sister group relationship of lungfishes with tetrapods. Holmes (1985), however, reviewed their paper and claimed the misinterpreted evolution of paired fins. Based on the detailed developmental studies, Shubin and Alberch (1986) gave a comprehensive review of the evolution of paired fins and limbs in vertebrates. Bendix-Almgreen (1975) and Zangerl (1973) examined the paired fins and shoulder girdles of fossil and recent elasmobranchs and discussed the significance in the morphological and phylogenetic studies. Hulley (1972) and McEachran and Compagno (1979,1982) used the scapulocoracoid and pelvic girdles to elucidate phylogenetic interrelationships of skates. Nishida (1985) described the scapulocoracoids of Japanese batoids and discussed their significance in the phylogeny of stingrays. Other descriptions of pelvic girdles of batoid fishes are: electric ray Diplobatis (Fechhelm and McEachran, 1984), skates and some stingrays (Hulley, 1972), several Atlantic stingrays (Capape, 1983), six-gilled stingray Hexatrygon (Heemstra and Smith, 1980), stingray Himantura (Compagno and Roberts, 1982), several Japanese batoid fishes (Nishida, 1985) and fresh-water stingrays (Rosa, 1985).

Jungersen (1899) and Huber (1901a) described the male copulatory organs (claspers) of recent holocephalans and elasmobranchs. Leigh-Sharpe (1920,1921,1922a,b,c,1924a,b,1926,a,b,c,d) described the claspers of a number of recent elasmobranchs. Zangerl (1981) gave a brief description of the clasper of the Paleozoic elasmobranchs and

discussed their homology with those of recent groups. White (1937) described the claspers of some sharks and batoid fishes and inferred the phylogenetic interrelationships of recent elasmobranchs. Gilbert and Heath (1972), Friedman (1935) and La-Marca (1964) investigated the morphology and function of claspers of the shark Squalus acanthias, skates and stingray Urolophus jamaicensis, respectively. Claspers were used in several systematic and phylogenetic studies of skates: Atlantic skates (Stehmann, 1970; Hulley, 1972; McEachran and Martin, 1978), Japanese skates (Ishiyama, 1958; Ishihara and Ishiyama, 1985), Sympterygia (McEachran, 1982b), Psammmobatis (McEachran, 1983), Gurgesiella (McEachran and Compagno, 1979) and Neoraja and Gurgesiella (McEachran and Compagno, 1982). Hulley (1972), Compagno and Roberts (1982) and Rosa (1985) described the morphology of claspers of several batoid genera, stingray Himantura signifer and freshwater stingray family Potamotrygonidae, respectively.

MATERIALS AND METHODS

Total 369 specimens of the species of Urotrygon, including all available type material, were examined. Several species of both amphi-American and Australian-western Pacific Urolophus were also examined for comparative purpose. All non-Urotrygon specimens that were examined are listed in Appendix 1. Acronoms of museums or institutions through which specimens or information were gained are as follows (Leviton et al., 1985):

BMNH-- British Museum (Natural History), Department of Zoology, London, England;

BOC--- Bingham Oceanographic Collection, The Peabody Museum of Natural History, Yale University, New Haven, Connecticut;

BPBM-- Bernice P. Bishop Museum, Honolulu, Hawaii;

CAS and CAS-Su-- California Academy of Sciences, San Francisco, California;

FAKU-- Department of Fisheries, Faculty of Agriculture, Kyoto University, Maizuru, Japan;

FMNH-- Field Museum of Natural History, Chicago, Illinois;

FSFL-- Far Seas Fisheries Research Laboratory, Distant-water Trawl Resources Section, Japanese Fisheries Agency, Ministry of Agriculture and Fisheries, Shimizu, Japan;

GCRL-- Gulf Coast Research Laboratory Museum, Ocean Spring, Mississippi;

IMARPE-- Instituto de Mar del Peru, Lima, Peru;

LACM-- Los Angeles County Museum of Natural History, Los Angeles, California;

MCZ--- Museum of Comparative Zoology, Harvard University, Cambridge, Massachusettes;

RMNH-- Rijksmuseum van Natuurlijke Historie, Leiden, Holland

RUSI-- J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa;

SIO--- Scripps Institute of Oceanography, Marine Vertebrate Collection, University of California, La Jolla, California;

TBT--- Dr. T.B. Thorson's Collection, University of Nebraska, Lincoln, Nebraska;

TCWC-- Texas Cooperative Wildlife Collection, Texas A&M University, College Station, Texas;

UFPB-- Universidade Federal de Paraiba, Departamento de Sistematica e Ecologia, João Pessoa, Brasil;

USNM-- National Museum of Natural History, Smithsonian Institution, Washington, D.C.;

ZMA--- Universiteit van Amsterdam Zoologisch Museum, Amsterdam, Holland.

Thirty two morphometric measurements were made with dial calipers or dividers to the nearest 0.01 mm. These measurements were taken on a horizontal between perpendiculars at given points (Fig. 1,2).

1 Total length (TL): from tip of snout to tip of caudal fin.

2 Disc width (DW): distance between outermost tips of pectoral fin.

3 Disc length (DL): distance between tip of snout and posterior-most tip of pectoral fin.

Fig. 1. Schematic presentation of dorsal body and caudal fin measurements taken on specimens of Urotrygon. Names of measurements and their abbreviations are given in text.

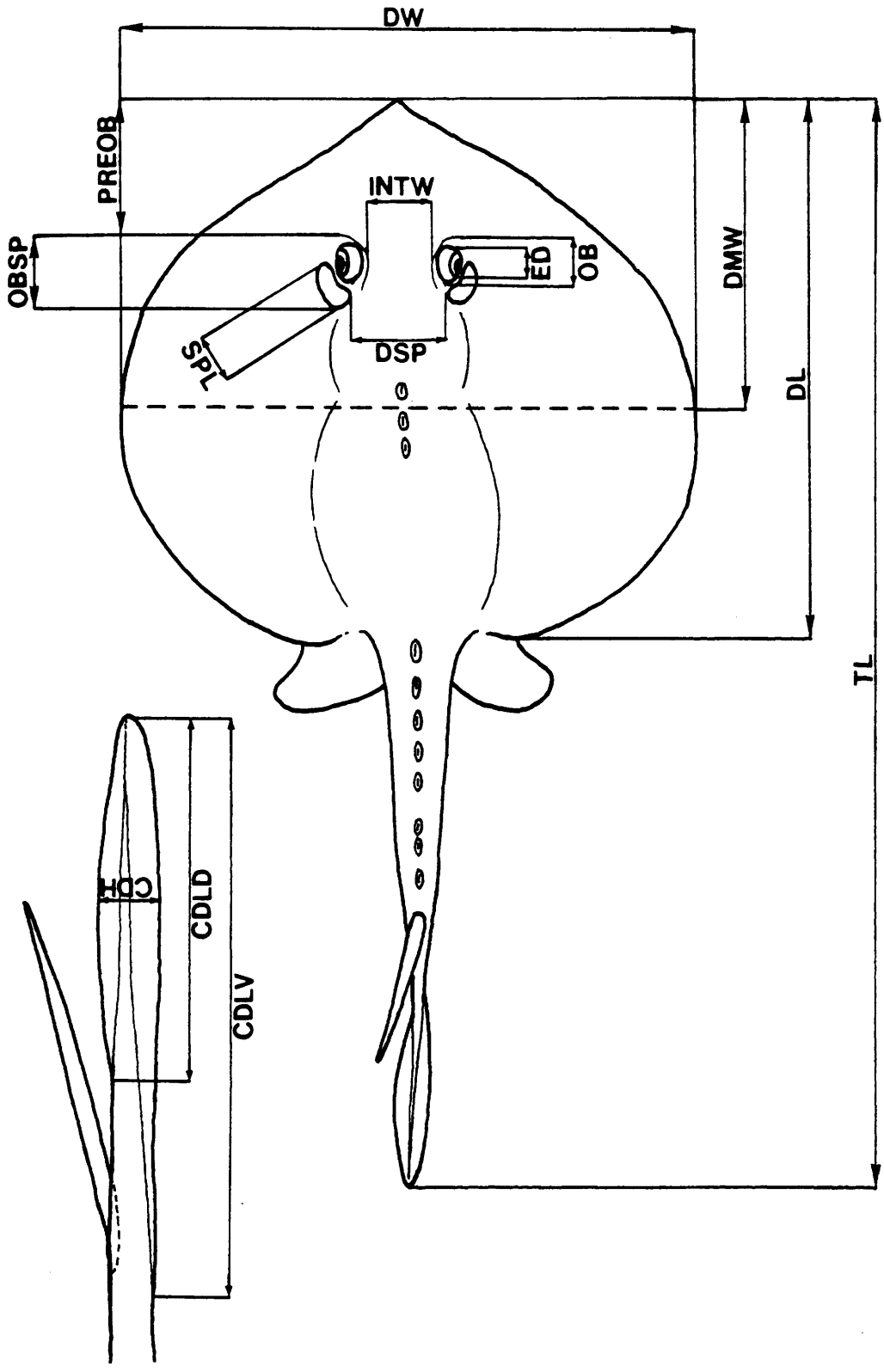
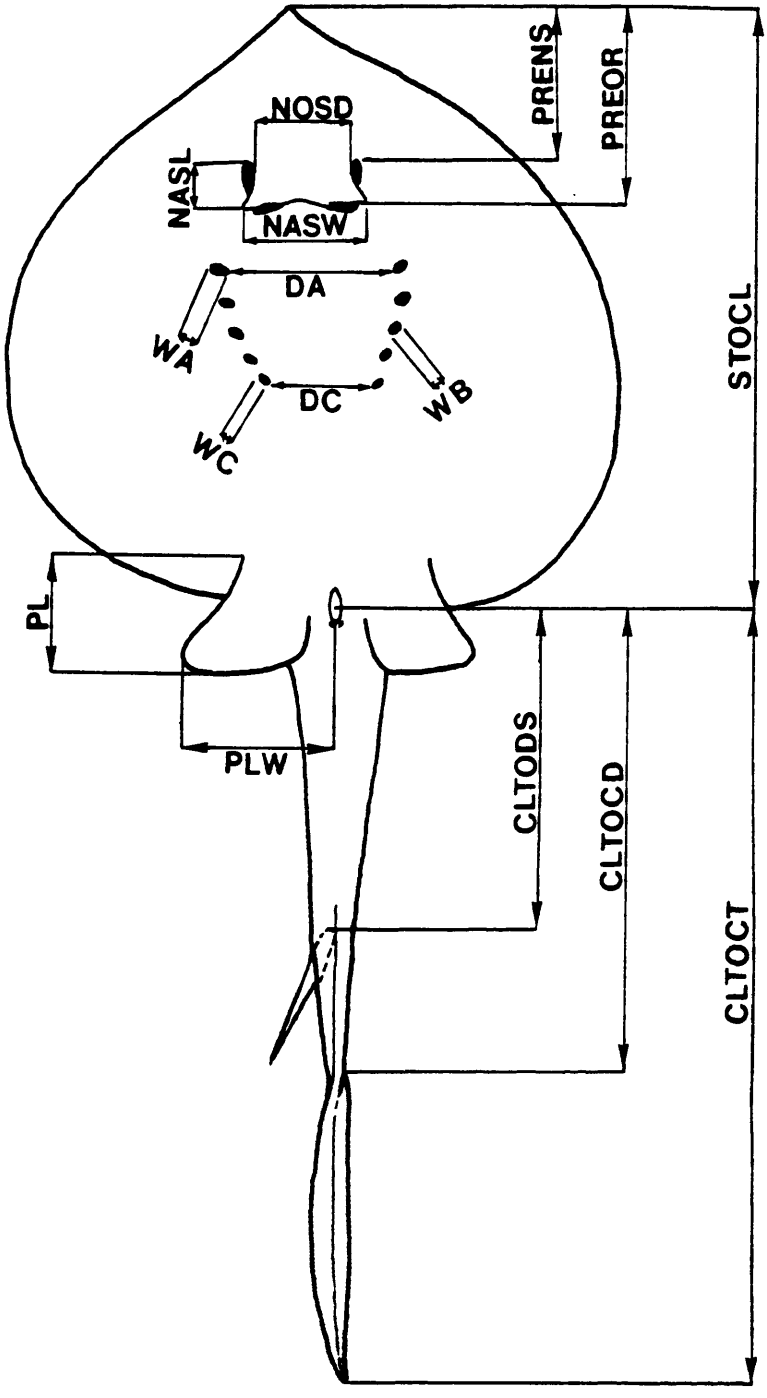

DW
PREOB
INTW
OBSP
ED
OB
DMW
DL
TL
SPL
DSP
CDLD
CDLV
CD

Fig. 2. Schematic presentation of ventral measurements taken on specimens of Urotrygon. Names of measurements and their abbreviations were given in text. Preoral lenght, mouth width and tail width at axil of pelvic fins are not shown here.


PRENS
PREOR
NOSD
NASL
NASW
DA
WA
DC
WB
WC
STOCL
PL
PLW
CLTODS
CLTOCD
CLTOCT

4 Disc length to maximum width (DMW): distance between tip of snout and horizontal line connecting points of maximum width of pectoral fin.

5 Preorbital length (PREOB): from tip of snout to tip of preorbital process taken by pressing calipers lightly against skin.

6 Preoral length (PREOR): from tip of snout to mouth slit on midline.

7 Prenasal length (PRENS): from tip of snout to nearest point on outer rim of nostrils.

8 Length of nasal curtain (NASL): from anterior rim of nostrils to posterior margin of nasal curtain.

9 Width of nasal curtain (NASW): maximum distance of posterior margin of nasal curtain.

10 Orbit diameter (OD): distance between tip of preorbital process and posterior margin of eyeballs.

11 Eye diameter (ED): greatest diameter of eyeballs.

12 Interorbital width (INTW): least distance between inner edges of left and right aspects of neurocranium taken by pressing calipers lightly against skin.

13 Orbit to spiracle length (OBSP): from tip of preorbital process to posterior margin of eyeballs.

14 Spiracle length (SPL): greatest diameter across spiracular depression.

15 Distance between spiracles (DSP): least distance between inner most corner of left and right spiracle openings.

16 Mouth width (MW): greatest dimension across tooth band of upper jaw.

17 Distance between nostrils (NOSD): least distance between left and right lateral margin of nasal curtain.

18 Length of pelvic fins (PL): distance from anterior insertion of pelvic fins to farthest points of posterior margin of pelvic fins.

19 Width of pelvic fins (PLW): distance between midline of cloaca to outermost points of pelvic fins.

20 Height of caudal fin (CDH): maximum height of caudal fin.

21 Length of dorsal lobe of caudal fin (CDLD): from anterior most point of dorsal margin of lobe to tip of caudal fin.

22 Length of ventral lobe of caudal fin (CDLV): from anterior most point of ventral margin of lobe to tip of caudal fin.

23 Tail heigth at axil of pelvic fins (TAMH): maximum height of tail at axil of pelvic fins.

24 Width of first gill slit (WA): maximum diameter across first gill slit.

25 Width of third gill slit (WB): maximum diameter across third gill slit.

26 Width of fifth gill slit (WC): maximum diameter across fifth gill slit.

27 Distance between first gill slits (DA): distance between inner most corner of left and right first gill slits.

28 Distance between fifth gill slits (DC): distance between inner most corner of left and right fifth gill slits.

29 Distance from tip of snout to cloaca (STOCL): from tip of snout to center of cloaca.

30 Distance from cloaca to origin of tail spine (CLTODS): distance from center of cloaca to origin of tail spine taken by pressing calipers against skin (the origin is embedded in skin).

31 Distance from cloaca to origin of dorsal lobe of caudal fin (CLTOCD): from center of cloaca to anterior most point of dorsal margin of lobe of caudal fin.

32 Distance from cloaca to tip of caudal fin (CLTOCT): distance from center of cloaca to tip of caudal fin.

Non-parametric characters included angle of snout (Bigelow and Schroeder, 1953), rows of teeth on upper jaw (Hubbs and Ishiyama, 1968) and number of vertebral centra. Number of vertebral centra were counted from radiographs. The counts were made from the anterior most recognizable centrum embedded in the thoracolumber synarcuum to that at the origin of tail spine.

The morphometric characters defined above were expressed as a ratio of total length, log-transformed, then subjected to Principal Component Analysis (PCA) available in the Statistical Analysis System (SAS) (Ray, 1982). This method does not require a prior group assigment for individuals (Pimental, 1979) and thus was used to detect the first approximation of groupings of Urotrygon species. The components were calculated with the covariance matrix. The relative contribution of components of PCA to separation of groups is explained by loadings of original variables on each component. Those which load heavily on a given component were thus taken as important variables for the taxonomy and were subjected to further analysis. The analyses consisted of nine different combinations of the known species of Urotrygon. Since the holotype of Urotrygon binghami and the specimens

of U. sp (3) were obtained after two-thirds of all PCAs were performed, they could not be included in the first two analyses. In addition, Urotrygon daviesi were excluded from the analyses because of a lack of specimens.

The analysis of variance for unbalanced data was used to test the significant differences of morphometric and meristic characters among the known species of Urotrygon. Several morphometric characters with highly loadings in the PCA were expressed as a percentage of total length and then subjected to ANOVA (Analysis of Variance), pairwise t-tests and Duncan's multiple range tests. The statistical comparisons of the characters were made only between or among the species which have an adequate sample size, i.e., > 20. All univariate analyses were performed using the programs available in the Statistical Analysis System (SAS) (Ray, 1982).

Descriptions and comparisons of denticles and thorns among species were based on specimens of comparable stages of development. The structure of dermal denticles of skates and rays basically agrees with the placoid scales in recent sharks (Reif, 1979). They consist of an enameroid cap, a dentine crown and basal plate with or without vascular canals. However, the denticles of recent sharks and rays are more morphologically differentiated than those of recent sharks. Smaller ones, comparable to placoid scales, are called denticles whereas the larger ones are called thorns or dermal tubercles (Bigelow and Schroeder, 1953; Reif, 1979). Furthermore, larger denticles (=thorns) in several fossil and recent skates and rays have a similar pattern of histological organization but vary in details from taxon to

taxon, especially structures associated with the basal plates (Reif, 1979).

The observation of coloration was based on specimens which were fixed with formalin and stored in alcohol.

The structure of neurocrania, skeleton of ventral gill arches, pectoral and pelvic girdles, scapulocoracoids, claspers, cranial arterial system, cranial nervous patterns and muscles associated with neurocrania and ventral gill arches were examined from gross dissection of specimens, cleared and stained specimens and X-radiographs. Embryos and juvenile specimens of selected batoid fishes were cleared and double-stained with Alcian Blue (Kodak 14091) and Alizarine (Alizarine Sodium Monosulfonate, Fisher Scientific Company) for cartilages and calcified structures, respectively (Dingerkus and Uhler, 1977; Dingerkus, 1981). Photo micrographies of several morphological structures were taken with the WILD MPS 12 system equipped with WILD MPD 05 Microphoto Automatic Exposure Meter. Abbreviations of anatomical characters are given in Appendix 2.

The analysis of phylogenetic interrelationships of Urolophidae and related genera was performed using a cladistic method (Wiley, 1981). This methodology is based on determining the polarity of character states. Symplesiomorphic characters are primitive characters shared by two or more taxa and are of no significance in phylogenetic reconstruction. Synapomorphic characters are derived characters shared by two or more taxa which suggest phylogenetic affinity. There is, however, still controverty over the criteria used to hypothesize the polarity of characters.

In the present study the polarity of character states was determined by outgroup comparison and ontogenetic analysis. Most researchers employ the outgroup method (Watrous and Wheeler, 1981) in conjuction with the rule of parsimony (Maddison et al., 1984) to minimize homoplasies (character reversals, parallelism and convergence). However, Watrous and Wheeler (1981) maintained that the rule of parsimony is unnecessary for the construction of cladograms (phylogenetic hypotheses) and Panchen (1982) noted that nature is not necessarily parsimonious, but exhibits a variety of homoplastic attributes. Felsenstein (1983) argued that the rule of parsimony is statistically inconsistent, while Sober (1983) claimed that parsimonious cladograms are the ones with the highest likelihood. To avoid these conceptual difficulties, Farris (1983) pointed out that the rule of parsimony is operational but does not necessarily reflect reality. Thus cladograms constructed by the rule of parsimony are treated as character state relationships rather than phylogenetic trees. This is the procedure adopted in the present study.

There are two problems in using the criterion of ontogeny for the determination of the polarity of characters: conceptual and practical problems. Nelson (1978,1985), Nelson and Platnick (1981) and Patterson (1982) claimed that the ontogenetic criterion invokes the least number of ad hoc assumptions and is a direct technique for estimating the polarity of characters. However, Brooks and Wiley (1985) and Kluge (1985) stated that genealogical relationships can not be deduced solely from this method. Kluge and Strauss (1985) showed convincingly that the transformation series of ontogenetic stages can not be used to elucidate the polarity of characters without outgroup

comparison. In addition, Alberch (1985) demonstrated that strict use of ontogenetic sequence in phylogenetic analysis can lead to errors because the sequence often involved reversals and non-terminal deletions. de Queiroz (1985) distinguished instantaneous morphologies from ontogenetic transformation, arguing that the latter is uninformative in elucidating the polarity of characters unless they are viewed as characters. If such is the case, the ontogenetic method is equivalent to comparative phylogenetic or outgroup method without invoking any other methods.

However, information on ontogenetic sequences is crucial in determining character homologies prior to analysis of the polarity of character states. Thus homologies are regarded as distinct from synapomorphies (de Queiroz, 1985), unlike the opinion of Patterson (1982). The statement by Kluge (1985) makes my position regarding the ontogenetic criterion clear: "since each criterion [ontogeny and outgroup] serves to cover the assumptions of the other, one might argue that they should be used in concert whenever possible."

In the present study, comparative anatomy and ontogenetic information from the findings of the present study and published results were used to elucidate homolgy of characters.

PRINCIPAL COMPONENT ANALYSES

Analysis 1.-- Analysis 1 compared eight species of Urotrygon: U. microphthalmum, U. venezuelae, U. munda, U. sp (1), U. sp (2), U. rogersi, U. asterias and U. aspidura (Fig. 3 and Table 1). The first two components accounted for 91 % of total variance. PC1 was a size component with a relatively wide range of character loadings. PC2 was highly loaded on eye and orbit diameters (Fig. 3). The analysis clearly separated Urotrygon microphthalmum and partially separated U. sp (1) from the other species along PC2 axis. Although Urotrygon sp (1) was partially separated from the remaining species along PC2 axis, the major separation along PC1 axis may be due to the fact that U. sp (1) is the smallest species in Urotrygon.

Analysis 2.-- Analysis 2 compared Urotrygon venezuelae, U. munda, U. sp (1), U. sp (2), U. rogersi, U. asterias and U. aspidura (Fig. 4 and Table 1). The first two components accounted for 93 % of total variance. PC1 was a size component with a relatively wide range of character loadings. The eye and orbit diameters were highly loaded but spiracle (orbit to spiracle and spiracle lengths) and caudal fin (height of caudal fin and length of dorsal lobe of caudal fin) measurements were moderately loaded on PC2. The exclusion of Urotrygon microphthalmum from the analysis produced two distinct clusters of the species with U. sp (2) positioned between them along the PC2 axis. One cluster consisted of Urotrygon venezuelae, U. munda and U. sp (1) and the other was composed of U. rogersi, U. asterias and U. aspidura (Fig. 4).

Fig. 3. Projection of individuals of eight species: Urotrygon microphthalmum (1), U. venezuelae (2), U. munda (3), U. sp (1) (4), U. sp (2) (5), U. rogersi (6), U. asterias (7) and U. aspidura (9); along the first two principal component axes.

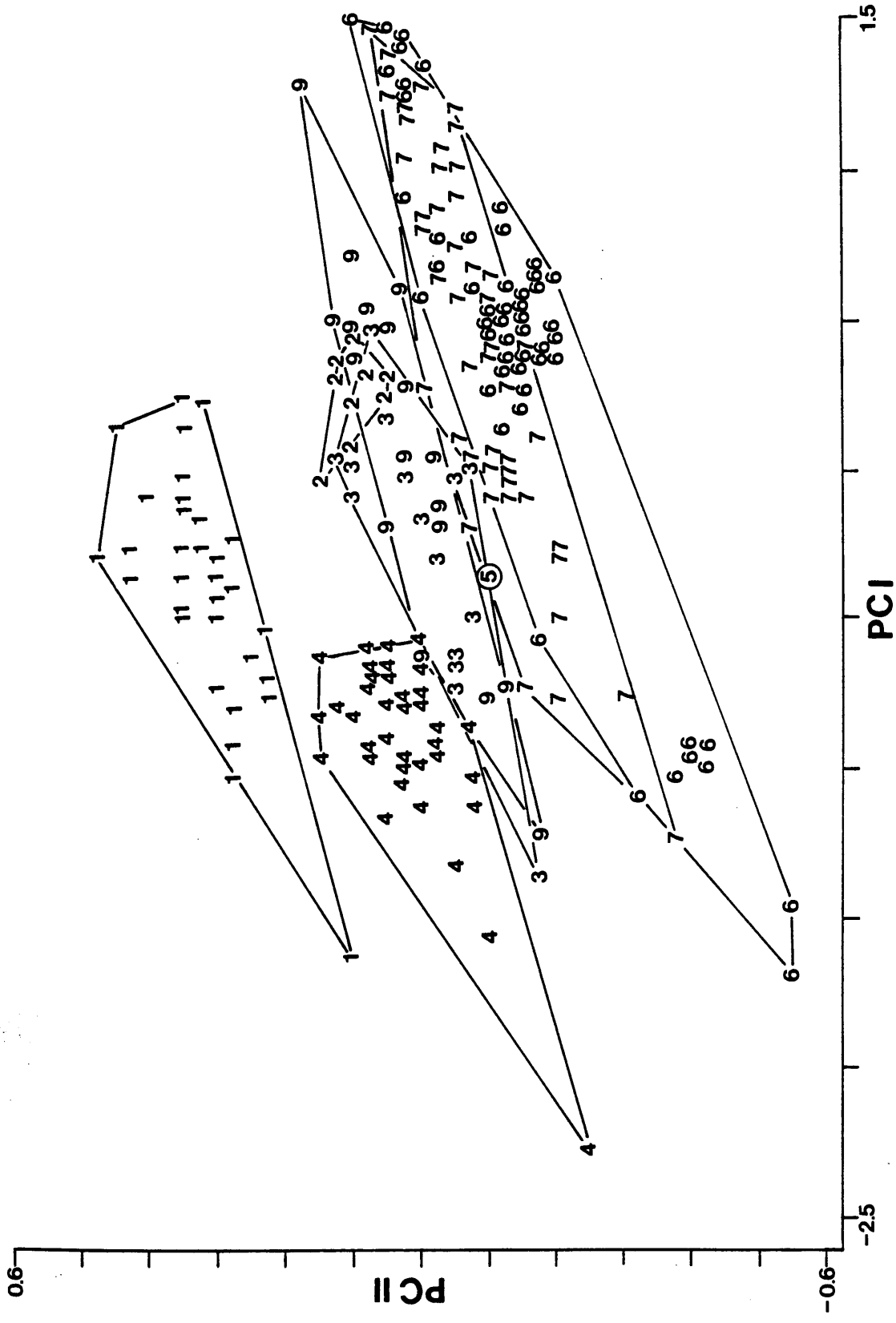

PC I
PC II
1.5
-2.5
0.6
-0.6

Fig. 4. Projection of individuals of seven species: Urotrygon venezuelae (2), U. munda (3), U. sp (1) (4), U. sp (2) (5), U. rogersi (6), U. asterias (7) and U. aspidura (9); along the first two principal component axes.

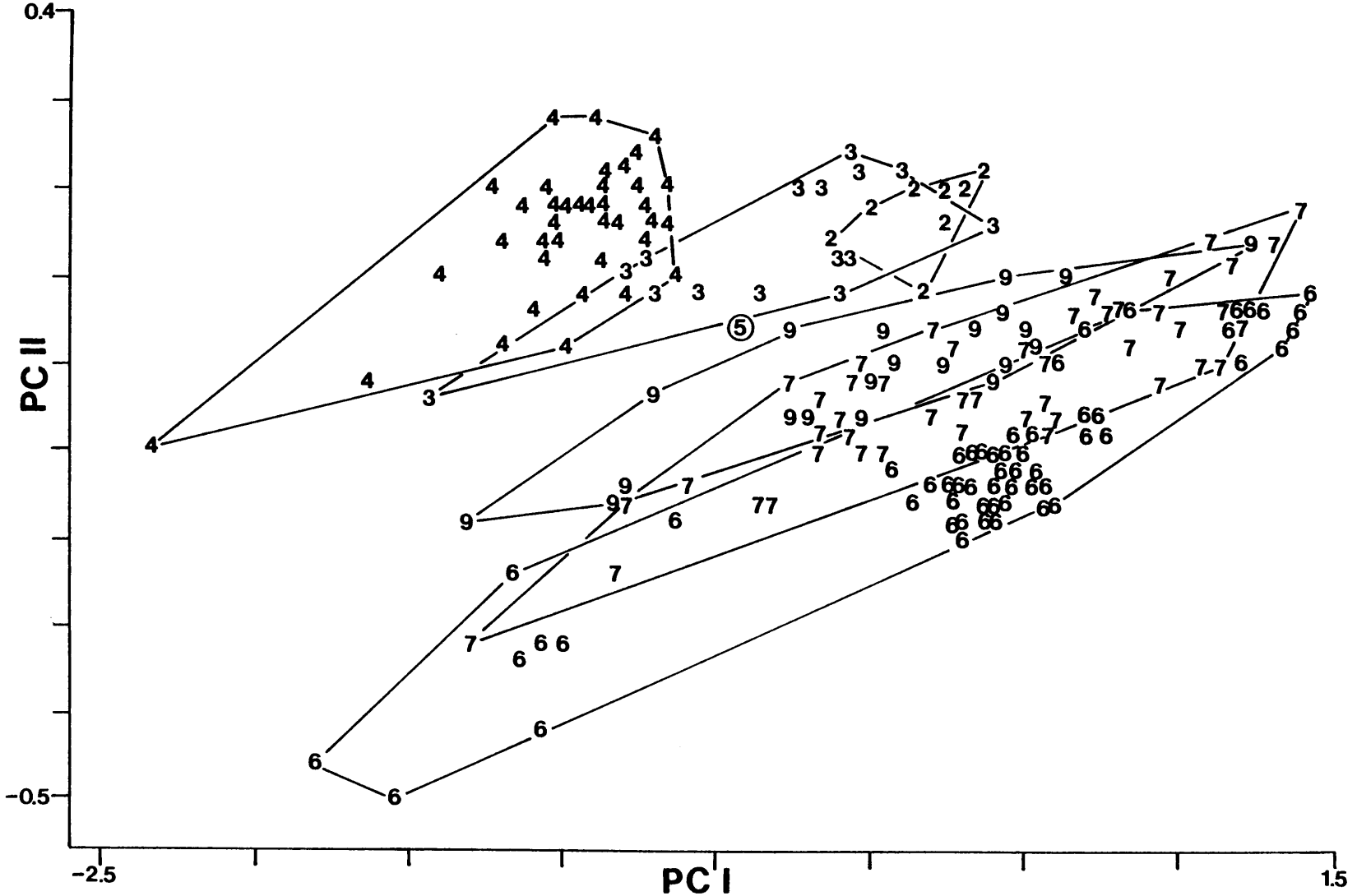

0.4
-0.5
PC II
-2.5
PC I
1.5

Fig. 5. Projection of individuals of three species: Urotrygon venezuelae (2), U. munda (3) and U. sp (1) (4); along the first two principal component axes.

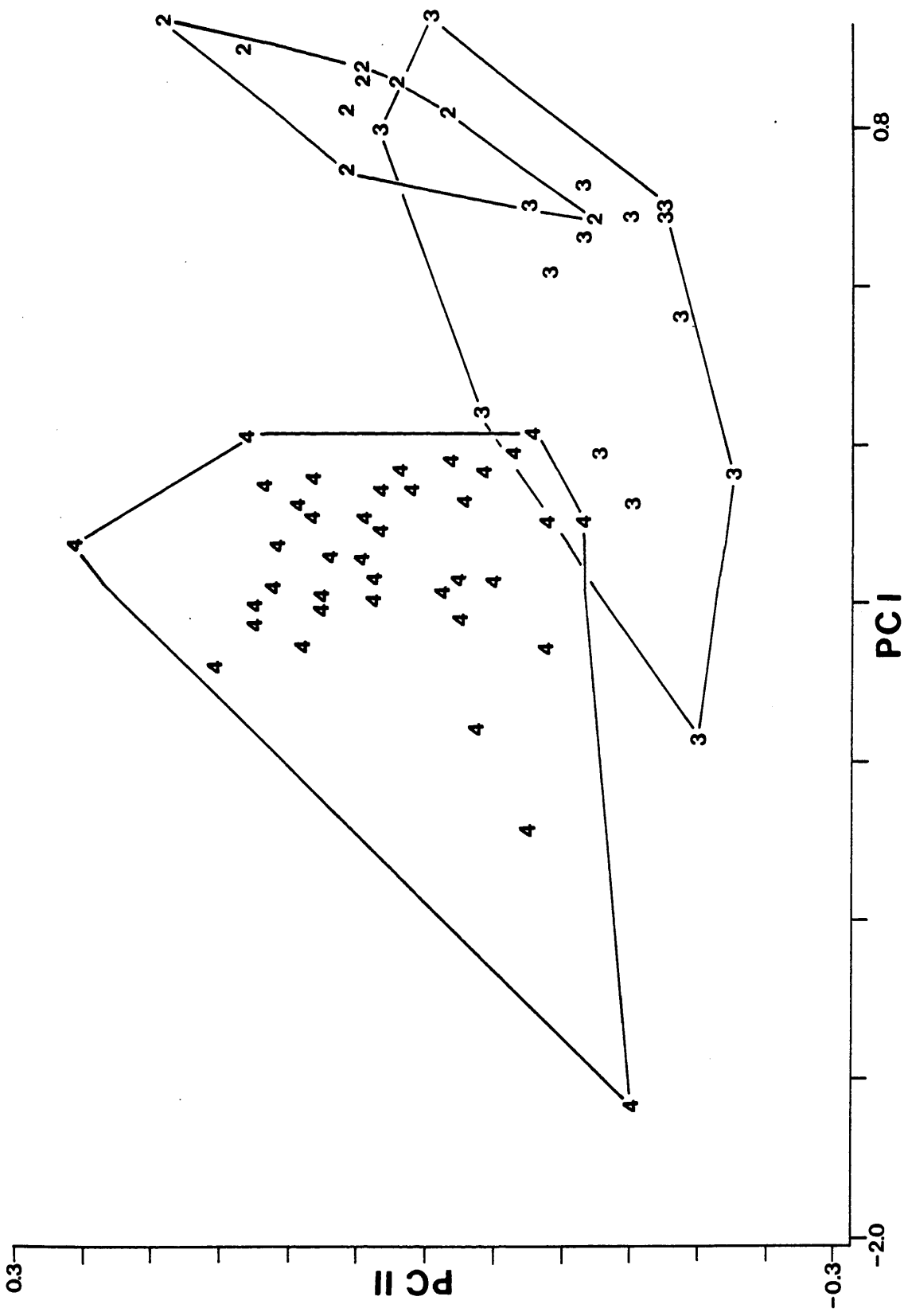

PC I
PC II
0.8
-2.0
0.3
-0.3

Table 1. PRINCIPAL COMPONENT ANALYSES OF MORPHOMETRIC VARIABLES: ANALYSIS 1 AND 2. Analysis 1-- Urotrygon microphthalmum (N=37), U. venezuelae (N=9), U. munda (N=15), U. sp (1) (N=40), U. sp. (2) (N=2), U. rogersi (N=70), U. asterias (N=49) and U. aspidura (N=21). Analysis 2-- Urotrygon venezuelae (N=9), U. munda (N=15), U. sp (1) (N=40), U. sp (2) (N=2), U. rogersi (N=71), U. asterias (N=48) and U. aspidura (N=21). Abbreviations for morphometric characters are explained in text.

	Analysis 1		Analysis 2	
Character	PC1	PC2	PC1	PC2
DMW	.16	.20	.17	.16
PREOB	.15	.27	.17	.16
PREOR	.16	.23	.17	.11
PRENS	.16	.26	.17	.09
NASL	.19	.05	.18	.13
NASW	.19	.14	.20	.12
OD	.21	-.32	.20	-.36
ED	.26	-.61	.24	-.57
INTW	.17	.05	.17	.09
OBST	.19	-.20	.19	-.27
SPL	.19	-.22	.18	-.28
DSP	.17	-.03	.17	-.10
PL	.19	.07	.19	.12
PLW	.17	.07	.16	.20
CDH	.15	-.22	.14	.12
CDLD	.20	.14	.21	-.20
TALW	.15	.04	.15	.28
WA	.21	-.07	.20	.02
WB	.19	-.08	.20	-.01
WC	.16	-.08	.19	-.06
DA	.16	.06	.16	.13
DC	.15	.08	.15	.16
STOCL	.18	.08	.18	.07
CLTOLD	.18	.11	.18	.06
CLTOCT	.18	.12	.19	-.02
% variance explained	86	5	90	3

Table 2. PRINCIPAL COMPONENT ANALYSES OF MORPHOMETRIC VARIABLES: ANALYSIS 3, 4 AND 5. Analysis 3.-- Urotrygon venezuelae (N=9), U. munda (N=15) and U. sp (1) (N=40). Analysis 4.-- Urotrygon venezuelae (N=9), U. munda (N=15) and U. sp (2) (N=2). Analysis 5.-- Urotrygon munda (N=5), U. sp (1) (N=40) and U. sp (2) (N=2). Abbreviations of morphometric characters are explained in text.

	Analysis 3		Analysis 4		Analysis 5	
Character	PC1	PC2	PC1	PC2	PC1	PC2
DMW	.17	.01	.17	-.02	.17	.06
PREOB	.14	.00	.15	-.04	.17	.05
PREOR	.13	.08	.15	-.03	.17	.05
PRENS	.13	.08	.15	-.01	.16	.08
NASL	.18	-.44	.17	.17	.15	.36
NASW	.20	-.20	.22	-.06	.21	.10
OD	.11	.27	.16	-.15	.18	-.23
ED	.10	.35	.25	-.55	.28	-.60
INTW	.17	.00	.18	-.09	.18	-.03
OBST	.17	.03	.14	.03	.14	-.05
SPL	.17	-.07	.15	.03	.14	-.01
DSP	.18	.05	.17	-.04	.17	-.06
PL	.17	.24	.19	-.03	.19	-.01
PLW	.17	.28	.17	.03	.18	.01
CDH	.11	.15	.11	.04	.13	.14
CDLD	.27	-.36	.17	.22	.12	.17
TALW	.20	-.09	.20	-.04	.20	.03
WA	.26	.13	.20	.41	.19	.34
WB	.19	.11	.17	.34	.16	.25
WC	.22	-.18	.16	.48	.13	.33
DA	.17	.17	.15	.07	.15	.03
DC	.16	.22	.14	-.04	.17	-.05
STOCL	.19	.12	.17	.04	.18	.03
CLTOLD	.20	.00	.24	-.16	.24	-.19
CLTOCT	.22	-.08	.22	-.03	.21	-.03
% variance explained	84	4	85	3	80	4

Analysis 3.-- Analysis 3 compared Urotrygon venezuelae, U. munda and U. sp (1) (Fig. 5 and Table 2). The first two components accounted for 88 % of total variance. PC1 was a size component and exhibited a relatively wide range of character loadings. Length of nasal curtain, length of dorsal lobe of caudal fin and eye diameter were highly loaded on PC2 axis. At least part of the separation of Urotrygon sp (1) from U. venezuelae was due to the small size of the former species.

Analysis 4.-- Analysis 4 compared Urotrygon venezuelae, U. munda and U. sp (2) (Fig. 6 and Table 2). The first two components accounted for 88 % of total variance. PC1 was size component with a relatively wide range of character loadings. Eye diameter and widths of first, third and fifth gill slits were highly loaded on PC2. Urotrygon venezuelae partially overlapped U. munda along PC2 axis. The two specimens of Urotrygon sp (2) were clustered with U. munda.

Analysis 5.-- Analysis 5 compared Urotrygon munda, U. sp (1) and U. sp (2) (Fig. 7 and Table 2). The first two components accounted for 84 % of total variance. PC1 was a size component with a wide range of character loadings. Eye diameter was heavily loaded and length of nasal curtain and first and fifth gill slits were moderately loaded on PC2. Two clusters were obliquely oriented in component space and not well separated along PC2 axis, but overlapped along PC1 axis, suggesting that the components were in part confounded with a size factor. A part of the separation of Urotrygon sp (1) from U. munda and U. sp (2) on PC2 was explained by high loading of eye diameter.

Fig. 6. Projection of individuals of three species: Urotrygon venezuelae (2), U. munda (3) and U. sp (2) (5); along the first two principal component axes.

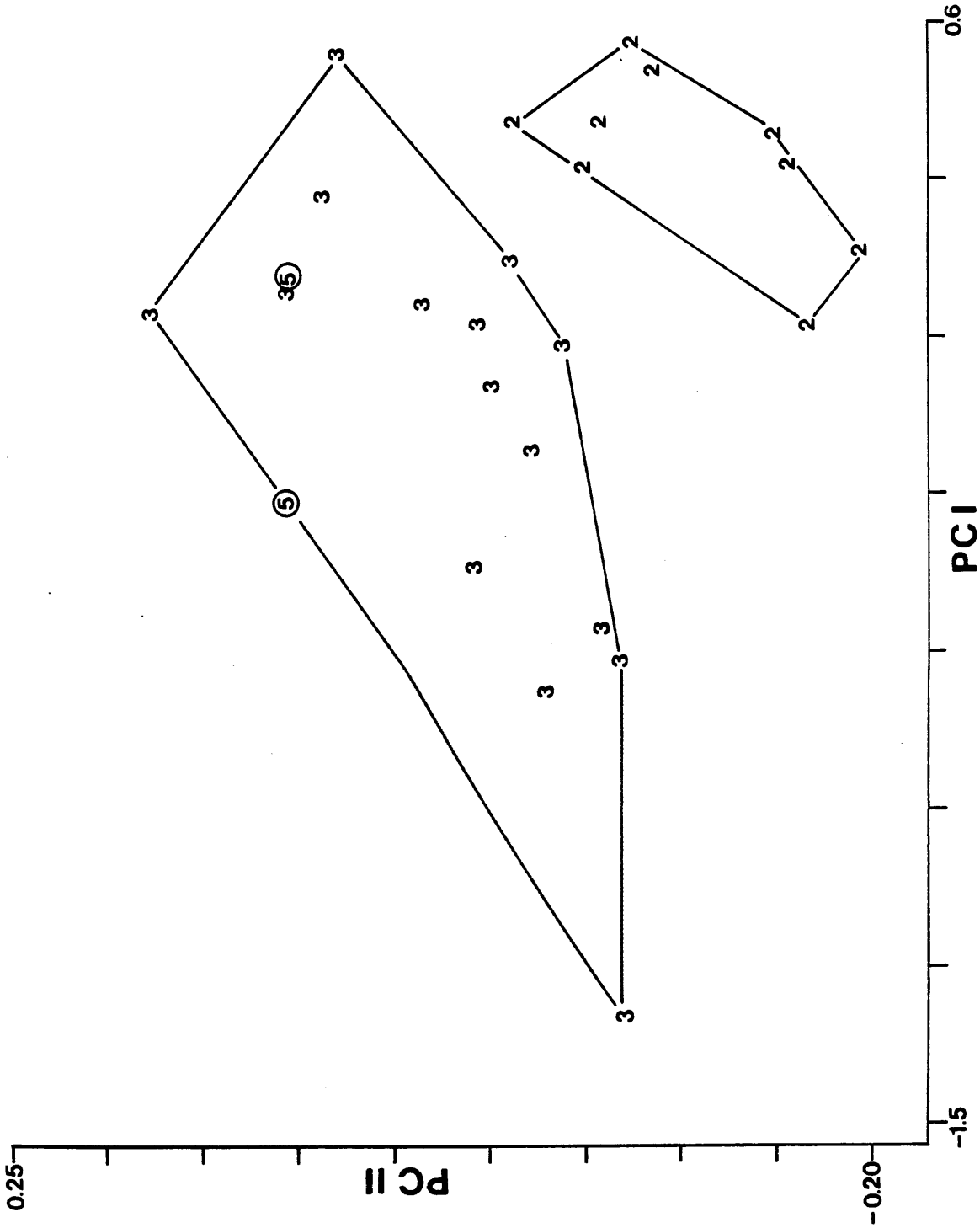
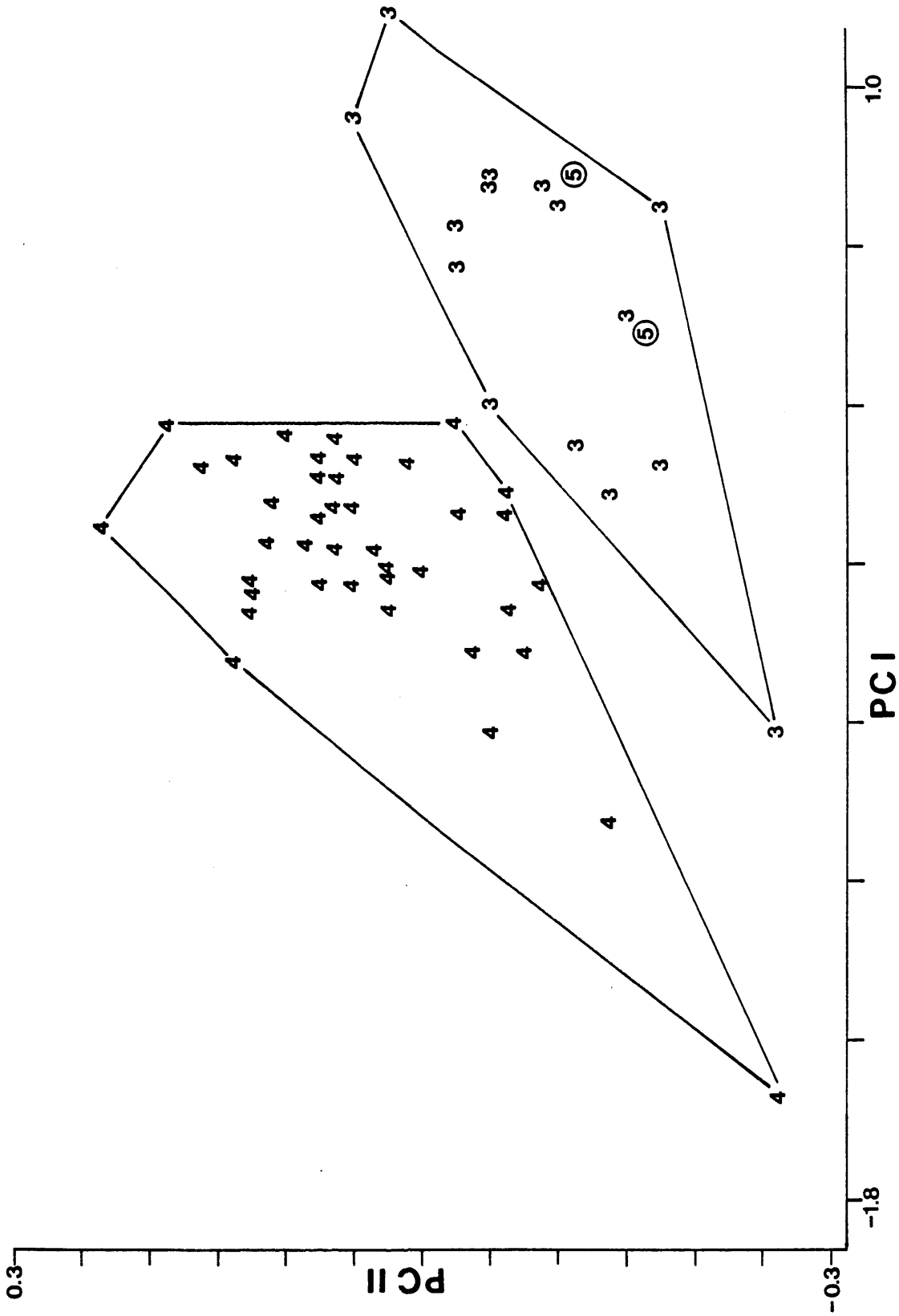

0.25
PC II
-0.20
-1.5
PC I
0.6
3
2
5

Fig. 7. Projection of individuals of three species: Urotrygon munda (3), U. sp (1) (4) and U. sp (2) (5); along the first two principal component axes.


PC II
PC I
0.3
-0.3
-1.8
1.0

Analysis 6.-- Analysis 6 comapred Urotrygon rogersi, U. asterias, U. aspidura and U. binghami (Fig. 8 and Table 3). The first two components accounted for 92 % of total variance. PC1 was a size component with a narrow range of character loadings. PC2 was highly loaded on tail height at axil of pelvic fins and eye diameter. Urotrygon aspidura was well separated from U. rogersi, whereas Urotrygon asterias overlapped both U. aspidura and U. rogersi. The holotype of Urotrygon binghami fell in the cluster of U. rogersi.

Analysis 7.-- Analysis 7 compared Urotrygon asterias and U. aspidura (Fig. 9 and Table 3). The first two components accounted for 93 % of total variance. PC1 was also a size component with a narrow range of character loadings. Two species were clearly separated along PC2 axis which was highly loaded on eye diameter and tail width at axil of pelvic fins and moderately on snout dimension.

Analysis 8.-- Analysis 8 compared Urotrygon munda, U. asterias and U. sp (3) (Fig. 10 and Table 4). The first two components accounted for 93 % of total variance. PC1 was a size component with a narrow range of character loadings. PC2 was highly loaded on length of dorsal lobe of caudal fin and moderately on orbit/spiracle dimension and orbit diameter. Urotrygon munda and U. asterias were clearly separated along PC2 axis. Urotrygon sp (3) was clustered with U. asterias.

Analysis 9.-- Analysis 9 compared Urotrygon rogersi, U. asterias, U. sp (3), U. serrula, U. peruana, U. caudispinosa, U. goodei and U. chilensis (Fig. 11 and Table 4). The first two components accounted for 93 % of total variance. PC1 was a size component and exhibited a narrow range of character loadings. PC2 was highly loaded on tail

Fig. 8. Projection of individuals of four species: Urotrygon rogersi (6), U. asterias (7), U. binghami (a) and U. aspidura (9); along the first two principal component axes.

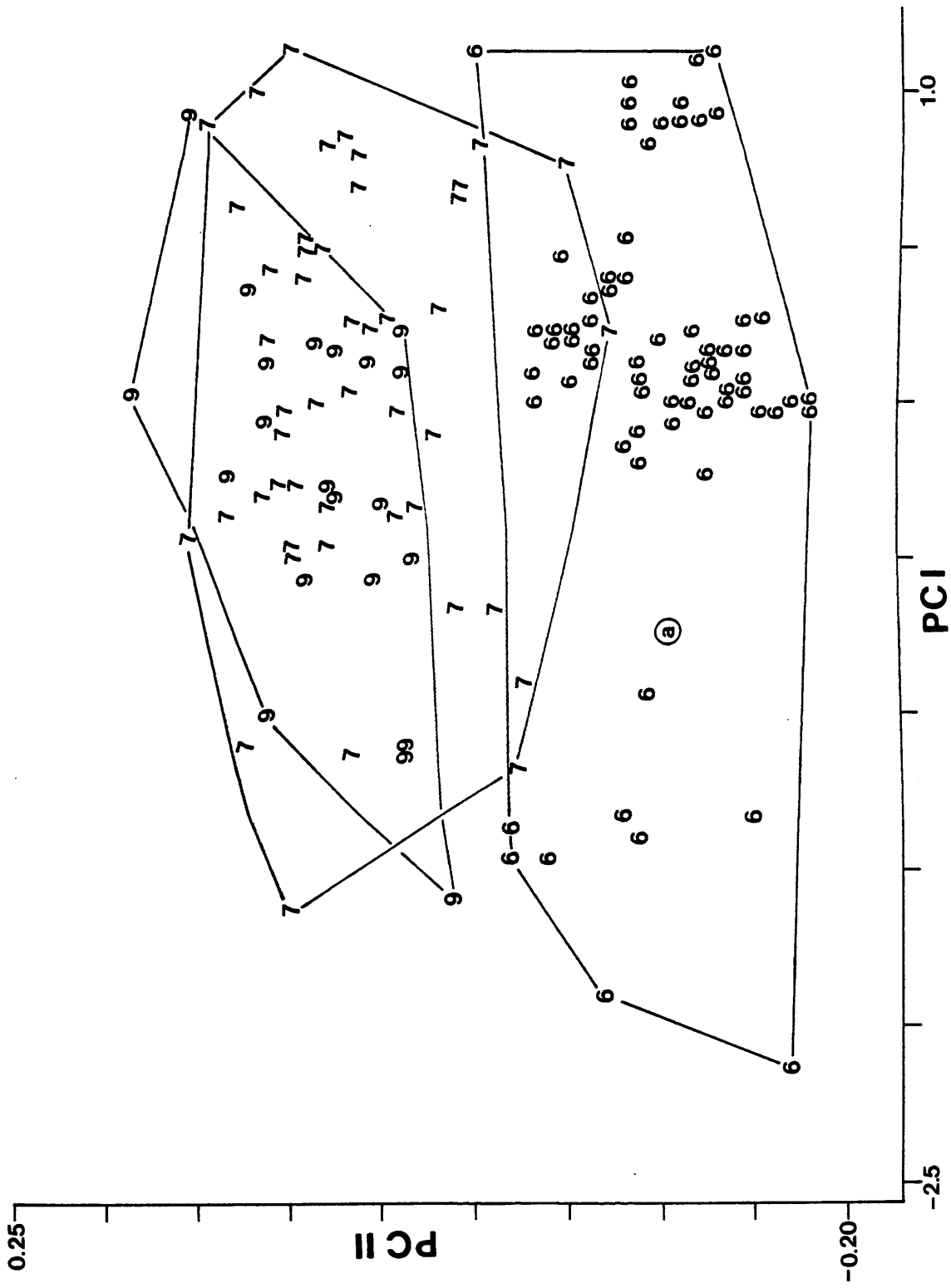

0.25
-0.20
PC II
-2.5
1.0
PC I
a

Fig. 9. Projection of individuals of Urotrygon asterias (7) and U. aspidura (9) along the first two principal component axes.

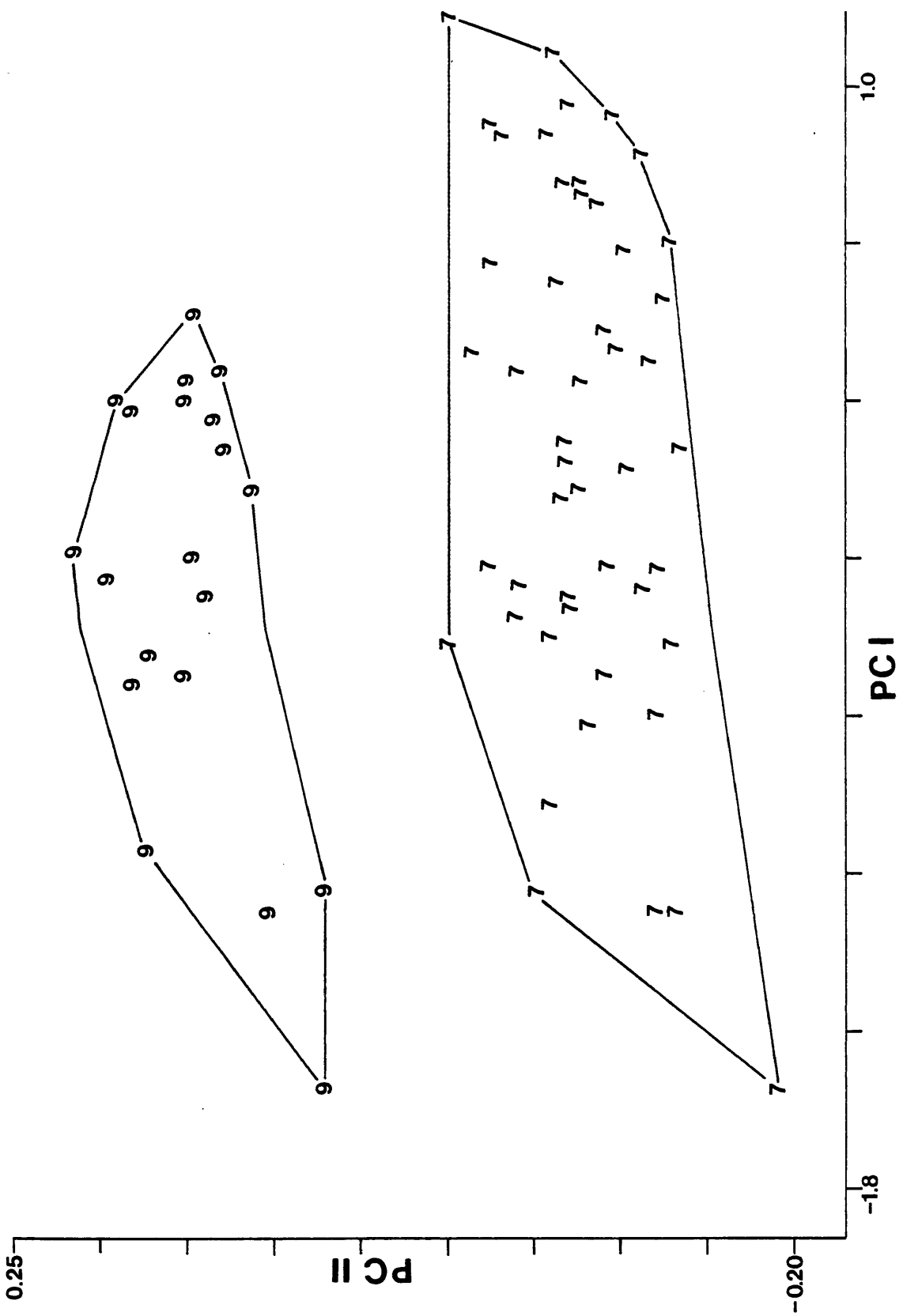

0.25
-0.20
PC II
-1.8
1.0
PC I

Fig. 10. Projection of individuals of three species: Urotrygon munda (3), U. asterias (7) and U. sp (3) (8); along the first two principal component axes.

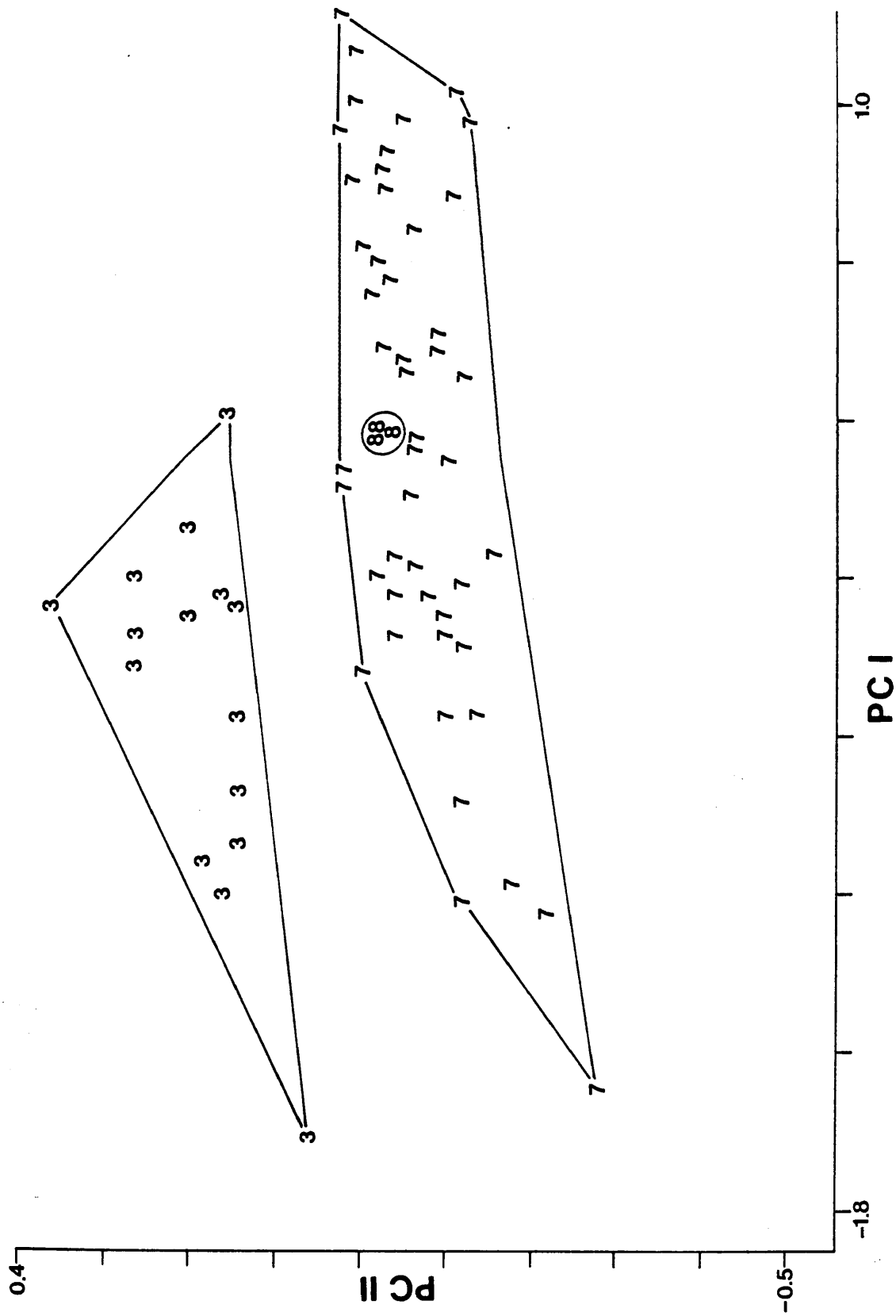

0.4
PC II
−0.5
−1.8
PC I
1.0

Fig. 11. Projection of individuals of eight species: Urotrygon rogersi (6), U. asterias (7), U. sp (3) (8), U. serrula (b), U. peruana (c), U. caudispinosa (d), U. goodei (e) and U. chilensis (f); along the first two principal component axes.

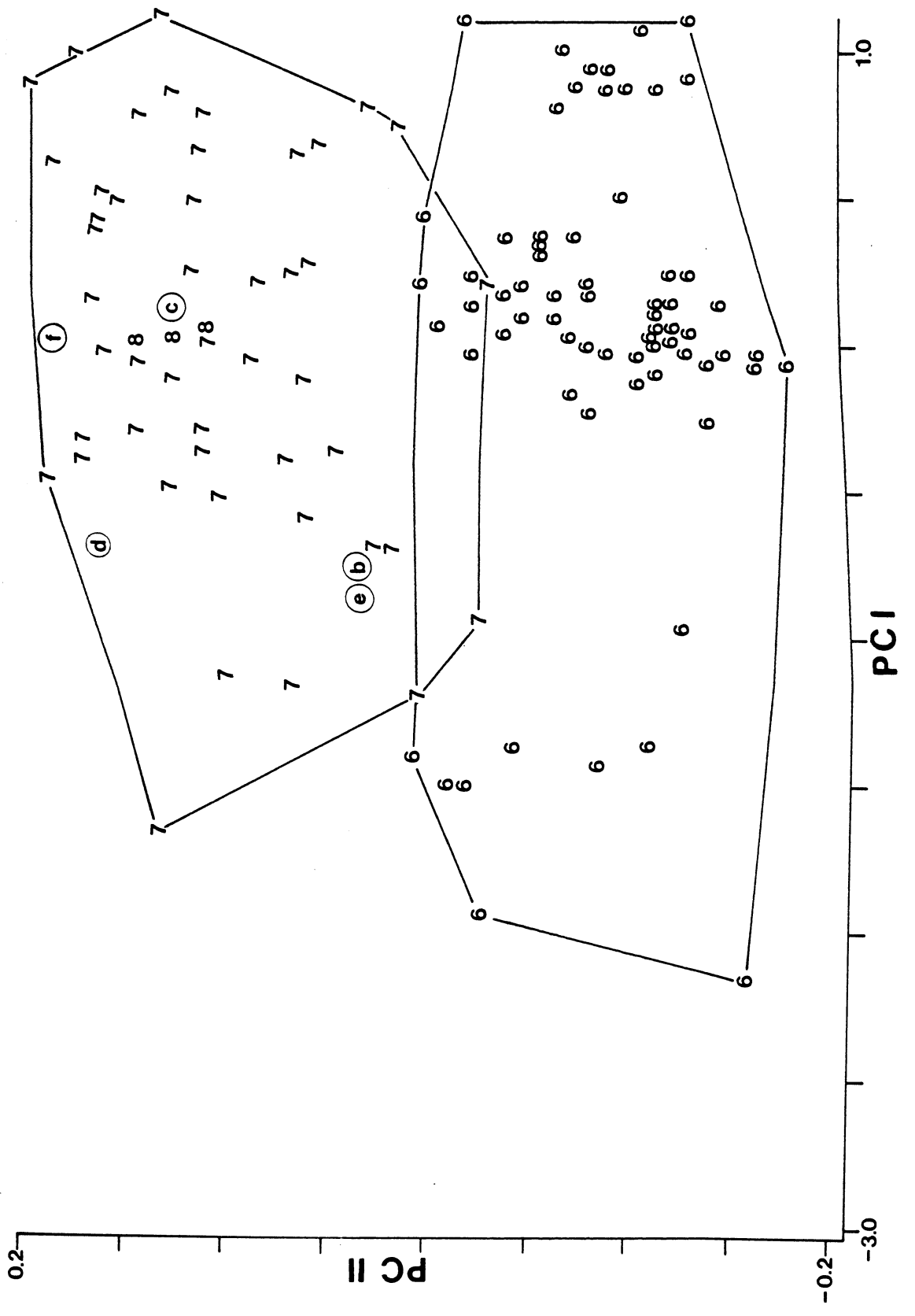

PC II
PC I
0.2
-0.2
-3.0
1.0
a
b
c
d
e
f

Table 3. PRINCIPAL COMPONENT ANALYSES OF MORPHOMETRIC VRIABLES: ANALYSIS 6 AND 7. Analysis 6.-- Urotrygon rogersi (N=70), U. asterias (N=48), U. binghami (N=1) and U. aspidura (N=24). Analysis 7.-- Urotrygon asterias (N=40) and U. aspidura (N=21). Abbreviations for morphometric characters are explained in text.

	Analysis 6		Analysis 7	
Character	PC1	PC2	PC1	PC2
DMW	.20	-.04	.19	.14
PREOB	.19	-.07	.17	.30
PREOR	.18	-.05	.16	.26
PRENS	.18	-.05	.16	.31
NASL	.21	-.25	.21	.06
NASW	.21	-.08	.20	-.10
OD	.16	-.33	.15	-.17
ED	.16	-.49	.17	-.53
INTW	.17	.06	.17	-.06
OBST	.15	-.12	.16	-.00
SPL	.14	.04	.16	-.04
DSP	.15	.00	.15	.08
PL	.20	.15	.20	-.09
PLW	.19	.28	.18	.01
CDH	.16	-.13	.18	-.11
CDLD	.18	.14	.18	.24
TALW	.17	.50	.21	-.40
WA	.20	-.11	.21	.23
WB	.21	-.11	.21	.07
WC	.18	.10	.20	.06
DA	.18	.08	.19	-.17
DC	.18	.06	.19	.14
STOCL	.19	.06	.19	.01
CLTOLD	.18	.17	.18	.08
CLTOCT	.17	.16	.18	.12
% variance explained	90	2	90	3

Table 4. PRINCIPAL COMPONENT ANALYSES OF MORPHOMETRIC VARIABLES: ANALYSIS 8 AND 9. Analysis 8.-- Urotrygon munda (N=15), U. asterias (N=48) and U. sp (3) (N=3). Analysis 9.-- Urotrygon rogersi (N=70), U. asterias (N=48), U. sp (3) (N=3), U. serrula (N=1), U. peruana (N=1), U. caudispinosa (N=1), U. goodei (N=1) and U. chilensis (N=1). Abbreviations for morphometric characters are explained in text.

	Analysis 8		Analysis 9	
Character	PC1	PC2	PC1	PC2
DMW	.18	.21	.20	-.09
PREOB	.16	.24	.20	-.20
PREOR	.16	.15	.19	-.18
PRENS	.12	.16	.19	-.20
NASL	.21	.16	.21	-.26
NASW	.19	.17	.21	-.06
OD	.17	-.28	.16	-.24
ED	.17	-.18	.15	-.27
INTW	.16	.10	.17	.07
OBST	.19	-.29	.15	-.09
SPL	.19	-.37	.13	.08
DSP	.16	-.05	.15	-.02
PL	.19	.07	.20	.18
PLW	.17	.10	.20	.28
CDH	.16	.15	.16	-.04
CDLD	.23	-.50	.18	.04
TALW	.19	.10	.17	.65
WA	.22	.20	.20	-.09
WB	.21	-.06	.21	-.07
WC	.21	-.24	.18	.11
DA	.18	.05	.17	.15
DC	.17	.19	.18	.11
STOCL	.19	.03	.20	.05
CLTOLD	.16	.15	.17	.11
CLTOCT	.18	-.05	.17	.08
% variance explained	90	3	91	2

width and eye diameter. Urotrygon rogersi and U. asterias overlap slightly along PC2 axis. The remaining species were all clustered with Urotrygon asterias.

The Principal Components Analyses distinguished, at least in part, among seven of 16 nominal and undescribed species of Urotrygon.

1) The first two analyses compared eight species largely grouped them into three phenetic assemblages, i.e., 1) Urotrygon microphthalmum; 2) U. venezuelae, U. munda and U. sp (1); 3) U. rogersi, U. asterias, U. aspidura, U. binghami and U. sp (3). U. sp (2) was located between the second and third assemblages.
2) Urotrygon venezuelae, U. munda and U. sp (1) were largely separated along PC1 axis, which in all analyses was a size component. Urotrygon sp (1) overlapped U. venezuelae and partially overlapped U. munda along PC2 axis.
3) Urotrygon sp (2) was clustered with U. munda.
4) Urotrygon aspidura was distinguished from U. rogersi; however, U. asterias partially overlapped both species. U. binghami was clustered with U. rogersi.
5) Urotrygon sp (3), U. serrula, U. peruana, U. caudispinosa, U. goodei and U. chilensis were all clustered with U. asterias.

UNIVARIATE ANALYSES

Characters with high loadings in the principal component analyses or which have been cited in the literature as distinguishing among the species were subjected to Analysis of Variance (ANOVA).

Despite the fact that disc width did not load heavily in any of the principal component analyses it distinguished several species of Urotrygon in the univariate analysis (Fig. 12). Urotrygon microphthalmum was clearly distinct from all other species in having a relatively narrow disc. Disc width also distinguished U. munda from U. sp (1) and U. asterias from U. rogersi (Table 5). In fact, the original description of U. rogersi clearly stated that it differs from U. asterias in having a wider disc (Jordan and Starks, 1895).

Snout length (preorbital and prenasal lengths) likewise did not load heavily in the principal component analyses but was significantly different between the following species pairs (Table 5): Urotrygon microphthalmum and U. venezuelae, U. munda and U. sp (1) and U. rogersi and U. asterias (Fig. 13, 14). The ANOVA for both lengths compared within the latter two species pairs showed the significant F-values at the $p=0.0001$.

Orbit diameter which loaded heavily in the several principal component analyses served to separate Urotrygon microphthalmum and U. venezuelae from the remaining species (Fig. 15 and Table 5). It also separated U. rogersi from U. asterias and U. aspidura from both of the former species. Both the pairwise t-test and Duncan's multiple range test showed the significant separation of three species (Table 6).

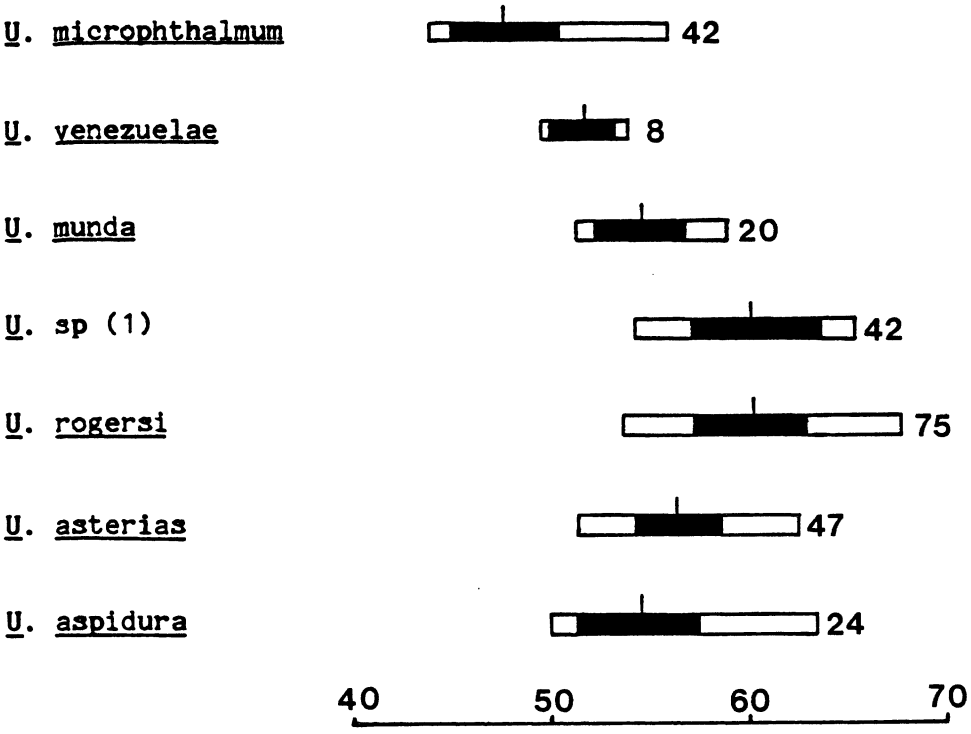


Fig. 12. Variation in disc width in hundredths of total length among seven species of Urotrygon. The number next to each diagram is the sample size. Vertical line: mean; solid rectangle: one standard deviation; open rectangle: range.

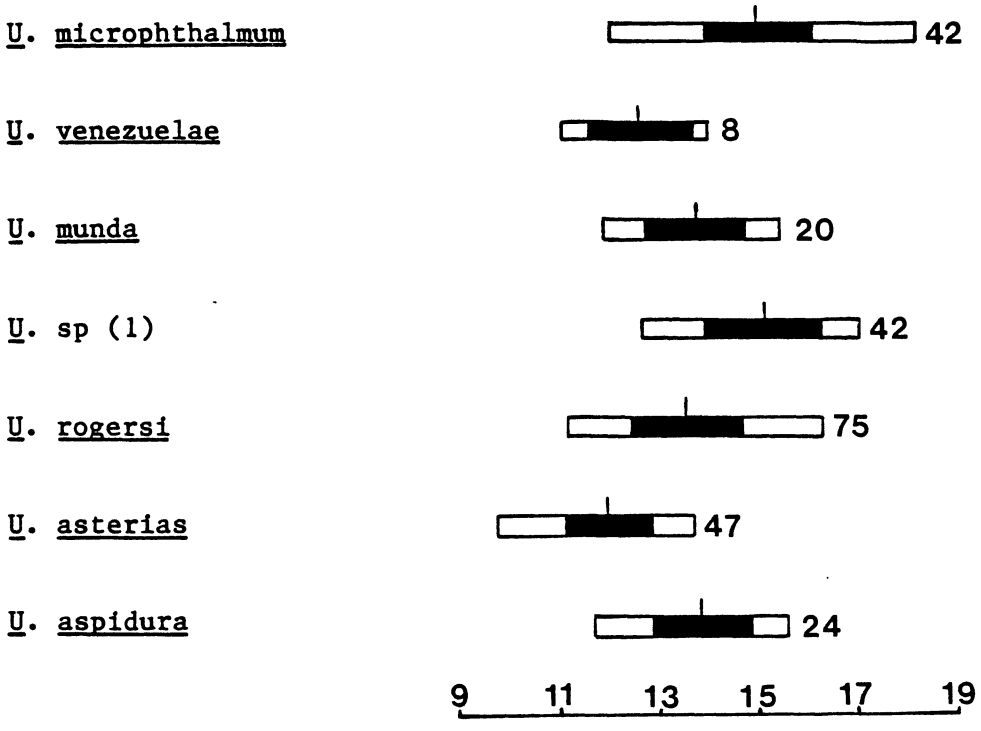


Fig. 13. Variation in preorbital length in hundredths of total length among seven species of Urotrygon. Refer to Figure 12 for the explanation of diagram.

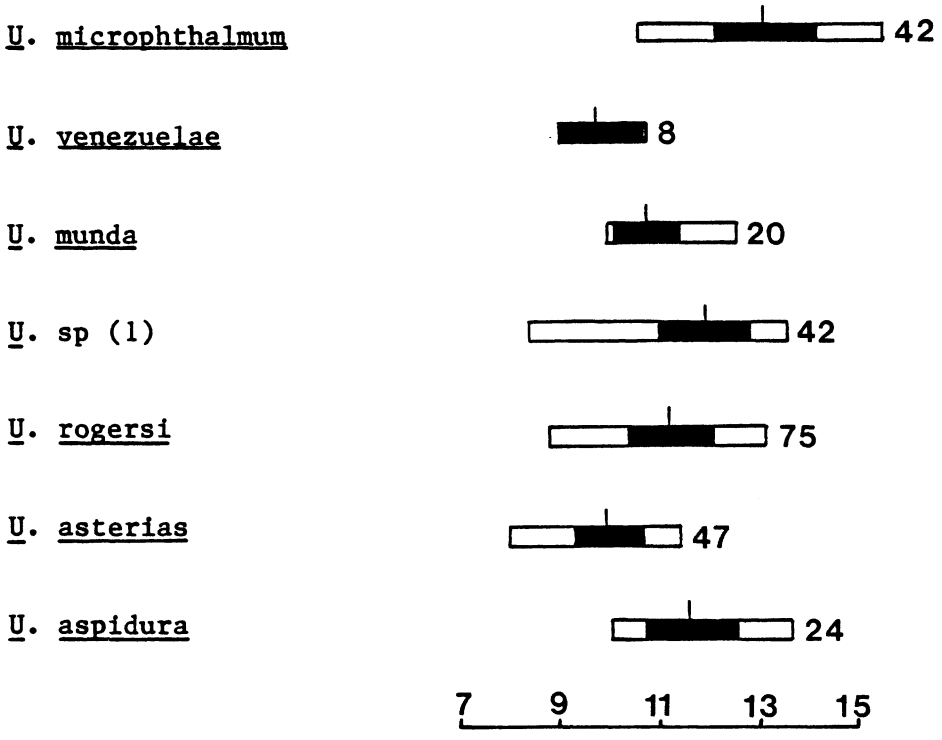


Fig. 14. Variation in prenasal length in hundredths of total length among seven species of Urotrygon. Refer to Figure 12 for the explanation of diagram.

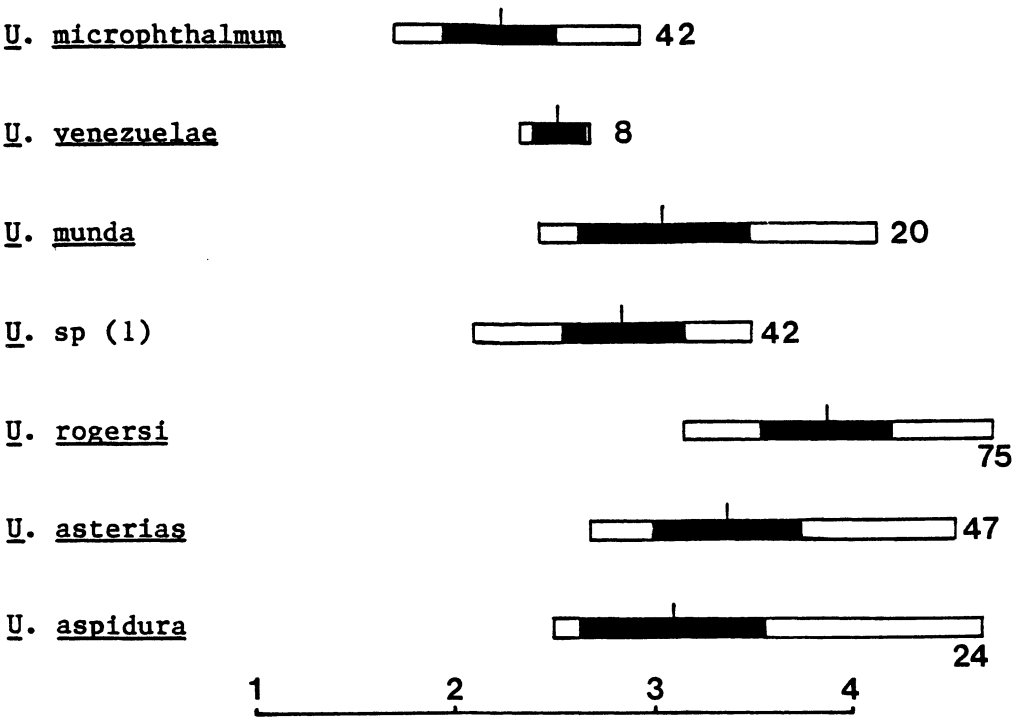


Fig. 15. Variation in orbit diameter in hundredths of total length among seven species of Urotrygon. Refer to Figure 12 for the explanation of diagram.

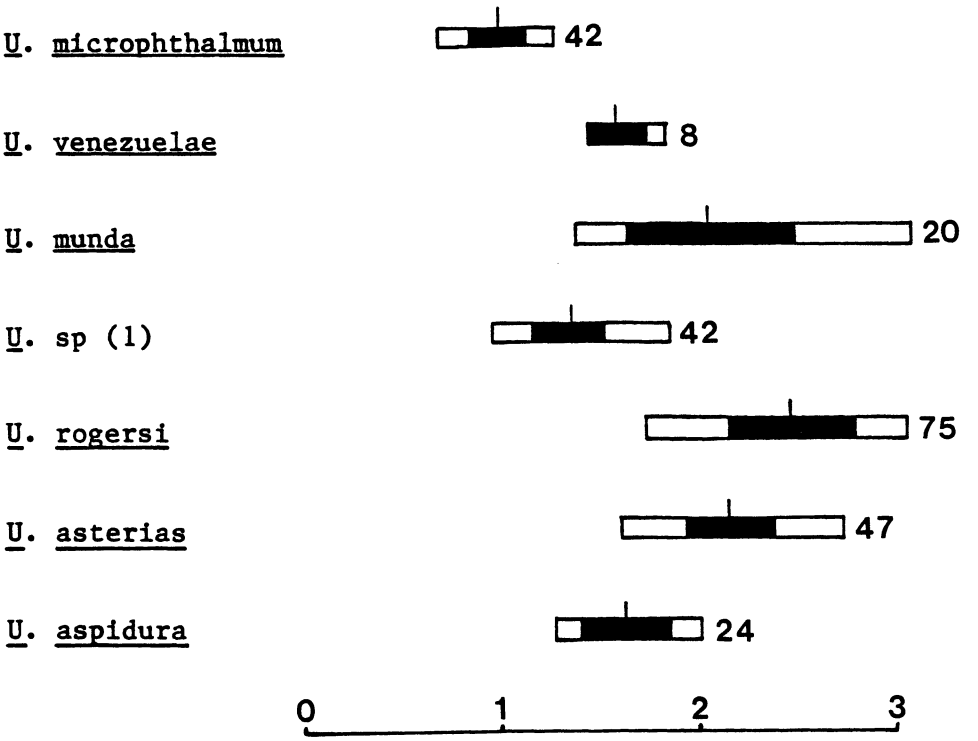


Fig. 16. Variation in eye diameter in hundredths of total length among seven species of Urotrygon. Refer to Figure 12 for the explanation of diagram.

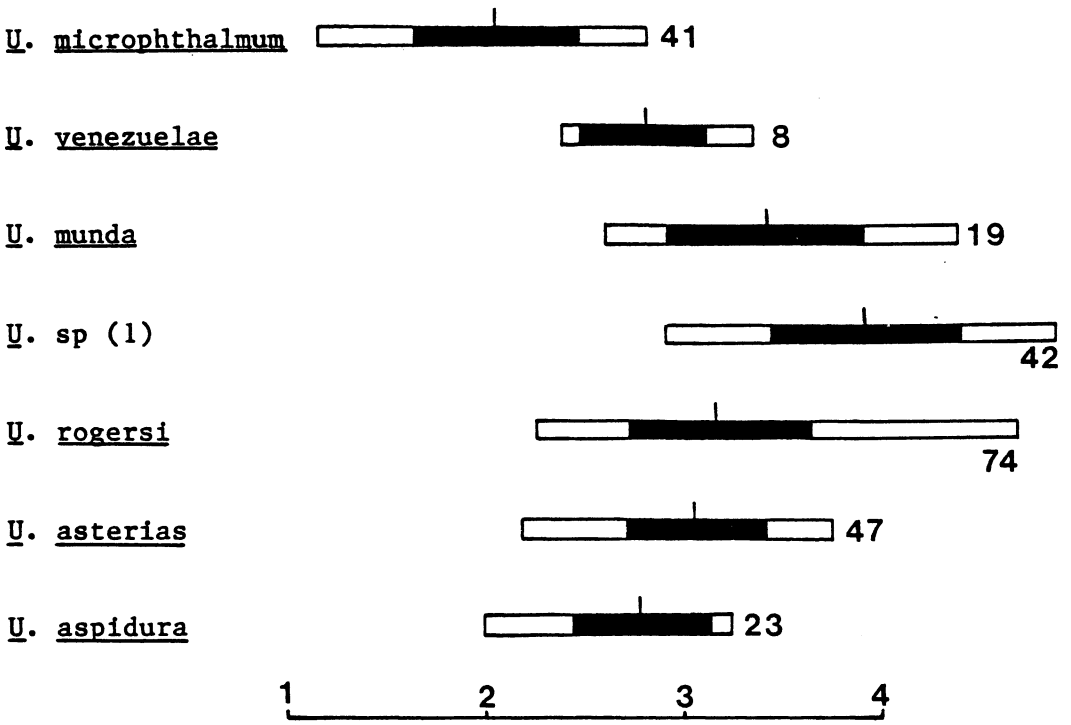
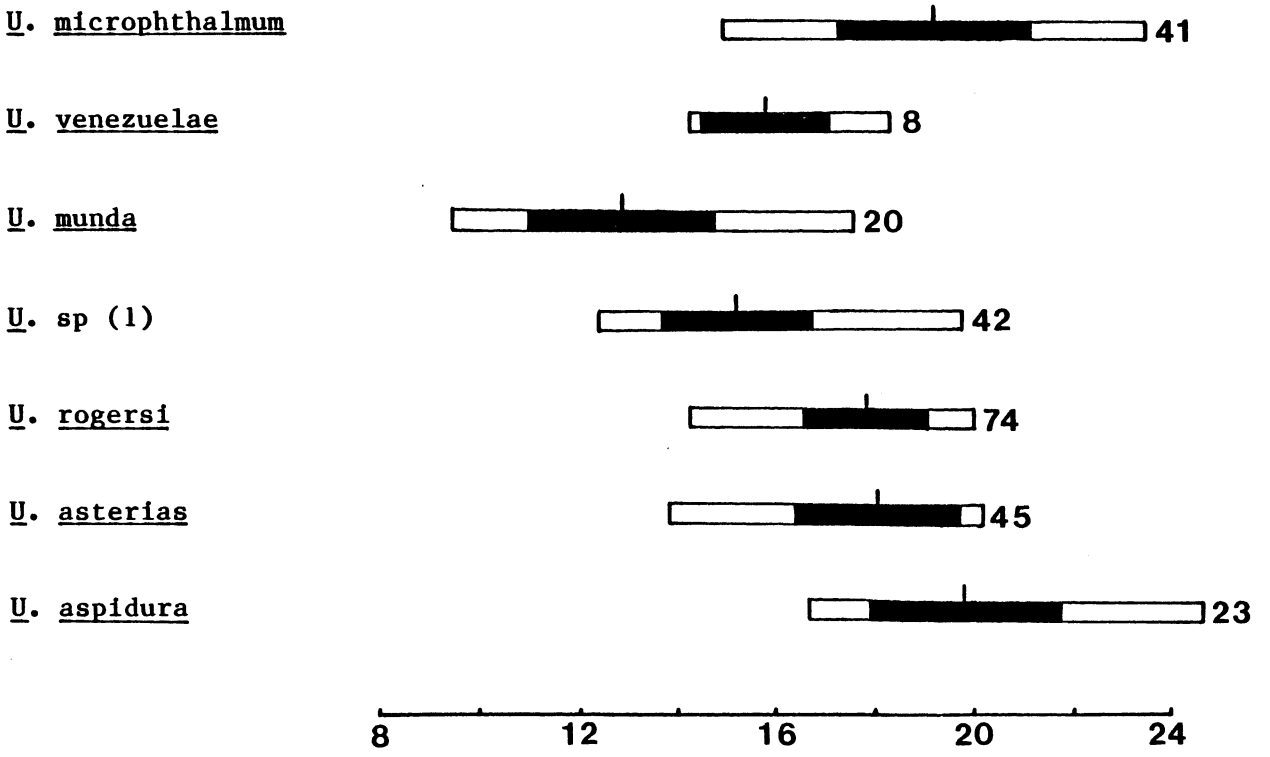


Fig. 17. Variation in height of caudal fin in hundredths of total length among seven species of Urotrygon. Refer to Figure 12 for the explanation of diagram.

Fig. 18. Variation in length of dorsal lobe of caudal fin in hundredths of total length among seven species of Urotrygon. Refer to Figure 12 for the explanation of diagram.


U. microphthalmum
41
U. venezuelae
8
U. munda
20
U. sp (1)
42
U. rogersi
74
U. asterias
45
U. aspidura
23
8
12
16
20
24

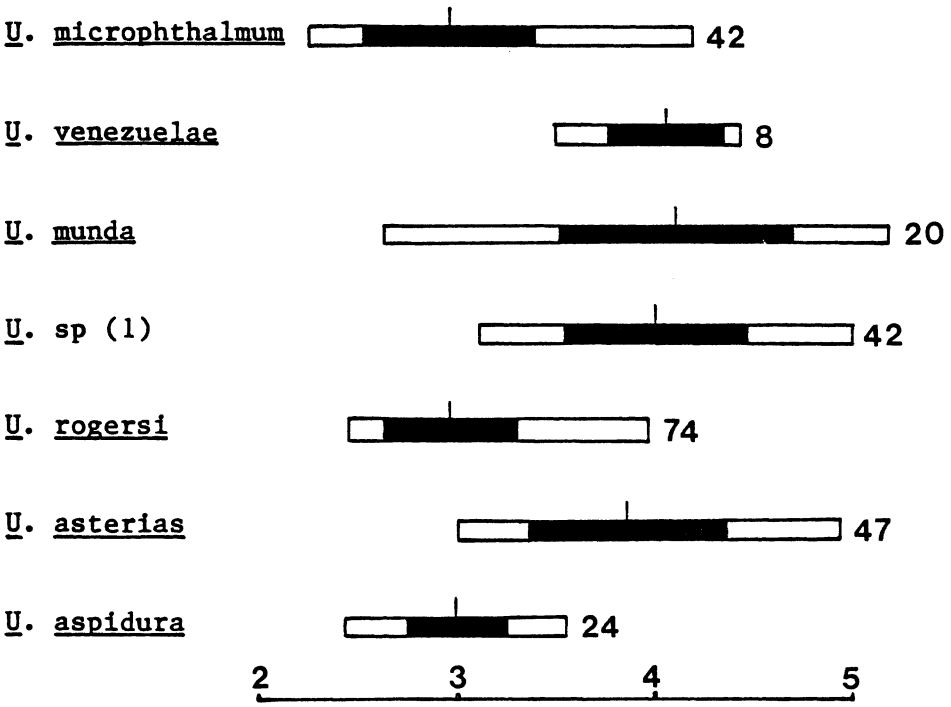


Fig. 19. Variation in tail height at axil of pelvic fin in hundredths of total length among seven species of Urotrygon. Refer to Figure 12 for the explanation of diagram.

Urotrygon sp (2) had a larger orbital diameter (3.78 and 3.82 % of total length) than U. munda ($\bar{x}$=3.10) and U. sp (1) ($\bar{x}$=2.89) (Table 5).

Urotrygon microphthalmum was distinct in having smaller eyes from the rest of the species (Fig. 16), even from U. sp (1) and U. aspidura with small eyes. In addition, both the pairwise t-test and Duncan's multiple range test discriminated significantly the species among U. rogersi, U. asterias and U. aspidura (Table 6).

Height of caudal fin distinguished Urotrygon microphthalmum from the rest of the species. It also separated U. munda from U. sp (1) (Fig. 17).

Lenght of dorsal lobe of caudal fin distinguished Urotrygon microphthalmum from U. venezuelae (Table 5 and Fig. 18). The character also contributed to the separation of U. munda, U. sp (1), U. rogersi, U. asterias and U. aspidura (Fig. 18). Both the pairwise t-test and Duncan's multiple range test grouped the above species into four groups: U. munda, U. sp (1), U. rogersi and U. asterias and U. aspidura (Table 7).

Tail height at axil of pelvic fins contributed most effectively to the separation of Urotrygon rogersi from U. asterias (Fig. 19). The ANOVA showed the significant difference between two species at p=0.0001.

The number of vertebral centra divided Urotrygon into two groups (Table 8), yet this difference was of taxonomic value only for one case. U. daviesi was distinguished from the rest of the species in having the highest number of vertebral centra. The vertebral central ranged from 66 to 77 in U. microphthalmum, U. venezuelae, U. munda and U. sp (1) (Table 8). For the remaining species, the vertebral centra1

Table 5. SELECTED MORPHOMETRIC MEASUREMENTS OF SPECIES OF Urotrygon EXPRESSED AS PERCENTAGE OF TOTAL LENGTH. Those of Urotrygon daviesi were based on two specimens (BPBM 24578 and NTMS 10765-001). Abbreviation for characters are given in text. A) Urotrygon daviesi, U. microphthalmum and U. venezuelae; B) Urotrygon munda, U. sp (1) and U. sp (2); C) Urotrygon rogersi, U. sp (3) and U. asterias; D) Urotrygon aspidura, U. serrula, U. peruana and U. binghami; E) Urotrygon caudispinosa, U. goodei and U. chilensis.

A	U. daviesi		U. microphthalmum			U. venezuelae		
No. of specimens	N=2		N=42			N=8		
Total length (mm)	481	505	127 - 288			233 - 286		
			Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
DW	54.05	49.70	44.23-56.34	48.17	2.50	50.00-54.48	48.17	2.50
PREOB	16.61	16.20	12.37-18.47	15.77	1.13	11.34-14.25	12.90	1.01
PRENS	14.32	13.29	10.09-15.59	13.24	1.05	9.03-10.94	9.89	0.99
OB	3.53	2.97	1.74- 2.99	2.29	0.27	2.39- 2.73	2.56	0.11
ED	1.98	2.28	0.71- 1.32	1.01	0.15	1.46- 1.87	1.61	0.16
CDH	1.46	1.80	1.20- 2.85	2.07	0.40	2.41- 3.40	2.84	0.31
CDLD	16.22	16.73	15.07-23.53	19.24	1.93	14.37-18.29	15.89	1.22
TAMH	2.62	1.90	2.27- 4.23	2.98	0.43	3.52- 4.47	4.09	0.39

Table 5. Continued.

B	U. munda			U. sp (1)			U. sp (2)	
No. of specimens	N=20			N=42			N=2	
Total length (mm)	96 - 288			81 - 181			241	188
	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD		
DW	51.71-59.68	55.13	2.35	54.70-67.90	60.90	3.21	53.94	56.65
PREOB	12.11-15.65	14.05	1.02	12.87-17.32	15.40	1.11	13.98	15.48
PRENS	10.03-12.66	10.87	0.65	8.53-13.73	12.02	0.90	11.45	12.61
OB	2.46- 4.17	3.10	0.52	2.23- 3.54	2.89	0.32	3.78	3.82
ED	1.39- 3.10	2.08	0.42	0.96- 1.89	1.39	0.17	2.12	2.29
CDH	2.64- 4.42	3.46	0.49	2.94- 4.94	3.96	0.48	3.72	3.78
CDLD	9.49-17.61	12.99	1.84	12.44-19.93	15.28	1.48	10.73	14.27
TAMH	2.65- 5.21	4.14	0.60	3.13- 5.03	4.03	0.45	3.44	3.67

Table 5. Continued.

C	U. rogersi			U. sp (3)			U. asterias		
No. of specimens	N=76			N=3			N=47		
Total length (mm)	104 - 462			267	264	258	128 - 419		
	Range	$\bar{x}$	SD				Range	$\bar{x}$	SD
DW	53.85-67.90	60.10	3.00	51.03	54.17	51.94	51.57-62.09	56.61	2.30
PREOB	11.28-16.51	13.74	1.10	11.01	11.44	12.95	9.82-13.59	12.04	0.86
PRENS	8.85-13.21	11.29	0.84	8.02	8.41	9.42	8.05-11.47	10.00	0.71
OB	3.14- 4.74	3.88	0.35	3.04	3.41	3.41	2.69- 4.53	3.35	0.33
ED	1.73- 3.07	2.48	0.32	2.05	2.25	3.04	1.60- 2.75	2.16	0.23
CDH	2.26- 4.71	3.21	0.45	3.60	4.05	4.34	2.20- 3.79	3.04	0.38
CDLD	14.35-20.28	17.97	1.26	17.79	18.75	19.36	13.93-22.22	18.06	1.64
TAMH	2.49- 4.00	3.00	0.34	3.56	4.13	4.46	3.03- 4.97	3.91	0.49

Table 5. Continued.

D	U. aspidura			U. serrula	U. peruana	U. binghami
No. of specimens	N=24			N=1	N=1	N=1
Total length (mm)	Range	$\bar{x}$	SD			
DW	50.00-63.90	54.46	2.98	53.82	59.14	56.68
PREOB	11.76-15.61	13.92	0.98	11.99	12.62	14.01
PRENS	10.17-13.73	11.74	0.92	10.66	10.25	11.18
OB	2.52- 4.68	3.11	0.46	4.35	3.44	3.74
ED	1.26- 2.02	1.61	0.22	2.44	2.11	2.30
CDH	1.99- 3.24	2.78	0.35	3.50	2.80	3.74
CDLD	16.69-24.72	19.81	1.96	17.51	16.99	19.25
TAMH	2.45- 3.57	3.00	0.25	3.61	4.27	2.67

Table 5. Continued.

E	*U. caudispinosus*	*U. goodei*	*U. chilensis*
No. of specimens	N=1	N=1	N=1
Total length (mm)	192	183	265
DW	59.64	56.56	60.75
PREOB	12.29	11.53	11.40
PRENS	9.06	10.05	9.92
OB	3.59	3.83	3.36
ED	2.08	2.30	2.08
CDH	3.13	3.66	2.98
CDLD	19.06	19.02	16.45
TAMN	4.79	3.83	4.08

Table 6. PAIRWISE T-TEST FOR ORBIT AND EYE DIAMETERS (AS PERCENT TL) AMONG Urotrygon rogersi, U. asterias AND U. aspidura. The means with the same letter are not significantly different. Duncan's multiple range test showed the same results as the pairwise t-test.

		Orgit diameter			Eye diameter		
		Mean	N	Grouping	Mean	N	Grouping
Urotrygon	rogersi	3.89	76	A	2.45	76	A
U.	asterias	3.35	47	B	2.14	47	B
U.	aspidura	3.11	24	C	1.61	24	C

Table 7. PAIRWISE T-TEST FOR LENGTH OF DORSAL LOBE OF CAUDAL FIN (AS PERCENT TL) AMONG Urotrygon munda, U. sp (1), U. rogersi, U. asterias AND U. aspidura. The means with the same letter are not significantly different. Duncan's multiple range test showed the same results as pairwise t-test.

		Mean	N	Grouping
Urotrygon	munda	12.99	20	A
U.	sp (1)	15.29	42	B
U.	rogersi	17.97	75	C
U.	asterias	18.06	47	C
U.	aspidura	19.81	23	D

Table 8. NUMBER OF VERTEBRAL CENTRA OF THE SPECIES OF *Urotrygon*.

		Range	N
Urotrygon	*daviesi*	115	1
U.	*microphthalmum*	66 - 77	7
U.	*venezuelae*	74 - 76	7
U.	*munda*	72 - 77	7
U.	sp (1)	61 - 73	11
U.	sp (2)	68, 69	2
U.	*rogersi*	93 - 103	7
U.	*asterias*	84 - 97	9
U.	sp (3)	83, 86, 88	3
U.	*aspidura*	84 - 94	8
U.	*binghami*	?	
U.	*serrula*	86	1
U.	*peruana*	85	1
U.	*caudispinosa*	92	1
U.	*goodei*	93	1
U.	*chilensis*	85	1

ranged from 83 to 108. The number of tooth rows of upper jaw did not separate any species of Urotrygon (Fig. 20).

The angle of snout served to separate Urotrygon munda from U. sp (1) and U. rogersi from U. asterias (Fig. 21). The difference in the angle of the snout between the same sex of two species was statistically significant at p=0.0001. The ANOVA for angle of snout compared between two sexes of the same species of Urotrygon all showed the significant F-value at the p=0.0001, suggesting it to be a sexual dimorphic character.

The univariate analyses revealed the taxonomic importance in several morphometric characters which did not contribute highly to the separation of the species in the principal component analyses: disc width and snout dimension. The analyses thus reached the following conclusion:

1) U. microphthalmum differs from the other species in having the narrowest width of disc.
2) U. daviesi and U. microphthalmum have the longest snout.
3) U. daviesi has the highest number of vertebral centra.
4) U. munda differs from U. sp (1) in having a wider disc, shorter snout, larger eyes and broader angle of snout.
5) U. rogersi differs from U. asterias in having a wider disc, longer snout and more dorso-ventrally flattened tail.
6) U. aspidura differs from U. rogersi and U. asterias in having smaller eyes and slender, longer caudal fin.

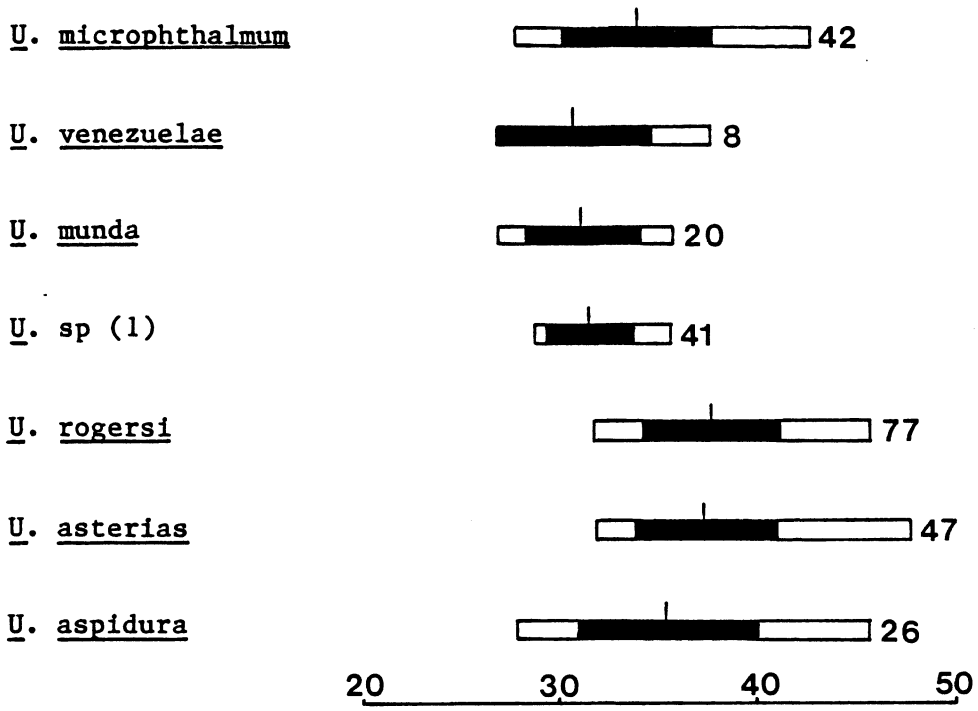
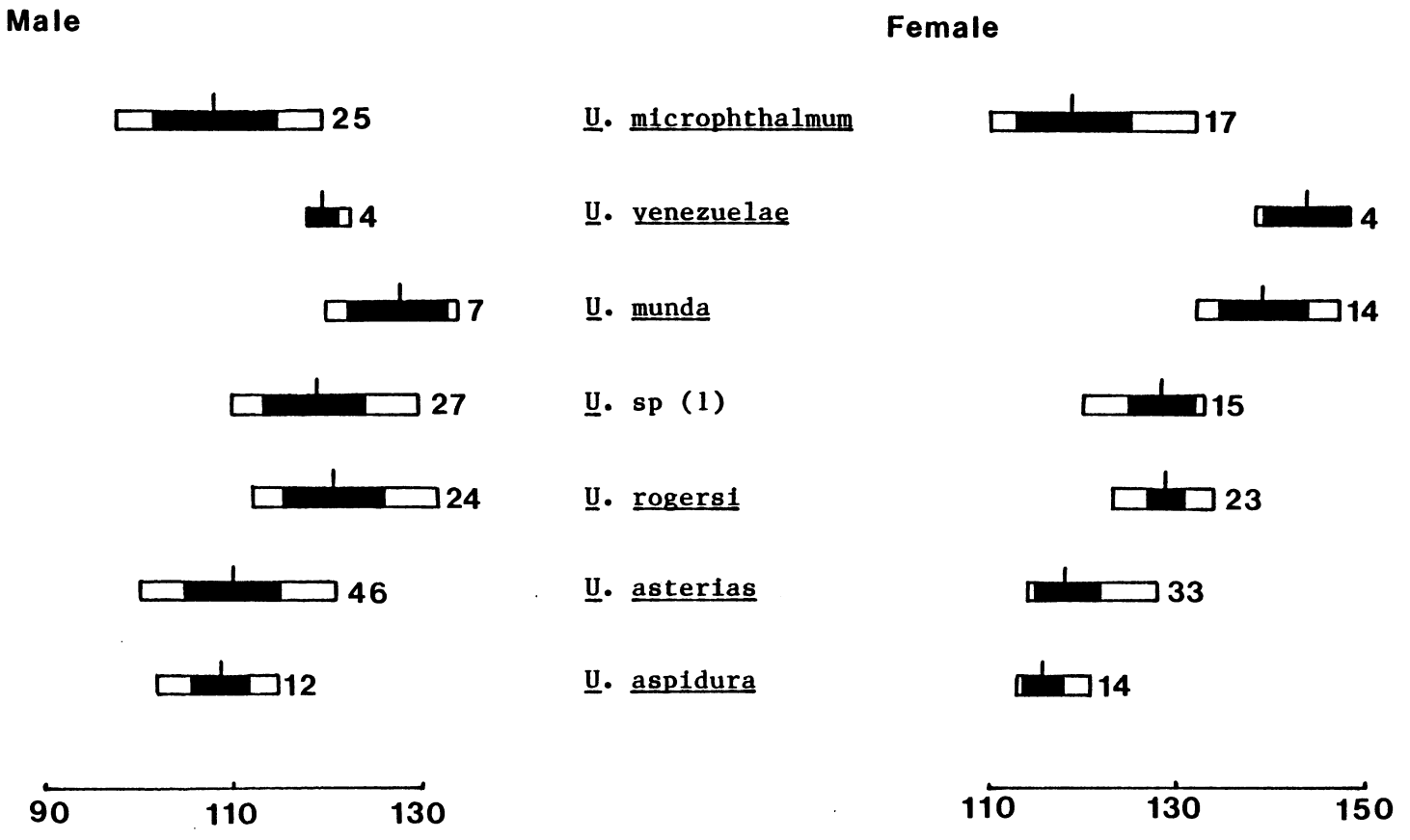


Fig. 20. Variation in the number of teeth in upper jaw among seven species of Urotrygon. Refer to Figure 12 for the explanation of diagram.

Fig. 21. Variation in angle of snout among seven species of Urotrygon. The measurements for two sexes of the species are separately given.


Male
Female
25
17
U. microphthalmum
4
4
U. venezuelae
7
14
U. munda
27
15
U. sp (1)
24
23
U. rogersi
46
33
U. asterias
12
14
U. aspidura
90
110
130
110
130
150

SQUAMATION

Urotrygon daviesi.-- The denticles are 0.3 to 0.4 mm in height with cone-shaped, straight crowns (Fig. 22A). The basal plates bear three or four narrow stellate ridges.

Specimens ranging from 480 mm to adults possess the denticles over the entire dorsal disc and both sides of tail (Fig. 22B). The ventral surface of the disc, pelvic fins, ventral side of tail at the base, between and behind pelvic fins and a small portion over the insertion of tail spine are devoid of denticles. The entire surface of the caudal fin is covered with denticles (Fig. 22 C). Occasionally, either the anterior portion of, or the entire dorsal surface of pelvic fins is covered with the denticles.

Urotrygon microphthalmum.-- The denticles are 0.3 to 0.5 mm in heigth with tear-drop-shaped crowns (Fig. 23). The basal plates do not extend lateral to the shaft of the denticles.

Individuals less than 100 mm TL are nearly naked. Those from 100 to 170 mm TL possess a sparse covering of denticles on the tip of the snout, area in front of eyes and anterior interorbital region (Fig. 23A). A few denticles are present along the inner margin of spiracles. The dorsal and lateral aspects of tail and the anterior region of dorsal lobe of caudal fin have a sparse covering of denticles. Specimens ranging from 170 to 200 mm TL are densely covered with denticles on the tip of the snout but sparsely covered with the denticles along the margin of the disc from the snout to the level of spiracles, on the interorbital region and along the midline from the nuchal to visceral region (Fig. 23B). The dorsal and lateral

Fig. 22. Squamation and denticles in Urotrygon daviesi. A) denticle; B) squamation on dorsal aspect; C) squamation on ventral aspect of tail near tail axil.

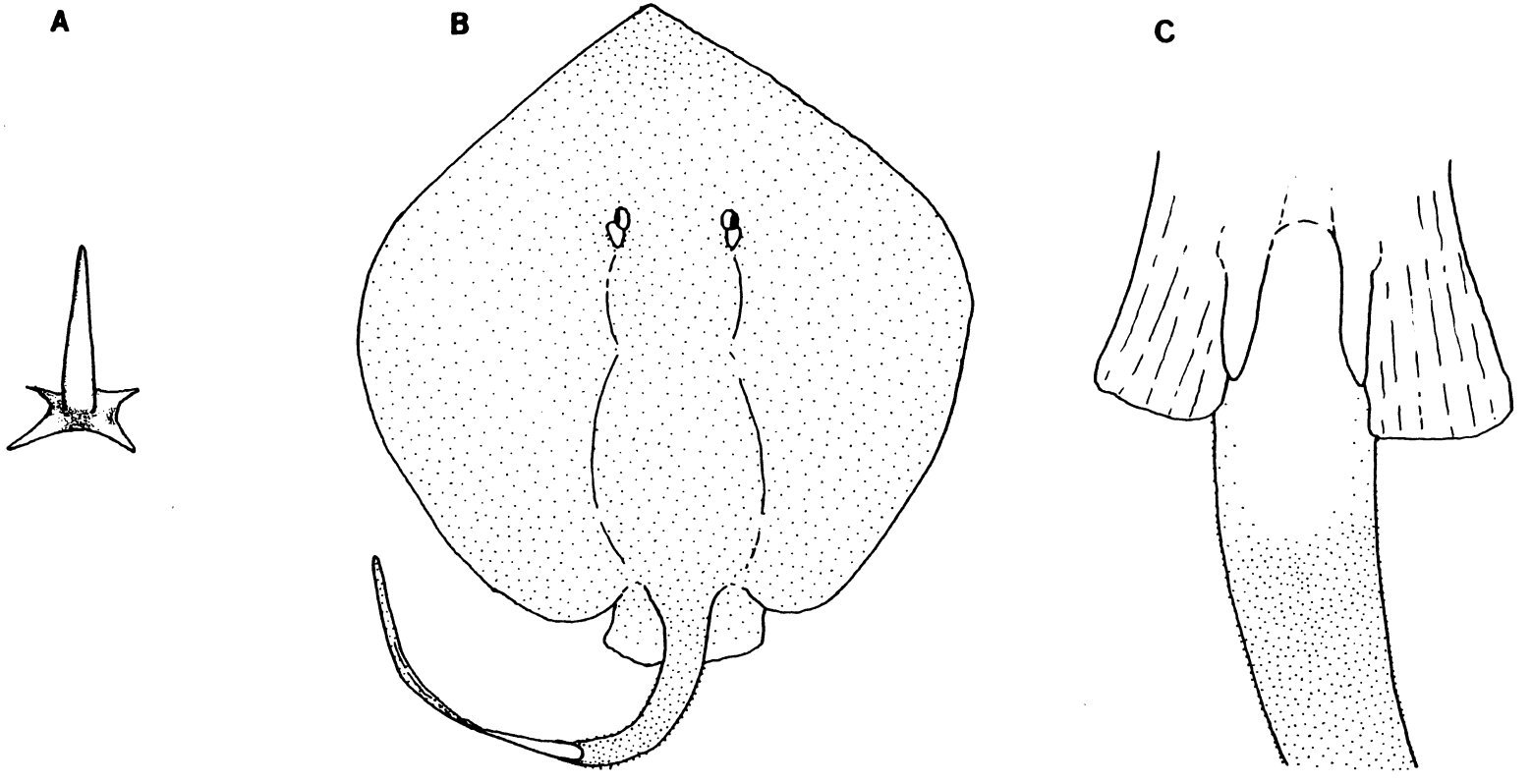
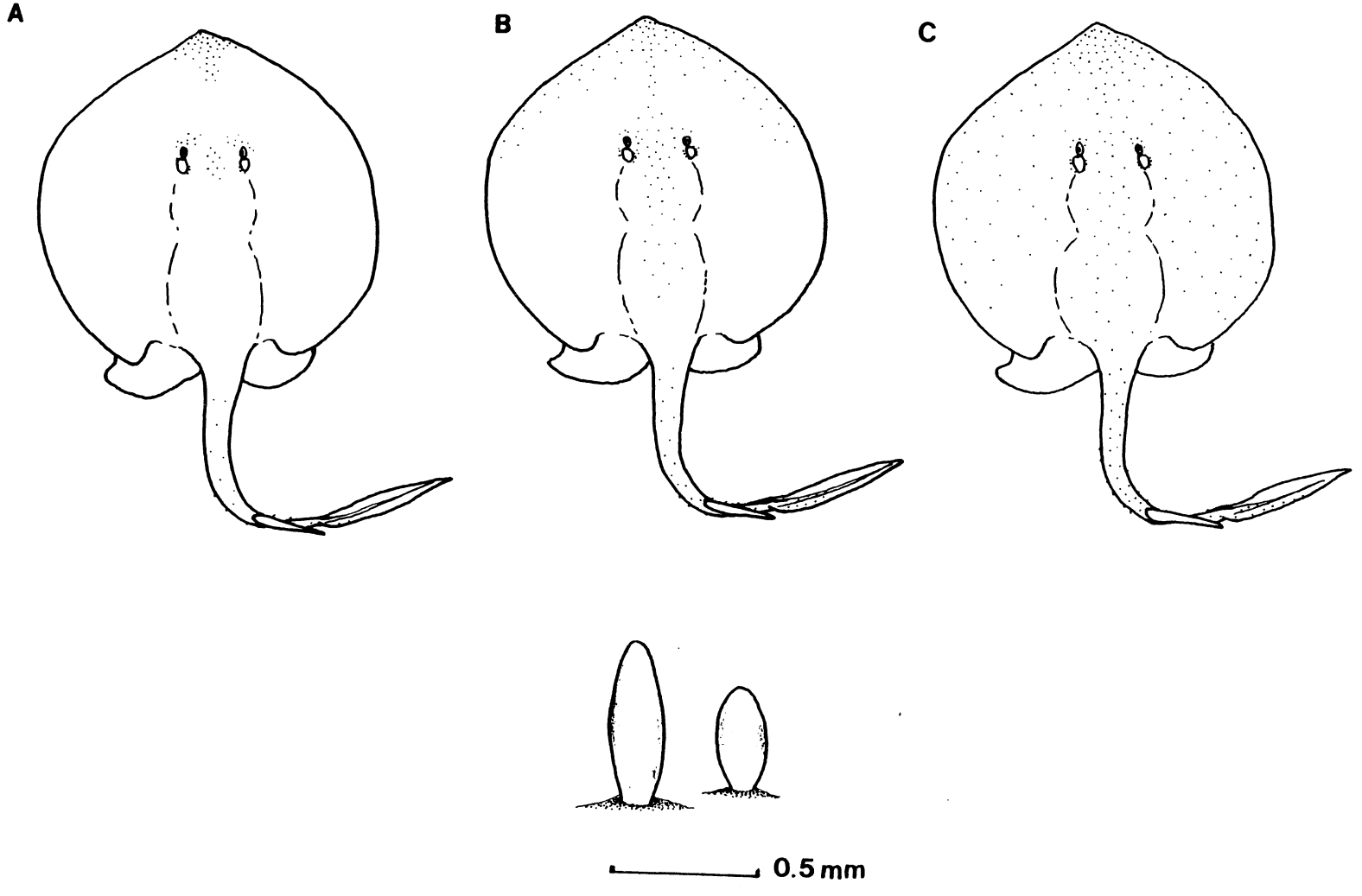

A
B
C

Fig. 23. Squamation and denticles in Urotrygon microphthalmum. A) squamation in individuals less than 100 mm TL; B) squamation in individuals ranging from 100 to 200 mm TL; C) squamation in individuals larger than 200 mm TL; D) denticles.

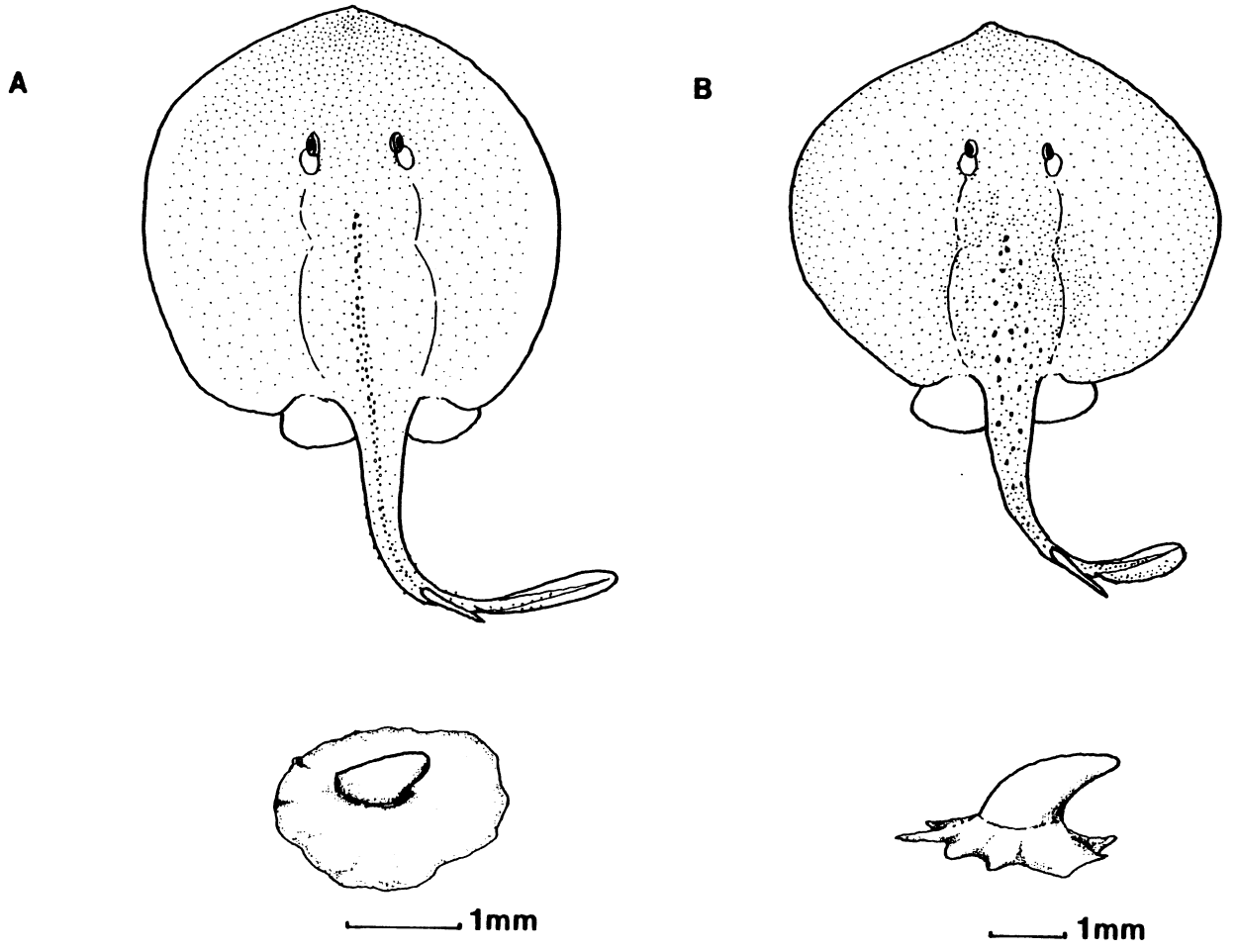

A
B
C
0.5 mm

aspects of tail and the anterior region of dorsal lobe of caudal fin are sparsely covered with the denticles. Individuals larger than 200 mm TL are covered with the denticles, sparsely distributed on the midline of the disc from the nuchal region to the area over the visceral cavity, but more densely on the snout and area lateral to eyes (Fig. 23C). The area lateral to the visceral cavity is devoid of denticles. The area at the posterior half of the outer margin of spiracles is covered with one to three denticles. The denticles are present along the edge of the disc from the tip of the snout to the mid-portion of the visceral cavity. They also cover the dorsal and lateral aspects of tail and the anterior region of dorsal lobe of caudal fin. The ventral surface of the disc, pelvic fins and tail is devoid of denticles.

Urotrygon venezuelae.-- The denticles are 0.3 to 0.6 mm in height with short, curved and cone-shaped crowns. The basal plates are broad and round (Fig. 24A).

The near term embryos are nearly naked. In adults the denticles are present over the dorsal disc, but much denser on the snout region. The extreme edge of the dorsal disc posterior to the level of eyes is devoid of denticles. A graded series of enlarged denticles is developed on the midline of the dorsal disc from either the nuchal or scapular region, forming one or two rows anteriorly but two or three rows posteriorly. In rare cases, the enlarged denticles on the midline of the dorsal disc are absent. The tail possesses two or three rows of the enlarged denticles on the midline, continuous with those on the dorsal disc. The dorsal and lateral aspects of tail are relatively densely covered with the denticles, extending to the dorsal

Fig. 24. Squamation and denticles in A) Urotrygon venezuelae and B) U. munda. Denticles of each species are shown in the bottom of each figure.


A
B
1mm
1mm

lobe and mid-lateral portion of the caudal fin. The ventral surface of the disc and tail and pelvic fins are devoid of denticles.

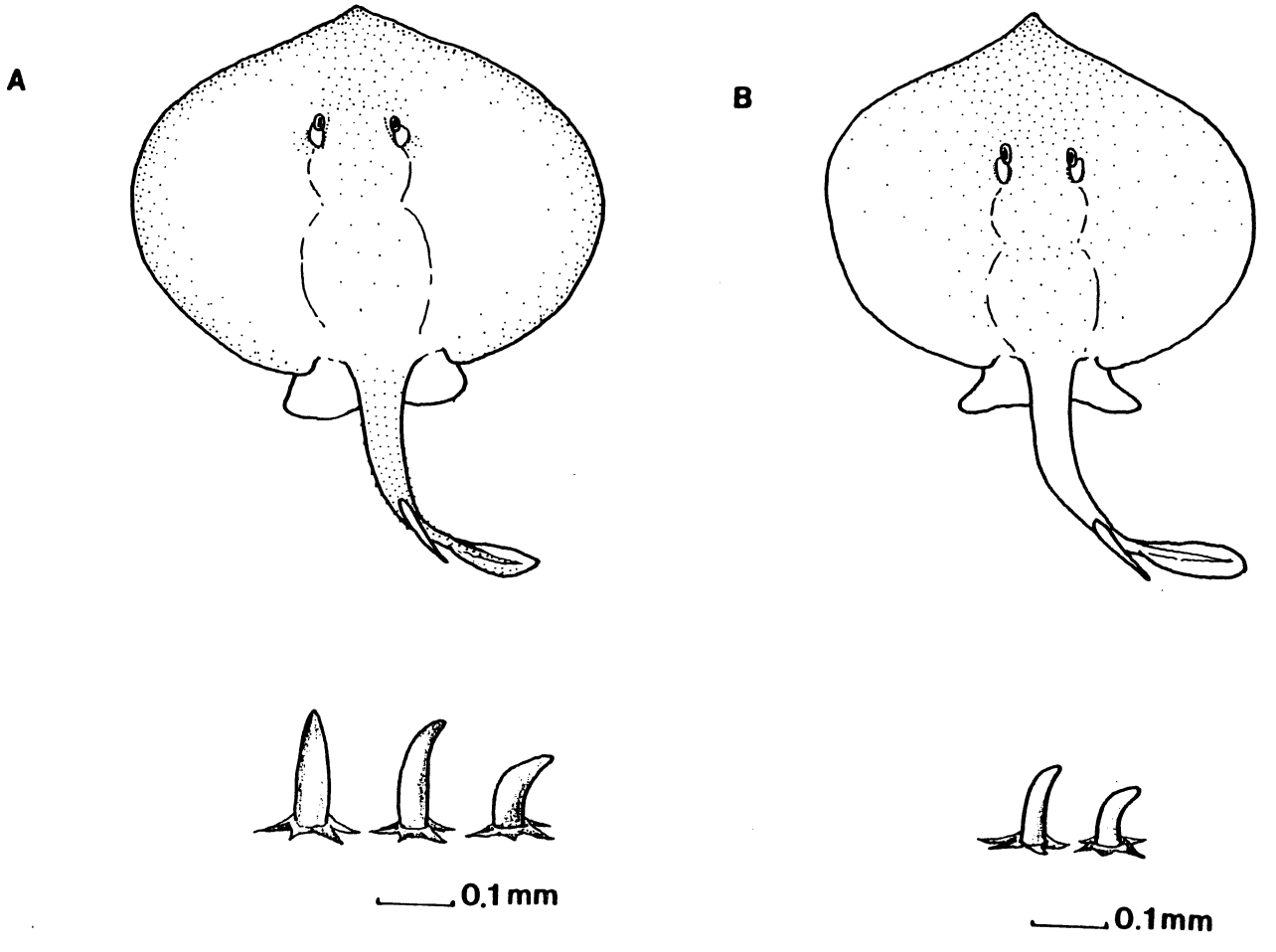
Urotrygon munda.-- The denticles are 2.00 to 3.00 mm in height with sharply recurved, cone-shaped crowns. The basal plates bear several stellate ridges (Fig. 24B).

In an embryo 96 mm TL, the disc and tail are completely naked. In an embryo 113 mm TL primodial denticle buds resembling the distribution pattern of those in adults are present on the disc. Specimens larger than 120 to 130 mm TL possess fully developed denticles on the entire dorsal disc and tail. The denticles are much denser and finer on the snout and become enlarged toward the midline of the dorsal disc and tail (Fig. 24B). The denticles cover the upper margin and mid-portion of the caudal fin. Pelvic fins are mostly naked, but in some individuals 3 to 4 small denticles are present on the dorsal aspect of the fins. The ventral surface of the disc and tail is devoid of the denticles.

Urotrygon sp (1).-- The denticles are 0.1 to 0.3 mm in height with slender, cone-shaped and curved crowns. The basal plates bear stelliform bases (Fig. 25A).

In the near term embryos and specimens smaller than 80 mm TL, the disc and tail are naked. Specimens larger 90 mm TL are covered with the denticles; densely developed on the snout area and the margin of the disc to near the posterior corner of the disc and sparsely on the interorbital and nuchal areas. In some specimens the denticles are sparsely developed on the scapular and visceral areas (Fig. 25A). One to two rows of slightly enlarged denticles are present along the inner and outer edges of spiracle openings, the inner of which occasionally

Fig. 25. Squamation and denticles in A) Urotrygon sp (1) and B) U. sp (2). Denticles of each species are shown in the bottom of each figure.


A
B
0.1 mm
0.1mm

extends forward to form a single row of the denticles along the inner side of eyes. The dorsal and lateral aspects of tail are densely covered with the denticles, extending to the anterior portion of dorsal lobe of caudal fin. The entire dorsal disc of the specimens taken from off Costa Rica is covered with uniformly distributed denticles.

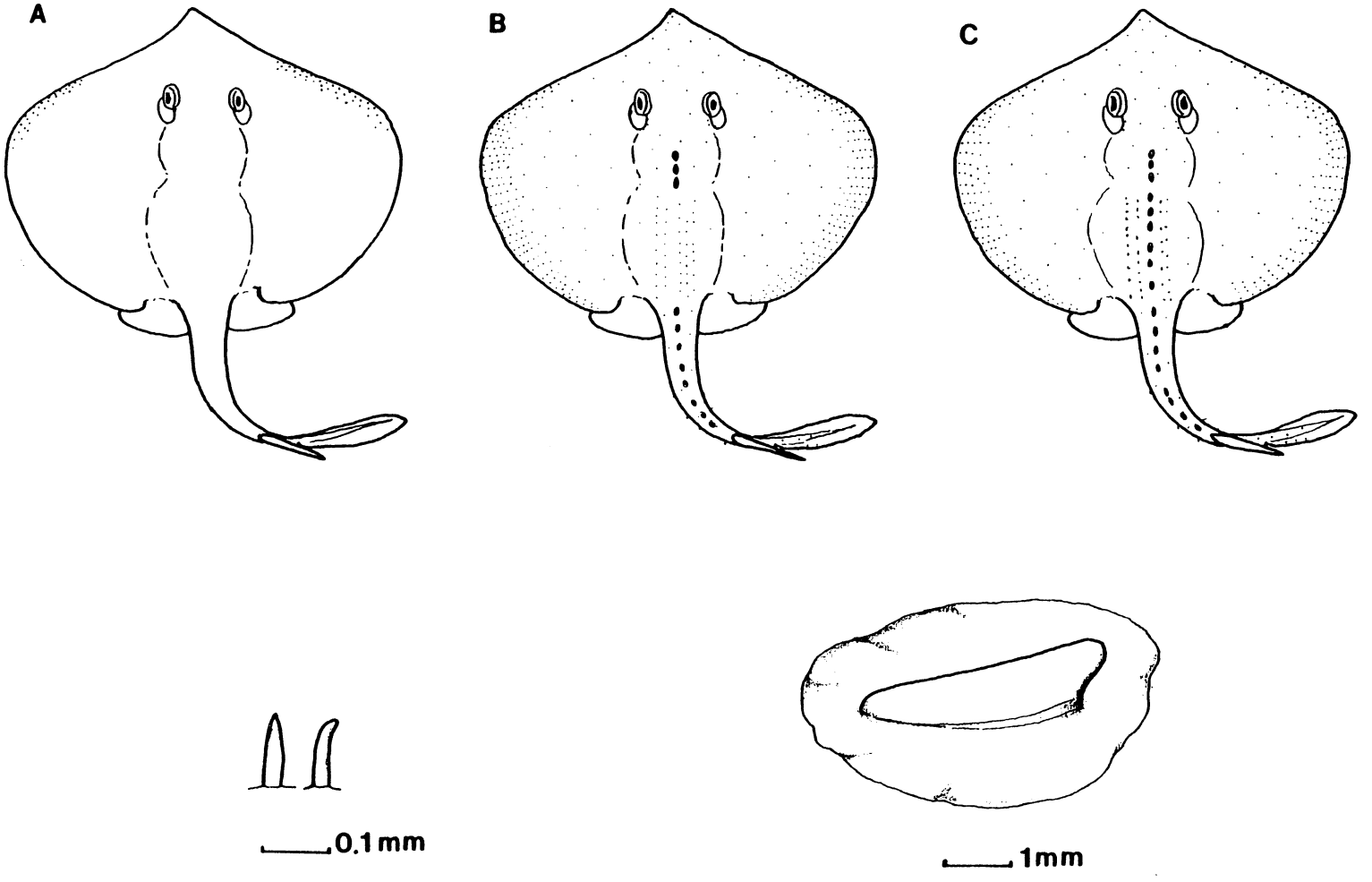
Urotrygon sp (2).-- The denticles are 0.1 to 0.2 mm in height with slender, cone-shaped and curved crowns (Fig. 25B). The basal plates bear small stelliform bases.

In the near term embryo, the disc, pelvic fins and tail are naked. In adults the denticles are densely distributed on the snout, areas in front of eyes, and the margin of the disc from the snout to the level of eyes, but sparsely covering the interorbital, nuchal, scapular regions and mid-portion of visceral cavity (Fig. 25B). Two to three rows of denticles are present around the inner and outer margins of spiracles. The ventral sides of the disc and both sides of pelvic fins and tail are entirely naked.

Urotrygon rogersi.-- The denticles are 0.1 to 0.2 mm in heigth with cone-shaped and straight or slightly curved crowns. The thorns are composed of elongated tube-like crowns with large oval basal plates. In most cases, the basal plates of thorns form a smooth margin, but occasionally the plates have several narrow depressions running toward the center (Fig. 26).

In the near term embryos and specimens less than about 130 mm TL, the disc and tail are naked. In individuals ranging from 140 to 200 mm TL, the denticles are restricted to along the anterior lateral margin of the disc from the level of eyes to the scapular region.

Fig. 26. Squamation, denticles and thorns in Urotrygon rogersi. A) squamation in individuals ranging from 140 to 200 mm TL; B) squamation in individuals larger than 200 mm TL with a discontinuous row of thorns; C) squamation in individuals larger than 200 mm TL with a continuous row of thorns. Bottom left: denticles; bottom right: thorn.

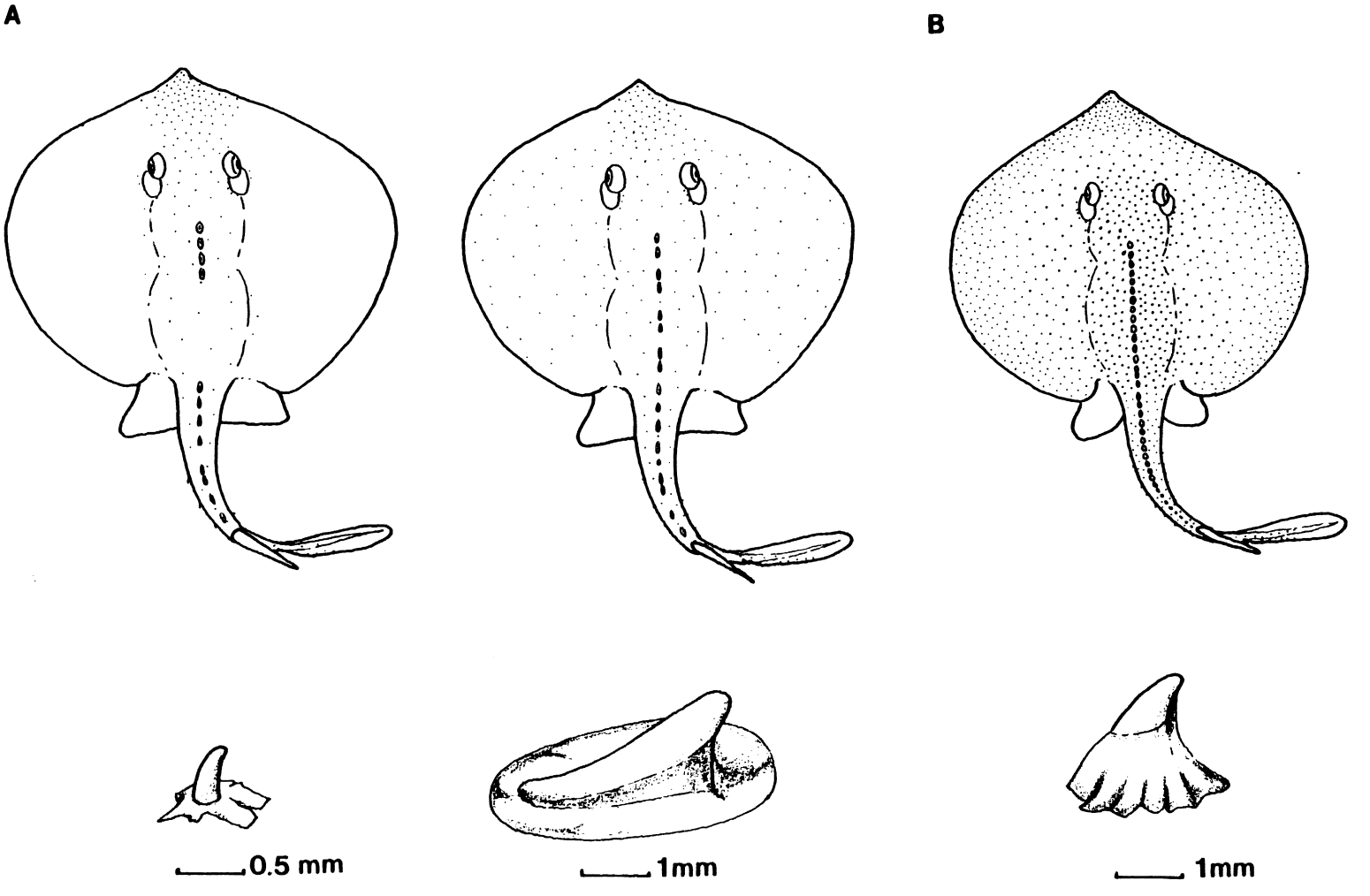

A
B
C
0.1mm
1mm

Three or four denticles are developed along each pectoral radial at the level of eyes to the scapular region (Fig. 26A). The specimens larger than 200 mm TL possess the denticles on the entire dorsal disc. The denticles are arranged irregularily in several rows and running parallel to each other over the midline from the visceral cavity to the level of the insertion of pelvic fins; laterally each pectoral radial from the level of eyes to the posterior corner of the pectoral fin bear denticles. Occasionally, the entire snout, the area over gill arches, the posterior corner of the pectoral fin and the lateral area of the visceral cavity are devoid of the denticles (Fig. 26B). The dorsal and lateral aspect of tail and the medio-lateral and dorsal margin of caudal fin are very sparsely covered with the denticles. The ventral surface of the disc and tail and both surfaces of pelvic fins are devoid of the denticles. The thorns appear along the midline from the nuchal to scaplular region on the specimens ranging from 200 to 300 mm TL. Specimens larger than 300 mm TL possess thorns either disjunctly along the midline from the nuchal to scapular region and along the midline of tail (Fig. 26B) or continuously along the midline from the nuchal to in front of origin of tail spine (Fig. 26C).

Urotrygon asterias.-- The denticles are 0.5 mm to 0.8 mm in height with cone-shaped but slightly curved crowns. The basal plates are stelliform (Fig. 27A). The thorns possess elongated tube-like crowns, distally elevated slightly. In some specimens the thorns are cone-shaped with short crowns and basal plates exhibit stelliform.

In near term embryos and specimens smaller than about 120 to 130 mm TL, the disc and tail are almost naked. In specimens between 130 to 200 mm TL, the denticles cover the snout, interorbital, areas over

Fig. 27. Squamation, denticles and thorns in Urotrygon asterias and Urotrygon sp (3). A) Urotrygon asterias: upper left: squamation in individuals ranging from 130 to 200 mm TL; upper right: squamation in individuals larger than 200 mm TL; bottom left: denticle; bottom right: thorn and B) Urotrygon sp (3): upper: squamation; bottom: thorn-like denticle.


A
B
0.5 mm
1mm
1mm

gill and visceral cavities (Fig. 27A). The denticles on the snout are dense but smaller, while those on the rest of the mid-portion of the disc are slightly large, but sparsely distributed. The antero-lateral margin of the snout is devoid of denticles. The denticles are very sparse on the dorsal and lateral aspects of tail. Several denticles are present in the mid-portion and dorsal lobe of caudal fin. Specimens larger than about 230 mm TL to adults possess the denticles over almost the entire disc; denser on the snout but sparsely and slightly enlarged toward the midline of the disc (Fig. 27A). Occasionally, the denticles are absent along the antero-lateral margin of the disc, mid-portion of the disc margin at the level of spiracles and posterior corner of disc. Specimens between 130 to 200 mm TL thorns possess an incomplete row of thorns along the midline from the nuchal or scapular region to along the midline of tail. In specimens larger than 230 mm TL thorns form a continuous row from the nuchal to origin of tail spine (Fig. 27A), althought some adults lack a continuous row of the thorns.

Urotrygon sp (3).-- Urotrygon sp (3) possesses an identical shape of denticles and thorns, and can be only indistinguishnable by size. They are 0.5 to 2.0 mm in height with tall cone-shaped crowns. The crowns and basal plates are externally indistiguishnable and form a continuous base with shallow longitudinal depressions. The curvature of crowns seems to increase with size (Fig. 27B).

In a near term embryo (93 mm TL) the disc and tail are naked. In adults, the denticles densely cover the entire dorsal disc and tail; being densest on the snout, interorbital, mid-portion of the disc from the nuchal to the level of the axil of pelvic fins, over the visceral

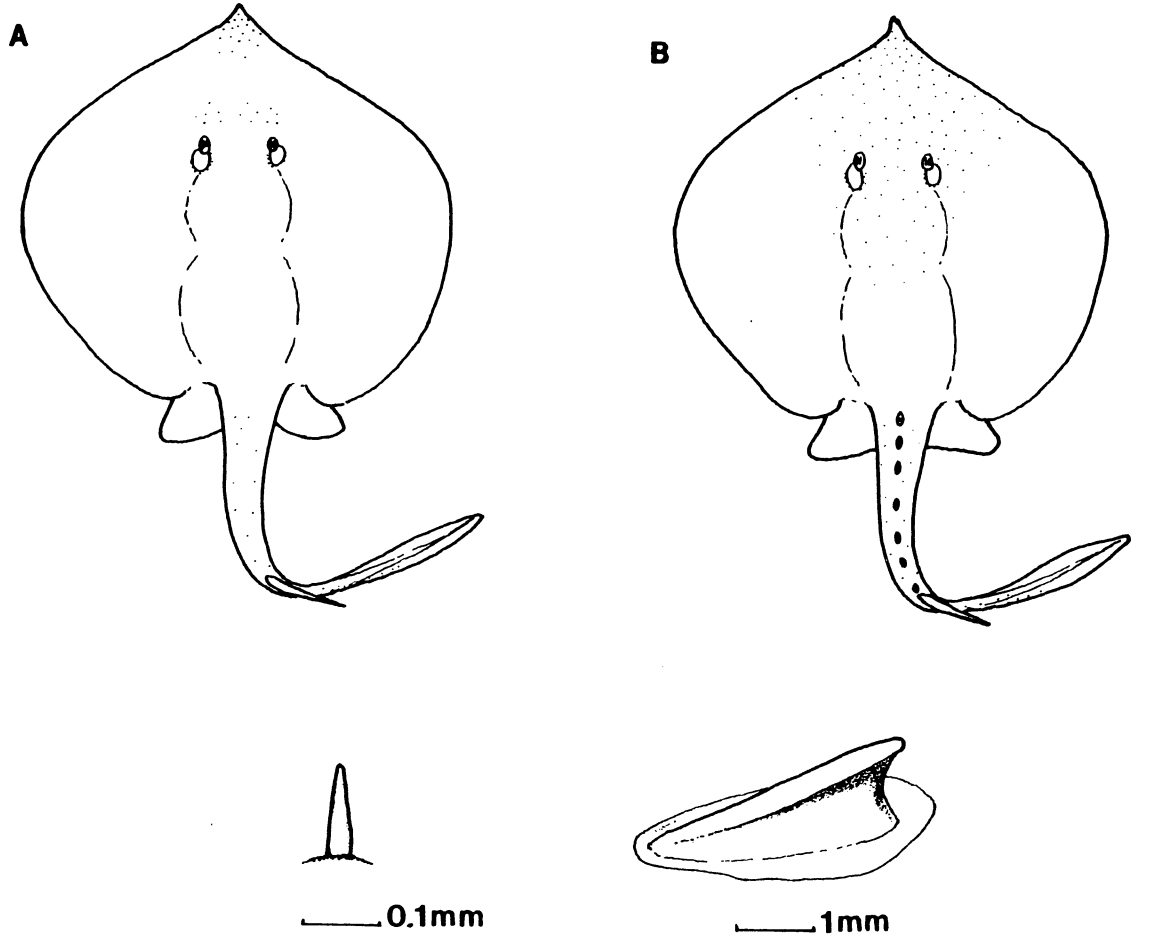
cavity and dorsal aspect of tail. The denticles are graded into thorns, enlarged toward the midline of the disc where a row of thorns form a continuous series from the nuchal to origin of tail spine. The denticles densely cover the anterior portion of dorsal lobe of caudal fin. The pelvic fins and ventral surface of the disc and tail are devoid of the denticles.

Urotrygon aspidura.-- The denticles are 0.1 to 0.2 mm in heigth with straight cone-shaped crowns (Fig. 28). The thorns possess a keel-shaped crown with elongated oval basal plates. The dorsal portion of the crowns is somewhat separated from the underlying base by a groove running the entire length of the crown.

In near term embryos, the disc and tail are naked. In individuals ranging from 100 to 200 mm TL (Fig. 28A), the denticles sparsely cover the tip of the snout and, in some cases, the area in front of the anterior margin of the neurocranium. Slightly larger denticles are present along the inner and posterior one-half of the outer margins of spiracles. The dorsal and lateral sides of tail are very sparsely covered with the denticles. In individuals larger than 200 mm TL (Fig. 28B), the denticles sparsely cover the tip of the snout, the area along the antero-lateral margin of the disc and snout, extending to interorbital and nuchal-scapular regions. In some individuals, the entire mid-portion of the disc is sparsely covered with the denticles. A row of three to eight thorns is present on the midline of tail.

The other species.-- The disc and tail of the holotypes of Urotrygon binghami and U. serrula are naked. The holotype of Urotrygon peruana possesses several minute denticles (0.1 to 0.2 mm in

Fig. 28. Squamation, denticles and thorns in Urotrygon aspidura. A) squamation in individuals ranging from 100 to 200 mm TL; B) squamation in individuals larger than 200 mm TL. Bottom left: denticle; bottom right: thorn.


A
B
0.1mm
1mm

height) on the tip of the snout and small areas behind spiracles. U. peruana possesses two types of thorns at the midline of the dorsal disc and tail (Fig. 29A). One type resembles those of Urotrygon asterias while the other resembled those of U. sp (3). Thus a series of thorns at midline is composed of both types of thorns. The dorsal disc of the holotype of Urotrygon caudispinosa possesses several minute denticles on the tip of the snout and over the scapular region (Fig. 29B). The holotype of Urotrygon goodei possesses several minute dentices on the anterior half of the outer margins of spiralces (Fig. 30A). The holotype of Urotrygon chilensis possesses several minute denticles on the tip of snout, inner margins of spiralce openings, and at the midline of the scapular region. Three thorns which resemble those of Urotrygon asterias are present on the nuchal region (Fig. 30B).

Conclusion.-- When ontogenetic variation is taken into consideration, the pattern and shape of denticles and thorns are of importance in distinguishing among species.

1) Urotrygon daviesi is unique in having small denticles on the ventral side of tail.
2) The denticles of Urotrygon microphthalmum are distinct in being tear-drop-shaped with rounded tips.
3) Urotrygon munda is distinguishnable from U. sp (1) in having denser and stronger denticles covering the entire dorsal disc and tail.
4) Urotrygon rogersi can be separable from U. asterias by having several rows of denticles running parallel on the midline of the visceral cavity and denticles along the pectoral fin

Fig. 29. Squamation, denticles and thorns in Urotrygon peruana and U. caudispinosa. A) Urotrygon peruana: upper: squamation; bottom far left: denticle; bottom right: two types of thorns and B) Urotrygon caudispinosa: upper: squamation; bottom: denticle.

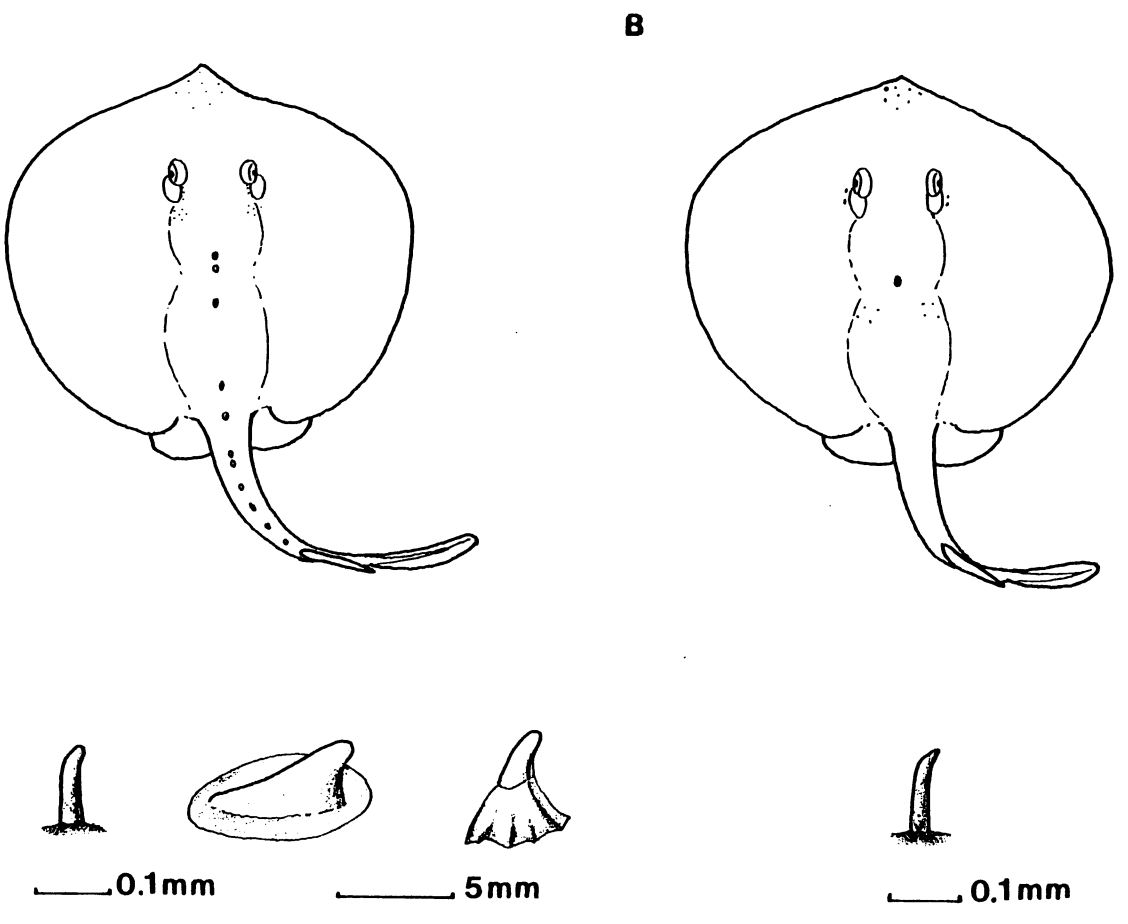
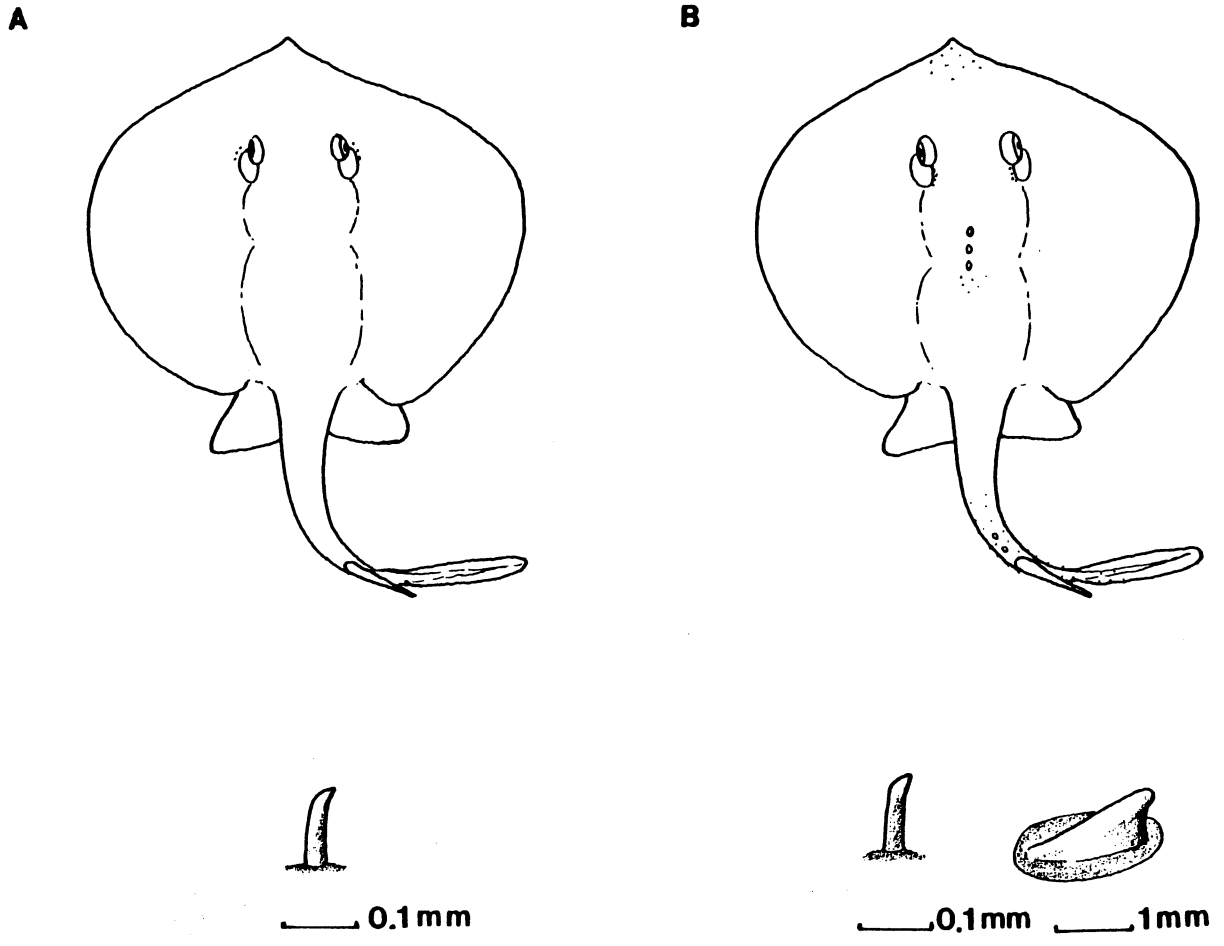

A
B
0.1mm
5mm
0.1mm

Fig. 30. Squamation, denticles and thorns in Urotrygon goodei and U. chilensis. A) Urotrygon goodei: upper: squamation; bottom: denticle and B) U. chilensis: upper: squamation; bottom left: denticle; bottom right: thorn.


A
B
0.1mm
0.1mm
1mm

radials.

5) Urotrygon sp (3) would be separable from U. asterias by having denser denticles on the dorsal disc and tail. Unlike the denticles of Urotrygon asterias, those of Urotrygon sp (3) is morphologically indistinguishnable from thorns. The morphology of thorns in both the species could not be of specific value, because Urotrygon asterias occasionally possesses several thorns typical to U. sp (3) with those of its own type. Urotrygon peruana also possesses thorns typical to both U. sp (3) and U. asterias.

6) The Urotrygon serrula group (U. serrula, U. peruana, U. caudispinosa, U. goodei and U. chilensis) do not exhibit the pattern found in the adults of U. asterias so that it is difficult to evaluate the specific value in details. Even so, the general pattern and shape of denticles and thorns rather resemble those of comparable size of U. asterias, supporting the results of univariate and multivariate comparisons among these species.

TAXONOMIC CONCLUSION

The following conclusions result from the above taxonomic analyses. Urotrygon daviesi, U. microphthalmum, U. venezuelae, U. munda, U. sp (1), U. sp (2), U. rogersi, U. chilensis, U. sp (3) and U. aspidura are considered separate species.

1) Urotrygon sp (3) is very similar to U. asterias in morphology but distinct in denticle pattern.
2) Urotrygon binghami is considered a junior synonym of U. rogersi.
3) Urotrygon asterias, U. serrula, U. peruana, U. caudispinosa and U. goodei are in synonymy with U. chilensis. Urotrygon serrula, U. peruana, U. caudispinosa and U. goodei were described from one specimen and the lack of materials made it diffcult to compare these specimens with those of U. asterias. However, there was no morphological or meristic evidence to support that any one of them was distinct from U. asterias, so that I treat them plus U. asterias under the name U. chilensis. The variations in denticle pattern and thorns of these species should be further investigated in order to confirm this result.

Urotrygon daviesi Wallace, 1967

Urotrygon daviesi Wallace, 1967: 6-10; Nair and Soundararajan, 1973:245-249; Tinker, 1978:46-47; Nakaya, 1982:56-57; Nakaya, 1984:70-71; Miyake and McEachran, 1986:291-302.

Urolophus marmoratus Chu, Meng, Hu and Li, 1981:108-111 (preoccupied by Urolophus marmoratus Philippi, 1892).

? Urotrygon mundus; Chen and Chung, 1971:28-29 (not U. munda Gill; possibly U. daviesi according to the description and figure).

Holotype.-- RUSI-7861, male (1717 mm), South Africa, Limpopo River mouth, 376 to 384 meters, Sept. 1966.

Paratype.-- RUSI-unknown, male (596 mm), South Africa, Limpopo River mouth, 376 to 384 meters, Sept. 1966.

Other material.-- BPBM 24578, male (481 mm), Hawaii, Maui, Pailolo Channel, TOWNSEND CROMWELL station 66, 4 Mar. 1971; MTUF 24994, juvenile specimen, Japan; NTMS 10765-001, 1 male (505 mm), Indonesia, off the coast of Java Island in Indian Ocean, 08° 03'S 110° 05'E, 50 to 70 meters, Mar. 1981.

Diagnosis.-- Long snout: preorbital length 16.61 to 19.86 % of total length. Small denticles on dorsal disc, pelvic fins and tail and on ventral aspect of tail.

Description.-- Disc round in shape, 1.01 and 1.00 in specimen BPBM 24578 and (0.96 to 1.10) in specimen NTMS 10765-001 (from the published data) times long; disc length to maximum width of disc 48.27 and 57.45 % (55.49 %) of disc width; anterior lateral margin of disc almost straight or slightly convex from tip of snout to level of spiralces and widely rounded toward pectoral axil; angle of snout 110° and 108°(106°to 115°); pelvic fins forming long rectangular, lateral margin much longer than posterior margin and straight or slightly convex, posterior margin slightly rounded; width of pelvic fins 0.74

and 0.98 times long. Tail slender and dorso-ventrally convex, height at axil of pelvic fins 5.12 and 3.59 % of distance from cloaca to tip of caudal fin; tail with lateral keels; distance from cloaca to origin of tail spine 43.61 and 46.37 % of distance from cloaca to tip of caudal fin; distance from cloaca to tip of caudal fin 51.21 and 52.95 % (49.62 %) of total length. Caudal fin considerably slender with narrow dorsal and ventral lobes; distance from cloaca to origin of dorsal fin 35.55 and 36.67 % of total length; height of dorsal lobe of caudal fin 8.97 and 10.77 % of length of dorsal lobe of caudal fin. Thin membrane forming a semi-circular blind pocket over proximal margin of cloaca.

Preorbital length 4.70 and 5.45 times orbit diameter; preoral length 2.34 and 2.36 times distance between nostrils; interorbital width 1.48 and 1.60 times orbit diameter; eye moderately large and oriented almost laterally, diameter 4.19 and 4.98 % (4.26 %) of distance from snout to cloaca. Length of spiralce 0.64 and 0.81 (0.59) times interorbital width. Nasal curtain with fringed and slightly concave or convex posterior margin, length 46.34 and 45.08 % of its width. Lobe-like expansion of posterior margin of nostrils poorly developed inwardly. Teeth in both jaws, arranged in quincunx, with sharply pointed cusp in matured males; 39 and 38 (21-45) rows of teeth on upper jaw.

Distance between first gill slits 1.46 and 1.65 times distance between nostrils; distance between fifth gill slits 0.98 and 0.98 times distance between nostrils.

Coloration.-- In fresh specimens, dorsal surface grayish brown, disc and pelvic fins with narrow black margins. Ventral surface of

disc and pelvic fins whitish with black margin. Ventral surface of tail grayish brown with blackish dorsal and ventral lobes of caudal fin. After preservation in formalin and storage in alcohol, dorsal surface of disc and pelvic fins and both surfaces of tail light brown, disc and pelvic fins with black margins. Ventral surface of disc and pelvic fins whitish with black margin.

Range.-- Limpopo River mouth in South Africa, the east coast of India, off the coast of Java Island in Indian Ocean, South China Sea, Okinawa Trough and Kyushu-Palau Ridge in Japan, and Maui in Hawaii.

Remarks.-- The species reported from South China Sea as Urolophus marmoratus by Chu et al. (1981) agrees with the description of Urotrygon daviesi. The specific name Urolophus marmoratus is preoccupied by Urolophus marmoratus Philippi, 1892 which was reported from the Chile. The description and figure for U. munda reported from Taiwan by Chen and Chung (1971) rather agree with those of U. daviesi.

Urotrygon microphthalmum Delsman, 1941

Urotrygon microphthalmum Delsman, 1941:65-66; Bigelow and Schroeder, 1953:428-430; Bigelow and Schroeder, 1962:235-241 (detailed description based on additional material from the mouth of Amazon River and Venezuela); Boeseman, 1963:299-300; Cervigon, 1966:85-86; Uyeno and Miyake, 1983:81; Miyake and McEachran, 1986: 291-302.

Holotype.-- RMNH 24707, female (237 mm), 5 miles NW of lightship off Surinam River outlet, 21 Feb. 1963.

Other material.-- CAS 48879, French Guiana, OREGON II Station 19912, 04°43' 05''N, 51°34'W, 22 May 1976; FMNH 90096, 7 males (179 to 246 mm), 3 females (208 to 260 mm), Amapa, Brazil, 14 Nov. 1957; FMNH 90097, 2 females (208 to 260 mm), Venezuela, OREGON station 2215, 09° 14'N, 60°26'W, 27 Aug. 1958; FMNH 90098, 1 male (190 mm), Venezuela, OREGON Station 2216, 09°13'N, 60°11'W, 27 Aug. 1958; FMNH 90099, 2 males (77.0 and 223 mm), 1 female (277 mm), Surinam, 1957; FMNH 90100, 1 male (176 mm), 1 female (234 mm), Surinam, 1957; MCZ 55451, 3 males (202 to 235 mm), 1 female (288mm), British Guiana, OREGON Station 4306, 06°54'N, 57°47'W, 25 Mar. 1963; UFPB 1230, 1 female (208 mm), Cabo Branco, Joao Pessoa, Paraiba, Brazil, 8-9 Sept. 1979; UFPB 1231, 1 female (231 mm), Cabo Branco, Joao Pessoa, Paraiba, Brazil, Feb. 1982; UFPB uncataloged, 1 female (80.0 mm), coast of Paraiba, Brazil; USNM 197109, 2 males (169 to 175 mm), 2 females (187 to 241 mm), British Guiana, OREGON II Station 17636 and 17637, 04°26'N, 50°55'W, 7 May 1975; USNM 222695, 1 male (211 mm), Trinidad, CALAMAR Station 660, 17 Jan. 1969; ZMA 116-142, 1 male (206mm), 1 female (147 mm), British Guiana, CALAMAR Station 671, 08°45'N, 59°15'W, 25 Jan. 1969; ZMA 116-143, 1 male (175 mm), British Guiana, CALAMAR Station 665, 08° 45'N, 59°15'W, 22-23 Jan. 1969; ZMA 116-144, 1 female (215 mm), CALAMAR Station 583, 06°15'N, 56°45'W, 25 Sept. 1968; ZMA 116-145, 1 male (246 mm), off the Surinam River, Surinam, 3 Nov. 1972; ZMA 116-146, 1 male (196 mm), Surinam, CALAMAR Station 577, 06°15'N, 54° 45'W, 29 Sept. 1968; ZMA 116-147, 3 males (179 to 205 mm), British Guiana, CALAMAR Station 651, 08°45'N, 59°15'W, 14 Jan. 1969; ZMA

116-148, 1 female (274 mm), Surinam, CALAMAR Station 552, 06°15'N, 54° 45'W, 9 Sept. 1968; ZMA 119-149, 1 male (235 mm), Surinam, CALAMAR Station 702, 06°15'N, 54°45'W, 21 Mar. 1969.

Diagnosis.-- Small eyes and oriented nearly dorsally: eye diameter 1.57 to 2.95 % ($\bar{x}$=2.26 %) of distance from snout to cloaca. Disc width, 44.23 to 56.34 % ($\bar{x}$=48.17 %) of total length. Caudal fin slender and long: length of dorsal lobe of caudal fin 15.07 to 23.53 % ($\bar{x}$=19.24 %) of total length. Dorsal disc and tail sparsely covered with minute tear drop-shaped denticles.

Description.-- Proportional dimensions of embryos are not included. Disc round in shape, 0.93 to 1.09 times ($\bar{x}$=1.00) long; disc length to maximum width of disc 49.55 to 66.37 % ($\bar{x}$=54.37 %) of disc width; antero-lateral margin of disc deeply concave in males but slightly convex in females and juvenile males; angle of snout 98° to 120° ($\bar{x}$=115°) in males and 110° to 132° ($\bar{x}$=126°) in females; tip of snout sometimes well marked off from rest of disc and forming a projection in matured males. Pelvic fins forming an equalateral triangle, lateral margin more or less straight or weakly convex and posterior margin broadly rounded; width of pelvic fins 0.85 to 1.54 times ($\bar{x}$=1.15) long. Tail slender and strongly depressed anterior to insertion of spine, height at axil of pelvic fins 4.31 to 8.00 % ($\bar{x}$=5.46 %) of distance from cloaca to tip of caudal fin; tail with or without weak lateral keels; distance from cloaca to origin of tail spine 35.00 to 46.50 % ($\bar{x}$=39.70 %) of distance from cloaca to tip of caudal fin; distance from cloaca to tip of caudal fin 51.49 to 57.88 % ($\bar{x}$=54.68 %) of total length. Caudal fin very slender with dorsal lobe

shorter than ventral lobe, the latter originating just behind origin of tail spine; distance from cloaca to origin of dorsal lobe of caudal fin 30.40 to 40.65 % ($\bar{x}$=35.32 %) of total length; height of dorsal lobe of caudal fin 6.36 to 16.55 % ($\bar{x}$=10.93 %) of length of dorsal lobe of caudal fin.

Preorbital length 4.95 to 8.95 times ($\bar{x}$=6.98) orbit diameter; preoral lenght 2.36 to 3.41 times ($\bar{x}$=2.75) distance between nostrils; interorbital width 1.64 to 3.25 times ($\bar{x}$=2.20) orbit diameter; eye situated at antero-medial corner of spiracle openings, eyes and spiralces in longitudinal row; eye minute and oriented almost dorsally, diameter 1.57 to 2.95 % ($\bar{x}$=2.26 %) of distance from snout to cloaca. Length of spiralce 0.42 to 0.80 times ($\bar{x}$=0.60) interorbital length. Nasal curtain with fringed and slightly concave or convex posterior margin, length 26.56 to 57.38 % ($\bar{x}$=42.88 %) of its width. Lobe-like expansion of posterior margin of nostrils developed inwardly and accommodating expansion of nasal curtain; two to ten papillae on proximal margin of lobe-like expansion. Teeth in both jaws, arranged in quincunx, with sharply pointed cusp in males larger than about 160 to 180 mm TL; 28 to 43 ($\bar{x}$=34) rows of teeth in upper jaw.

Distance between first gill slits 1.31 to 1.71 times ($\bar{x}$=1.66) distance between nostrils; distance between fifth gill slits 1.01 to 1.71 times ($\bar{x}$=1.29) distance between nostrils. Number of vertebral centra 66 to 77 ($\bar{x}$=72).

Coloration.-- After preservation in formalin and storage in alcohol, dorsal surface uniformly light brown to dark brown. Ventral surface of disc light tan to white, occasionally broad blackish band along margin of disc and several specks or spots scattered on area

between right and left gill slits. Ventral margin of pelvic fins blackish. Ventral surface of tail light tan to white, rarely with a brownish longitudinal band near insertion of pelvic fins.

Range.-- From western Venezuela, off the mouth of the Orinoco River, to off the mouth of the Amazon River. One specimen was recorded from Cabo Branco, Paraiba, Brazil, south of the Amazon River (Ricardo Rosa, personal communication).

Urotrygon venezuelae Schultz, 1949

Urotrygon venezuelae Schultz, 1949:24-27; Bigelow and Schroeder, 1953:430-433; Cervigon, 1966:86; Miyake and McEachran, 1986: 291-302.

Holotype.-- USNM 121966, female (256 mm), Gulf of Venezuela, Point Macolla, 19 Apr. 1925.

Other material.-- GCRL 15264, 1 male (255 mm), Colombia, Cartegena, vicinity of Boca Grande, 28 July 1976; TBT 75-2, 1 male (252 mm), Colombia, Tasajeras, 6 June 1975; TBT 76-10, 3 female (60, 65, and 268 mm), Colombia, Cartegena, 6 June 1976, collected by T. B. Thorson; TBT 76-26, 1 female (268 mm), Colombia, Cartegena, 8 July, 1976, collected by T. B. Thorson; TBT 76-28, (27 mm), Colombia, Cartegena, 13 July 1976, collected by T. B. Thorson; TBT 76-34 or 35 ?, 1 male (235 mm), Colombia, Cartegena, 13 July 1976, collected by T. B. Thorson; TBT 76-71, 1 female (256 mm), Colombia, Cartegena, 25 July 1976, collected by T. B. Thorson; TBT uncataloged, 1 female (286 mm),

Colombia, Atlantic side, collected by T. B. Thorson; TBT 80-8, 1 male (233 mm), Colombia, 1980, collected by T. B. Thorson.

Diagnosis.-- Two or three rows of small enlarged denticles on midline of dorsal disc and tail. Small denticles absent on narrow margin of dorsal disc except along snout. Angle of snout in females exceeding 140 degrees.

Description.-- Proportional dimensions of embryos are not included. Disc almost oval in shape, 1.05 to 1.18 times ($\bar{x}$=1.10) long; disc length to maximum width of disc 47.62 to 59.19 % ($\bar{x}$=51.64 %) of disc width; antero-lateral margin of disc moderately concave in males but broadly convex in females; angle of snout 118°to 123°($\bar{x}$=120°) in males and 138°to 148°($\bar{x}$=144°) in females; tip of snout not marked off from rest of disc. Pelvic fins resembling an equalateral triangle, lateral margin nearly straight and posterior margin broadly rounded; width of pelvic fins 1.10 to 1.39 times ($\bar{x}$=1.20) long. Tail relatively robust and thick, dorsal aspect slightly convex; tail height at axil of pelvic fins 6.25 to 8.63 % ($\bar{x}$=7.44 %) of distance from cloaca to tip of caudal fin; lateral keels well developed, originating near insertion of tail to behind origin of tail spine; distance from cloaca to origin of tail spine 45.21 to 56.68 % ($\bar{x}$=50.83 %) of distance from cloaca to tip of caudal fin; distance from cloaca to tip of caudal fin 51.31 to 57.34 % ($\bar{x}$=54.98 %) of total length. Caudal fin moderately slender with dorsal lobe shorter than ventral lobe; distance from cloaca to origin of dorsal lobe of caudal fin 39.02 to 40.77 % ($\bar{x}$=39.71 %) of total length; height of dorsal lobe of

caudal fin 16.05 to 20.78 % ($\bar{x}$=17.89 %) of length of dorsal lobe of caudal fin.

Preorbital length 4.39 to 5.53 times ($\bar{x}$=5.06) orbit diameter; preoral length 1.86 to 2.10 times ($\bar{x}$=1.98) distance between nostrils; interorbital width 2.29 to 2.34 times orbit diameter; eye relatively large and oriented dorso-laterally, diameter 3.05 to 4.38 % ($\bar{x}$=3.50 %) of distance from snout to cloaca. Length of spiralce 0.50 to 0.65 times ($\bar{x}$=0.58) interorbital length. Posterior margin of nasal curtain well fringed and either straight or slightly concave; length of nasal curtain 42.86 to 51.83 % ($\bar{x}$=47.37 %) of its width. Lobe-like expansion of posterior margin of nostrils moderately developed and accommodating expansion of nasal curtain. Teeth in both jaws, arranged in quincunx, with sharply pointed cusps in males (size at which cusp starts to develop is unknown); 27 to 38 ($\bar{x}$=31) rows of teeth in upper jaw.

Distance between first gill slits 1.79 to 2.24 times ($\bar{x}$=2.05) distance between nostrils; distance between fifth gill slits 1.60 to 1.83 times ($\bar{x}$=1.68) distance between nostrils. Number of vertebral centra 74 to 76 ($\bar{x}$=75).

Coloration.-- After peservation in formalin and stroage in alcohol dorsal surface uniformly greyish brown to light tan. Ventral surface of disc and pelvic fins yellowish or whitish with dark margin. Several brownish specks and spots on area between right and left gill slits. Ventral surface of tail whitish to yellowish with irregular sized brownish markings or one or two narrow longitudinal bands behind insertion of pelvic fins.

Range.-- Gulf of Venezuela and the Atlantic coast of Colombia; Cartegena, vicinity of Boca Grande and Tasajeras (in part Thomas Thorson, personal comminucation).

Urotrygon munda Gill, 1863

Urotrygon mundus Gill, 1863:173-174; Garman, 1913:406-407 ; Meek and Hildebrand, 1923:82-83; ? Ulrey, 1929:3 (possibly either U. asterias or U. rogersi; only list of species in the Gulf of California); Jordan, Evermann, and Clark, 1930:30; Fowler, 1930:23; Beebe and Tee-Van, 1941:268; Chirichigno, 1963:3 (first record from Peru); Castro Aguirre, 1965b:224-225; Chen and Chung, 1971:28-29 (not U. munda Gill); Chirichigno, 1974:69; Ramirez Hernandez and Gonzalez Pages, 1976:65; Miyake and McEachran, 1986: 291-302.

Urolophus mundus: Jordan, 1885:364; Jordan and Evermann, 1896:81; ? Osburn and Nichols, 1916:145 (possibly either U. asterias or U. rogersi according to their record from the Gulf of California).

Holotype.-- USNM 7297, female (tail broken), Panama Bay.

Other material.-- GCRL 16735, 3 males (98 to 216 mm), El Salvador, Jisquiliso Bay, Punta San Juan, 13°10'N, 88°29'W, 4 Feb. 1976, collected by M. Miller; GCRL 16736, 3 females (244 to 288 mm), El Salvador, Jiquiliso Bay, Punta San Juan, 29 Sept. 1976, collected by P. Phillips; MCZ 831S, 1 male (99.1 mm in disc length), Panama, 1885; USNM 220612, 5 males (96 to 234 mm), 7 females (113 to 247 mm),

El Salvador, Jiquiliso Bay, Punta San Juan, 17 Mar. 1976, collected by M. Miller; USNM 220625, 4 females (159 to 175 mm), El Salvador, La Venadona, Jiquiliso Bay, 9 June 1976, collected by P. Phillips.

Diagnosis.-- Disc almost rounded; 0.97 to 1.24 times ($\bar{x}$=1.09) long. Small but strong recured denticles covering entire dorsal disc and tail, enlarged toward midline but not forming any definite rows of dentilces on midline of dorsal disc and tail. Short robust caudal fin: length of dorsal lobe of caudal fin 9.49 to 17.61 % ($\bar{x}$=12.99 %).

Description.-- Proportional dimensions of embryos are not included. Disc round in shape, 0.97 to 1.24 times ($\bar{x}$=1.09) long; disc length to maximum width of disc 42.50 to 59.27 % ($\bar{x}$=50.68 %) of disc width; antero-lateral margin of straight or slightly convex in males whereas broadly convex in females; angle of snout 120°to 134°($\bar{x}$=128°) in males and 132°to 147°($\bar{x}$=139°) in females; tip of snout not marked off from rest of disc. Pelvic fins forming an equalateral triangle, lateral margin nearly straight with acute angle of corner and posterior margin broadly rounded, rarely straight; width of pelvic fin 0.94 to 1.70 times ($\bar{x}$=1.24) long. Tail robust and anterior to insertion of tail spine broadly rounded dorsally but flattened ventrally, height at axil of pelvic fins 4.92 to 9.69 % ($\bar{x}$=7.92 %) of distance form cloaca to tip of caudal fin; tail with or without weak lateral keels; distance from cloaca to origin of tail spine 41.67 to 61.81 % ($\bar{x}$=47.50 %) of distance from cloaca to tip of caudal fin; distance from cloaca to tip of caudal fin 41.60 to 55.23 % ($\bar{x}$=52.22 %) of total length. Caudal fin relatively short and blunt, dorsal lobe shorter than ventral lobe; tip of caudal fin rounded; distance from

cloaca to origin of dorsal lobe of caudal fin 34.96 to 44.44 % ($\bar{x}$=39.61 %) of total length; height of dorsal lobe of caudal fin 22.19 to 34.68 % ($\bar{x}$=27.19 %) of length.

Preorbital length 3.03 to 6.29 times ($\bar{x}$=4.63) orbit diameter; preoral length 2.12 to 2.75 times ($\bar{x}$=2.45) distance between nostrils; interorbital width 1.53 to 2.37 times ($\bar{x}$=1.94) orbit diameter; eye relatively small and oriented somewhat dorsally, diameter 2.86 to 5.05 % ($\bar{x}$=4.03 %) of distance from snout to cloaca. Length of spiracle 0.47 to 0.92 times ($\bar{x}$=0.60) interorbital length. Nasal curtain relatively short, with fringed and slightly concave to straight posterior margin, length 28.47 to 52.08 % ($\bar{x}$=41.91 %) of its width. Lobe-like expansion of posterior margin of nostrils poorly developed; two to eight papillae on proximal end of lobe-like expansion. Teeth in both jaws, arranged in quincunx, with sharply pointed cusp in males greater than 190 to 200 mm TL; 27 to 36 ($\bar{x}$=31) rows of teeth in upper jaw.

Distance between first gill slits 1.40 to 1.70 times ($\bar{x}$=1.55) distance between nostrils; distance between fifth gill slits 1.33 to 1.92 times ($\bar{x}$=1.60) distance between nostrils. Number of vertebral centra 72 to 77 ($\bar{x}$=75).

Coloration.-- After preservation in formalin and storage in alcohol, dorsal surface whitish brown, occasionally 10 to 16 minute spots on disc. Ventral surface of disc and pelvic fins whitish with dark broad margin and mostly irregularly shaped dark markings on right and left gill slits, rarely in front of cloaca. Ventral surface of tail whitish with several dark spots on midline near axil of pelvic fins.

Range.-- Coast of El Salvador, Bay of Panama, and the coast of Peru.

Remarks.-- Urotrygon munda reported from lower California (Osburn and Nichols, 1916; Ulrey, 1929) may represent either U. rogersi or U. chilensis because U. munda is thought to be restricted to the Pacific side of Panamian water.

Urotrygon sp. (1)

(Fig. 31A)

Urotrygon nebulosus: Castro Aguirre, 1965b:230-231 (not Urolophus nebulosus Garman).

Urotrygon sp (1): Miyake and McEachran, 1986: 291-302.

Material.-- CAS 4734, 1 male (193 mm), Mexico, Nayarit, 22°44'N, 105°39'W, 29 July 1932; CAS-SU 46731, 1 male (150 mm), Guatemala, W of Champerico, 14°13'N, 92°02'W, 15 Dec. 1937; FMNH 72281, 6 females (113 to 181 mm), 2 males (148 to 169 mm), Mexico, Chiapas, 14-18 Dec. 1954, collected by L. P. Woods and others; SIO 65-167, 28 males (82 to 169 mm), 13 females (67 to 161 mm), Mexico, Golfo de Tehuantepec, 7 June 1965; LACM 30745-11, 1 male (202 mm), 3 females (207 to 243 mm), Costa Rica, Golfo de Nicoya, Alrededor Isla de Chira, 27 Nov. 1968, collected by P. Leon; LACM 33806-97, 1 female (194 mm), Costa Rica, Puntarenas, WSW of Boca Burranca, 12 June 1973.

Diagnosis.-- Small eyes and oriented nearly dorsally: eye diameter 1.88 to 3.76 % ($\bar{x}$=2.82 %) of distance from snout to cloaca.

Snout and extreme margin of disc densely but mid-portion of disc and tail sparsely covered with denticles. Maximum size about 250 mm in TL.

Description.-- Proportional dimensions of embryos are not included. Disc almost round in shape, 1.08 to 1.26 times ($\bar{x}$=1.14) long; disc length to maximum width of disc 46.09 to 58.35 % ($\bar{x}$=51.75 %) of disc width; antero-lateral margin of disc straigth or slightly convex in both sexes, but sometimes slightly concave in males; margin of disc from tip of snout to level of spiracles forming an acute angle and then broadly rounded up toward axil of pectoral fin; angle of snout 110°to 130°($\bar{x}$=118°) in males and 120°to 133°($\bar{x}$=128°) in females; tip of snout not forming a projection. Pelvic fins forming equalateral to right-angled triangle, lateral margin straight or slightly concave and posterior margin broadly rounded; width of pelvic fins 0.89 to 2.32 times ($\bar{x}$=1.35) long. Tail slender and flattened dorsally but slightly convex ventrally, height at axil of pelvic fins 5.96 to 9.94 % ($\bar{x}$=8.02 %) of distance from cloaca to tip of caudal fin; tail rarely with weak keels; distance from cloaca to origin of tail spine 37.89 to 59.22 % ($\bar{x}$=42.58 %) of distance from cloaca to tip of caudal fin; distance from cloaca to tip of caudal fin 46.64 to 53.31 % ($\bar{x}$=50.39 %) of total length. Caudal fin moderately slender with shorter dorsal lobe than ventral lobe; tip of caudal fin narrowly rounded; distance from cloaca to origin of dorsal lobe of caudal fin 32.36 to 41.26 % ($\bar{x}$=35.55 %) of total length; height of caudal fin 17.89 to 38.89 % ($\bar{x}$=26.20 %) of length of dorsal lobe of caudal fin.

Preorbital length 3.84 to 7.00 times ($\bar{x}$=5.39) orbit diameter; preoral length 2.10 to 3.18 times ($\bar{x}$=2.67) distance between nostrils;

interorbital width 1.55 to 2.58 times ($\bar{x}$=2.00) orbit diameter. Length of spiracles 0.48 to 0.79 times ($\bar{x}$=0.63) interorbital width. Nasal curtain with fringed and usually deeply concave posterior margin and concave lateral margin, length 29.25 to 65.93 % ($\bar{x}$=51.21 %) of width. Lobe-like expansion of posterior margin of nostrils weakly developed inwardly and accommodating expansion of nasal curtain; a cluster of several papillae on proximal edge of lobe-like expansion. Teeth in both jaws, arranged in quincunx, with sharply pointed cusp in males (cusp development begins in males 100 to 130 mm in TL); 29 to 36 ($\bar{x}$=33) rows of teeth in upper jaws.

Distance between first gill slits 2.07 to 3.50 times ($\bar{x}$=2.67) distance between nostrils; distance between fifth gill slits 1.26 to 2.12 times ($\bar{x}$=1.58) distance between nostrils. Number of vertebral centra 61 to 73 ($\bar{x}$=68).

Coloration.-- After preserved in formalin and storage in alcohol, dorsal surface chocolate brown to light brown. Margin of disc narrowly edged with white. Ventral surface white to yellowish white. A short and brownish band running longitudinally from axil of pelvic fins on midline of ventral surface of tail. In rare cases, a light brown, triangular shaped marking on posterior corner of ventral surface of pelvic fins.

Range.-- Along the coasts of northern Nayarit and Golfo de Tehuantepec, Chiapas in Mexico, Champerico in Guatemala, and Golfo de Nicoya in Costa Rica.

Remarks.-- Castro Aguirre (1965b) reported this species as Urotrygon nebulosus from Mexico. However, his description and figure clearly indicate that his specimen is actually Urotrygon sp (1). He

may have been referring to Urolophus nebulosus Garman, 1913 which was synonymized with U. halleri. Most specimens of Urotrygon sp (1) examined in this study had previously been identified as Urotrygon binghami (=U. rogersi).

Urotrygon sp. (2)

(Fig. 31B)

Urotrygon sp (2): Miyake and McEachran, 1986: 291-302.

Material.-- USNM 222644, 1 female (241 mm), 2 males (87 and 188 mm), Panama, Gulf of Panama, Bahia Santelmo, 8 Jan. 1967.

Diagnosis.-- Entire dorsal body with tan to brownish fine vermiculations. The pattern more diffused and consisting of speck-like markings on extreme margin of disc, pelvic fins, and dorsal lobe of caudal fin.

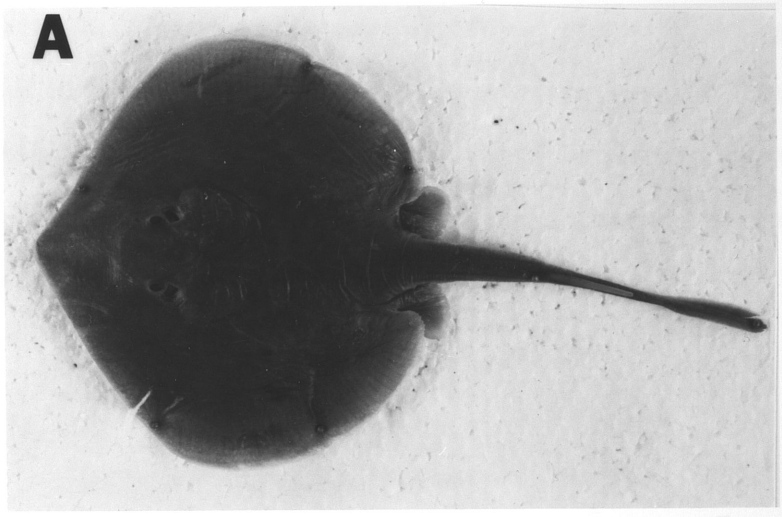
Description.-- Proportional dimensions of the embryo paratype (87 mm TL) are not included here. Disc almost oval in shape, 1.06 times (holotype) (1.05 in adult paratype) long; disc length to maximum width of disc 40.43 % (49.01 %) of disc width; antero-lateral margin of disc forming a relatively acute angle and straight or slightly convex to level of eyes, abruptly rounded toward axil of pectoral fin; angle of snout 122°(120°); tip of snout not forming a projection. Pelvic fins forming an equalateral triangle, lateral margin broadly concave and posterior margin nearly straight or slightly convex; width of pelvic fins 1.12 times (1.24) long. Tail moderately slender, flattened

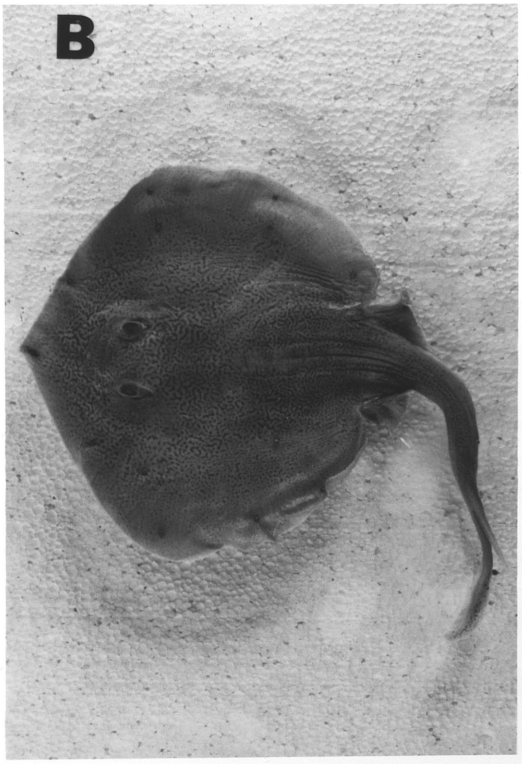
dorsally but slightly convex ventrally, width at axil of pelvic fins 6.81 % (7.42 %) of distance from cloaca to tip of caudal fin; Tail with weakly developed keels running from near level of tip of pelvic fins to insertion of tail spine; distance from cloaca to origin of tail spine 50.65 % (53.66 %) of distance from cloaca to tip of caudal fin; distance from cloaca to tip caudal fin 50.54 % (49.46 %) of total length. Caudal fin relatively robust and of equal height over most of length; tip of caudal fin broadly rounded; distance from cloaca to origin of dorsal lobe of caudal fin 36.68 % (39.63 %) of total length; height of dorsal lobe of caudal fin 26.49 % (35.33 %) of length.

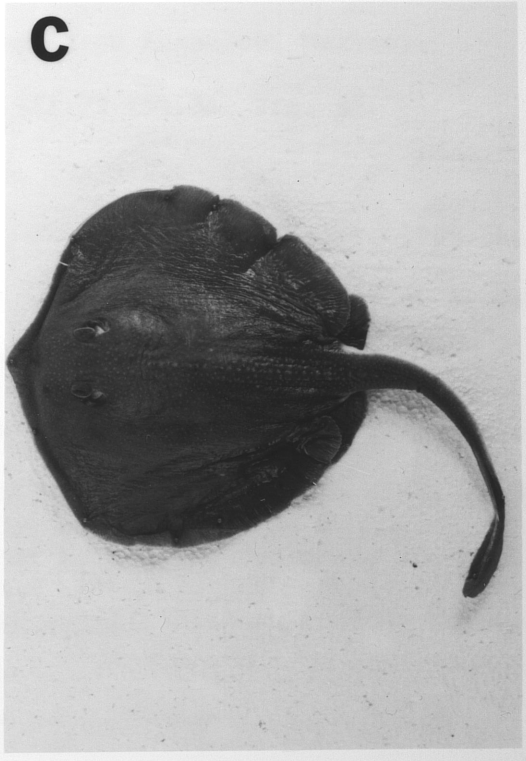
Preorbital length 3.65 times (4.10) orbit; preoral length 3.08 times (2.99) distance between nostrils; interorbital width 1.27 times (1.39) orbit diameter; eyes moderately large and oriented nearly dorsally, diameter 4.31 % (4.48 %) of distance from snout to cloaca. Length of spiralces 0.64 times (0.65) interorbital width. Nasal curtain relatively long, posterior margin straight or slightly convex and fringed; length of nasal curtain 53.55 % (55.78 %) of its width. Lobe-like expansion of nostrils weakly developed inwardly and accommodating distal expansion of nasal curtain; one to two papillae on proximal edge of lobe-like expansion. Teeth in both jaws, arranged in quincunx, with cusps in male adult (embryo in 87 mm TL possessing teeth in both jaws); number of teeth in upper jaw 38 (34 in embryo paratype and 38 in adult paratype).

Distance between first gill slits 3.11 times (2.80) distance between nostrils; distance between fifth gill slits 1.74 times (1.55) distance between nostrils. Number of vertebral centra 68 (in holotype) and 69 (in adult paratype).

Fig. 31. Three undescribed species of Urotrygon. A). U. sp (1) (FMNH 72281, male, 148 mm TL). B). U. sp (2) (USNM 222644, male, 241 mm TL). C). U. sp (3) (GCRL 13064, female, 264 mm TL).


A


B


C

Coloration.-- After preservation in formalin and storage in alcohol, entire dorsal surface covered with fine brownish vermiculations. The pattern more diffused and consisting of speck-like markings on extreme margin of disc, pelvic fin and dorsal lobe of caudal fin. Vermiculation pattern in embryo paratype more coarse and large on disc and tail. Ventral surface of body white.

Range.-- Bahia Santelmo, Gulf of Panama.

Urotrygon rogersi (Jordan and Starks, 1895)

Urolophus rogersi Jordan and Starks, 1895:388-389; Kendall and Radcliffe, 1912:80 (one specimen from Acapulco, Mexico).

Urolophus sp.: Kumada and Hiyama, 1937:23 (Pl.56, Fig. B).

Urotrygon aspidurus: Castro Aguirre, 1965b:226-227.

Urotrygon binghami Breder, 1926:11; Ulrey, 1929:3; Fowler, 1930:24; Terron, 1930:76; Beebe and Tee-Van, 1941:266-267; Castro Aguirre et al., 1970:120; Miyake and McEachran, 1986: 291-302.

Urotrygon rogersi: Garman, 1913:406-407 (as a synonym of U. munda); Jordan, Evermann, and Clark, 1930:30 (as a synonym of U. munda); Fowler, 1930:23 (as a synonym of U. munda); Beebe and Tee-Van. 1941:266 (as a synonym of U. asterias); Ricker, 1959:4; Miyake and McEachran, 1986: 291-302.

Holotype.-- CAS-SU 11700, female (437 mm), Mexico, Mazatlan, Astillero Hopkins Expedition, 1 Jan. 1895.

Other material.-- BOC 1019, 1 female (187 mm), Mexico, Gulf of California, Baja California, San Felipe, Rio Colorado, 16 to 22 meters, 19 May 1926; CAS 4400, 1 male (261 mm), Mexico, Guerreco, off Acapulco, 18°49'N, 99°05'W, "Zaca" Croker Expedition, 15 July 1932; CAS 42261, Mexico, Gulf of California, Baja California, Bahia San Felipe, 10 Apr. 1947, collected by C. L. Hubbs; CAS 47388, 2 males (440 and 468 mm), Mexico, Gulf of California, Baja California, Bahia San Felipe, 1 Mar. 1951; CAS 51836, 2 males (335 and 358 mm), Mexico, Nayarit, Bahia Matauchen, 6 Feb. 1958, collected by Rosenblatt and Stephens; CAS 51837, 4 males (135 to 250 mm), 2 females (136 to 142 mm), Mexico, Gulf of California, Sinaloa, Bahia Topolobampo, 2-3 June 1956, collected by W. Baldwin; CAS 51838, 1 male (462 mm), Mexico, Gulf of California, Baja California, Bahia San Felipe, 10 Apr. 1947, collected by C. L. Hubbs et al.; CAS-SU 17754, 1 female (427 mm), Mexico, Gulf of California, Sonora, Bahia San Francisco, 1 Apr. 1948, collected by Bohlke and Harry; CAS-SU 53842, 1 female (176 mm), Mexico, Gulf of California, Baja California, 11 km NW of San Felipe, 31 Jan. 1955, collected by Mahadera and Beadegue; FMNH 72677, 1 male (255 mm), 3 females (278 to 314 mm), Mexico, Chiapas, above San Benito, 14 to 18 Dec. 1954, collected by L. P. Woods; LACM W50-57, 13 males (281 to 395 mm), 4 females (227 to 384 mm), Mexico, Sonora, Kino, 3 Feb. 1950, collected by B. W. Walker et al.; SIO 65-162, 2 males (272 and376 mm), Mexico, Jalisco, El Golfo II Cruise, 15 m, 3 June 1965; SIO, 65-163, 4 females (166 to 325 mm), Mexico, Jalisco, El Golfo II Cruise, 30 m, 6 June 1965; SIO 73-238, 7 males (66 to 313 mm), 11 females (108 to 333 mm), Mexico, Jalisco, Bahia Chamels, 19° 34.8'N to 19°34.0'N, 105°08.0'W to 105°07.4'W, 8 to 10 fathoms, 2 Apr.

1973, collected by C. L. Hubbs; SIO 73-245, 22 males (244 to 277 mm), 10 females (246 to 301 mm), Mexico, Michoacan, Pt. Telmo, estuary, 18° 07.5'N to 18°06.7'N, 102°56.0'W to 102°57.3'W, 4 Apr. 1973, collected by C. L. Hubbs; TCWC 0444.3, 1 male (288 mm), Nicaragua, Brito San Juan, 11°30'N, 86°00'W, 15 Mar. 1972, collected by Gallaway and McAlpin; USNM 76574, 1 male (220 mm), Panama, 11 Oct. 1914; USNM 181309, 1 male (372 mm), Mexico, Gulf of California, Sinaloa, South of Bahia Topolobampo, collected by J. Stephens; USNM 181322, 4 females (138 to 285 mm), Mexico, Gulf of California, Baja California, Punta Diggs, 9 miles E of San Felipe, 1 to 2 Feb. 1955, collected by Hadaderao and Berdoque; USNM 222631, 1 male (220 mm), Mexico, Sonora, Puerto Penasco, "Puerto Arista" Cruise, 5 Jul. 1968.

Diagnosis.-- Disc rhomboid to diamond in shape and broadly laterally expanded, 1.01 to 1.32 times ($\bar{x}$=1.18) long. Eyes large, 3.63 to 6.58 % ($\bar{x}$=5.24 %) of distance from snout to cloaca. Midline of visceral cavity ornamented with several rows of denticles running parallel to each other; each pectoral radial on marginal area of disc from level of eyes to posterior corner of pectoral fin bearing small denticles.

Description.-- Proportional dimensions of embryos are not included. Disc rhomboid or diamond in shape, 1.01 to 1.32 times ($\bar{x}$=1.18) long; disc length to maximum width of disc 38.79 to 60.36 % ($\bar{x}$=48.01 %) of disc width; antero-lateral margin of disc broadly expanded laterally to level of spiracles, but abruptly rounded toward axil of pectoral fin in both sexes; in males antero-lateral margin slightly concave; angle of snout 100°to 121° ($\bar{x}$=109°) in males and 114

to 128°($\bar{x}$=118°) in females; tip of snout sometimes broadly marked off from rest of disc as a small projection. Pelvic fins forming an equalateral triangle, lateral margin straight and posterior margin broadly rounded; width of pelvic fins 0.80 to 1.41 times ($\bar{x}$=1.14) long. Tail slender, anterior to origin of tail spine moderately depressed, width at axil of pelvic fins 4.75 to 7.74 % ($\bar{x}$=5.69 %) of distance from cloaca to tip of caudal fin; tail rarely with weak lateral keels; distance from cloaca to origin of tail spine 40.31 to 51.41 % ($\bar{x}$=45.24 %) of distance from cloaca to tip of caudal fin; distance from cloaca to tip of caudal fin 48.98 to 56.58 % ($\bar{x}$=52.50 %) of total length. Caudal fin slender, dordal lobe much shorter than ventral lobe; tip of caudal fin usually broadly rounded; distance from cloaca to origin of dorsal lobe of caudal fin 31.29 to 38.24 % ($\bar{x}$=34.78 %) of total length; height of dorsal lobe of caudal fin 11.48 to 26.79 % ($\bar{x}$=18.04 %) of length.

Preorbital length 2.52 to 5.12 times ($\bar{x}$=3.53) orbit diameter; preoral length 1.82 to 2.97 times ($\bar{x}$=2.34) distance between nostrils; interorbital width 1.09 to 1.84 times ($\bar{x}$=1.36) orbit diameter; eye moderately large and oriented rather laterally, diameter 3.63 to 6.58 % ($\bar{x}$=5.24 %) of distance from snout to cloaca. Length of spiracle 0.59 to 1.20 times ($\bar{x}$=0.77) interorbital width. Nasal curtain relatively long, posterior margin fringed and either straight to moderately concave; length of nasal curtain 35.53 to 59.47 % ($\bar{x}$=48.15) of its width. Lobe-like expansion of posterior margin of nostrils relatively well developed and accommodating expansion of nasal curtain; one to four papillae on proximal margin of lobe-like expansion. Teeth in both jaws, arranged in quincunx, with sharply

pointed cusp in males larger than about 200 mm in TL; number of teeth in upper jaw 32 to 46 ($\bar{x}$=38).

Distance between first gill slits 1.75 to 2.60 times ($\bar{x}$=2.14) distance between nostrils; distance between fifth gill slits 1.00 to 1.67 times ($\bar{x}$=1.25) distance between nostrils. Number of vertebral centra 93 to 103 ($\bar{x}$=98).

Coloration.-- After preservation in formalin and storage in alcohol dorsal surface light chocorate brown to dark brown. Two specimens from off the coast of Jalisco and Michoacan, Mexico exhibit minute brownish specks scattered on dorsal surface of disc. Ventral surface yellowish white.

Range.-- Coast of Mexico from the Gulf of California from along the coast of Baja California near San Felipe area to off Brito San Juan, Nicaragua.

Urotrygon chilensis (Günther, 1871)

Urolophus chilensis Günther, 1871:653-654 (an immatured female from Chile).

Urolophus asterias Jordan and Gilbert, 1882:579; Jordan, 1885:364; Jordan, 1895:388; Jordan and Evermann, 1896:82; Kumada and Hiyama, 1937:23 (Pl.56, Fig.A).

Urolophus goodei Jordan and Bollman, 1889:151 (a juvenile specimen from Panama); Jordan and Evermann, 1899:81; Gilbert and Starks, 1904:16.

Urolophus mundus: Gilbert and Starks, 1904:16 (not U. munda Gill).

Urotrygon asterias: Meek and Hildebrand, 1923:83-84; Breder, 1926:11; Beebe and Tee-Van, 1941:266; Chirichigno, 1963:3-4; Castro Aguirre et al., 1970:120 (only list of species); Chirichigno, 1974:69; ? Ramirez Hernandez and Gonzalez Pages, 1976:65 (possibly U. rogersi according to Fig. 46; Miyake and McEachran, 1986: 291-302.

Urotrygon caudispinosus Hildebrand, 1946:67-69 (a juvenile specimen from Peru); Koepcke, 1959:85; Chirichigno, 1974:70; Miyake and McEachran, 1986: 291-302.

Urotrygon chilensis: Garman, 1913:405; Fowler, 1930:23; Beebe and Tee-Van, 1941:267; Fowler, 1951:276; Castro Aguirre, 1965 a:165-166 (a specimen from Guerrero, Chiapas, Mexico); Castro Aguirre, 1965b:231-232; Chirichigno, 1974:66; Ramirez Hernandez and Gonzalez Pages, 1976:64-65; Miyake and McEachran, 1986: 291-302.

Urotrygon goodei: Garman, 1913:405; Meek and Hildebrand, 1923:84-85; Jordan, Evermann, and Clark, 1930:30; Fowler, 1930:23; Beebe and Tee-Van, 1941:267; Ricker, 1959:4; Chirichigno, 1963:4; Castro Aguirre, 1965b:227-228; Chirichigno, 1974:70; Ramirez Hernandez and Gonzalez Pages, 1976:65; Miyake and McEachran, 1986: 291-302.

Urotrygon goodei caudispinosus: Ricker, 1959:4; Koepcke, 1962:15.

Urotrygon peruanus Hildebrand, 1946:69-71 (a specimen from Peru); Koepcke, 1959:85; Koepcke, 1962:15; Chirichigno, 1974:66; Miyake and McEachran, 1986: 291-302.

Urotrygon serrula Hildebrand, 1946:65-67 (a juvenile specimen from Peru); Koepcke, 1962:15; Chirichigno, 1974:69; Miyake and McEachran, 1986: 291-302.

Syntypes.-- USNM 29542, male (300 mm in TL), Mexico, Mazatlan, 1882, collected by C. H. Gilbert; USNM 28204; USNM 29524; USNM 29580; USNM 29318.

Other material.-- BMNH 1871.9.12.13:119, 1 female (265 mm), Chile, 13 Sept. 1871; CAS 42263, 1 female (335 mm), Mexico, Hancock Galapagos Expedition, 8 Dec. 1931; CAS 51839, 1 male (351 mm), Mexico, Nayarit, Estero at San Blas, 30 Jan. 1958, collected by J. Fitch and others; FMNH 62371, 1 male (123 mm), 3 females (153 to 380 mm), Mexico, Nayarit, Bahia Matenchen, 6 Feb. 1958, collected by R. H. Rosenblatt and J. Stevens; GCRL 12310, 3 males (200 to 332 mm), 2 females (203 to 260 mm), Panama, Gulf of Panama, 08°51.5'N, 79°33.5'W, 9 Nov. 1973, collected by C. Dawson; GCRL 15295, 1 male (136 mm), 2 females (296 to 332 mm), Panama, Gulf of Panama, 29 Oct. 1969; LACM 7013, 11 males (228 to 372 mm), 3 females (288 to 419 mm), Mexico, Sonora, Gulf of California, Bahia Kino, 3 Feb. 1950, collected by B. W. Walker and others; LACM 30745-10, 2 males (291 to 307 mm), 1 female (228 mm), Costa Rica, Puntarenes, Gulf of Nicoya, 27 Nov. 1968, collected by P. Leon; SIO 62-38, 1 female (387 mm), Mexico, Jalisco, Banderas Bay, 20°39'N, 105°11.8'W, 19 Aug. 1961, collected by F. H. Berry and others; SIO 62-39, 6 males (164 to 276 mm), Mexico, JaliscoBanderas Bay, 20°39'N, 105°11.8'W, 19 Aug. 1961, collected by F. H. Berry and others; SIO 64-78, 1 female (344 mm), Mexico, Gulf of California, Baja California, 25°12.2'N, 112°07.7'W, 10 meters, 1 Feb. 1964, collected by B. J. Zahuranec and others; SIO 71-224, 3 males (249 to 322 mm), Panama, Ft. Amador Officer's Club Beach, 13 Nov. 1970, collected by J. E. McCosker and others; TCWC uncat., 1 female (279mm), Peru, off Paita, 05°34.6'S, 81°02.1'W, 25 May 1976; USNM

41150, 1 female (183 mm), Panama, Magdalena Bay, Albatross Station 2797, 08°06.3'N, 78°51'W, 59.4 meters, 5 Mar. 1888; USNM 50373, 1 male (277 mm), Panama, collected by C. H. Gilbert; USNM 127790, 1 female (188 mm), Peru, Independecia Bay, 1941, collected by R. H. Fiedler and others; USNM 127793, 1 male (276 mm), Peru, Paita Bay, 1941, collected by R. H. Fiedler and others; USNM 127795, 1 male (187 mm), Peru, Lobos de Tierra Bay, 1941, collected by R. H. Fiedler and others; USNM 128425, 1 female (178 mm), Panama, Canal Zone, Fort Amador Beach, collected by W. H. W. Komp; USNM 183999, 9 males (140 to 306 mm), 5 females (231 to 292 mm), Mexico, Sinaloa, Topolobampo, 10-14 Feb. 1958, collected by W. J. Baldwin; USNM 222630, 1 male (204 mm), Colombia, Buenaventura, 06°58'N, 77°41'W, 4 Mar. 1969; USNM 222632, 1 male (272 mm), Colombia, south of Buenaventura, off Punta Aji, 03 18'N, 77 42'W, 38 meters, 21 Sept. 1969; USNM 222636, 12 females (125 to 280 mm), Colombia, south of Tumaco, off Cape Manglares, 01°39'N, 79° 02.3'W, 18.3 meters, 27 Oct. 1970; USNM 222638, 1 male (119 mm in DL), Colombia, south of Buenaventura, 02°48'N, 78°08'W, 18 meters, 20 Sept. 1969; USNM 222640, 3 males (223 to 254 mm), Colombia, south of Tumaco, off Cape Manglares, 01°39'N, 79°02.3'W, 18.3 meters, 27 Oct. 1970.

Diagnosis.-- Snout densely but disc and tail sparsely covered with denticles. Midline of disc and tail from nuchal to origin of tail spine with strong thorns either in a continuous row or in a discontinuous row. Tail relatively dorso-ventrally compressed: tail width at axil of pelvic fins 5.62 to 9.51 % ($\bar{x}$=7.35 %) of distance from cloaca to caudal fin.

Description.-- Proportional dimensions of embryos are not included. Disc almost rhomboid in shape, 1.07 to 1.19 times ($\bar{x}$=1.12) long; disc length to maximum width of disc 39.37 to 50.64 % ($\bar{x}$=44.8 %) of disc width; antero-lateral margin of disc slightly concave and expanded laterally to level of eyes, but abruptly rounded toward intersion of pectoral fin; angle of snout 112° to 132° ($\bar{x}$=121°) in males and 123° to 134° ($\bar{x}$=129°) in females; tip of snout not forming a projection. Pelvic fins forming an equalateral triangle, lateral margin straight and posterior margin broadly rounded; width of pelvic fins 0.90 tp 1.42 times ($\bar{x}$=1.18) long. Tail slender, dorsally slightly convex but ventrally flattened, width at axil of pelvic fins 5.62 to 9.51 % ($\bar{x}$=7.35 %) of distance from cloaca to caudal fin; tail rarely with weak keels; distance from cloaca to origin of tail spine 36.94 to 58.59 % ($\bar{x}$=45.03 %) of distance from cloaca to tip of caudal fin; distance from cloaca to tip of caudal fin 49.09 to 56.00 % ($\bar{x}$=53.12 %) of total length. Caudal fin moderately slender, dorsal lobe much shorter than lower lobe; tip of caudal fin narrowly rounded to slightly pointed; distance from cloaca to origin of dorsal lobe of caudal fin 13.93 to 22.22 % ($\bar{x}$=18.09 %) of total length; height of dorsal lobe of caudal fin 12.50 to 21.14 % ($\bar{x}$=17.06%) of length.

Preorbital length 2.59 tp 4.74 times ($\bar{x}$=3.61) orbit diameter; preoral length 1.92 to 2.82 times ($\bar{x}$=2.30) distance between nostrils; interorbital width 1.28 to 2.00 times ($\bar{x}$=1.61) orbit diameter; eye moderately large and oriented dorso-laterally, diameter 3.13 to 6.18 % ($\bar{x}$=4.59 %) of distance from snout to cloaca. Length of spiralces 0.60 to 1.02 times ($\bar{x}$=0.76) interorbital width. Nasal curtain relatively long, posterior margin narrowly concave and fringed; length of nasal

curtain 29.17 to 52.73 % ($\bar{x}$=45.74 %) of its width. Lobe-like expansion of posterior margin of nostril moderately developed inwardly and accommodating extension of nasal curtain; three to six papillae on proximal margin of lobe-like expansion. Teeth in both jaws, arranged in quincunx, with sharply pointed cusp in males larger than about 230 mm TL (one mature specimen (LACM 7013), 308 mm TL, lacked cusps on teeth); 32 to 48 ($\bar{x}$=38) rows of teeth in upper jaw.

Distance between first gill slits 1.56 to 1.90 times ($\bar{x}$=1.75) distance between nostrils; distance between fifth gill slits 1.10 to 1.62 times ($\bar{x}$=1.38) distance between nostrils. Number of vertebral centra 84 to 97 ($\bar{x}$=89).

Coloration.-- After preservation in formalin and storage in alcohol, dorsal surface dark brown to light brown. Most of specimens taken from off the coast of Sonora, Mazatlan, Nayarit, and Jalisco (Mexico) and Costa Rica have numerous small rounded and speck-like blackish markings on disc. The markings on mid-portion of disc much larger and more rounded while those toward the margin of disc are much smaller and speck-like markings. Distribution of markings seems to have no distinct pattern. The markings also present in some of specimens taken from Panama and Colombia. Specimens taken from Colombia (USNM 222640) did not have any markings at all. Ventral surface yellowish white.

Range.-- Coast of Mexico from the San Felipe region in the Gulf of California to Costa Rica, Panama, Colombia, northern parts of Peru and Chile.

Remarks.-- Urotrygon serrula, U. peruanus, U. caudispinosus and U. goodei were morphologically indistinguishnable and thus synonymized

with the oldest available name U. chilensis Günther. Unfortunately, Miyake and McEachran (1986) uncorrectly regarded Urotrygon asterias as the senior synonym.

Urotrygon sp. (3)

(Fig. 31C)

Urotrygon sp (3): Miyake and McEachran, 1986: 291-302.

Material.-- GCRL 13064, 1 female (264 mm), 2 males (93 and 267 mm), Panama, Punta Paitille, 8 Mar. 1974, collected by C. E. Dawson and others.

Diagnosis.-- Entire dorsal disc and tail covered with high cone-shaped and recured denticles. Denticles enlarged toward midline and forming one or two continuous rows on midline of disc and tail from nuchal to origin of tail spine. Dorsal surface of disc and tail uniformly dark grayish brown, relatively broadly edged with white.

Description.-- Proportional dimensions of the embryo (93 mm TL) are not included. Disc round to diamond in shape, 1.01 to 1.15 times ($\bar{x}$=1.07) long; disc length to maximum width of disc 45.54 to 51.01 % ($\bar{x}$=48.13 %) of disc width; antero-lateral margin of disc convex in both sexes and slightly expanded laterally to level of spiracles, but abruptly rounded toward axil of pectoral fin; angle of snout 117° in males and 131° and 137° in females; tip of snout without forming a projection. Pelvic fins forming an equalateral triangle, lateral margin straight or only slightly convex and posterior margin broadly

rounded; corner of pelvic fins very broadly rounded; width of pelvic fins 1.10 to 1.14 times ($\bar{x}$=1.13) long. Tail moderately slender, depressed dorsally but rather convex ventrally, width at axil of pelvic fins 6.92 to 8.73 % ($\bar{x}$=7.70 %) of distance from cloaca to tip of caudal fin; tail with well developed lateral keel running on sides from behind insertion of pelvic fins to insertion of tail spine; distance from cloaca to origin of tail spine 47.90 to 49.64 % ($\bar{x}$=48.95 %) of distance from cloaca to tip of caudal fin; distance from cloaca to tip of caudal fin 51.09 to 55.46 % ($\bar{x}$=53.22 %) of total length. Caudal fin moderately long, distally broaden; tip of caudal fin broadly rounded; distance from cloaca to origin of dorsal lobe of caudal fin 33.64 to 36.47 % ($\bar{x}$=35.11 %) of total length; height of dorsal lobe of caudal fin 18.60 to 24.40 % ($\bar{x}$=21.54 %) of length.

Preorbital length 3.26 to 3.80 times ($\bar{x}$=3.61) orbit diameter; preoral length 2.11 to 2.44 times ($\bar{x}$=2.66) distance between nostrils; interorbital width 1.60 to 1.80 times ($\bar{x}$=1.71) orbit diameter; eyes moderately large and oriented dorso-laterally, diameter 4.32 to 4.77 % ($\bar{x}$=4.62 %) of distance from snout to cloaca. Length of spiralces 0.72 to 0.77 times ($\bar{x}$=0.74) interorbital width. Nasal curtain relatively long, posterior margin deeply concave and fringed; length of nasal curtain 50.62 to 55.62 % ($\bar{x}$=53.64 %) of its width. Lobe-like expansion of nostrils well developed inwardly and accommodating expansion of nasal curtain; a cluster of one to three papillae on proximal edge of lobe-like expansion. Teeth in both jaws, arranged in quincunx, with sharp cusps in male (embryo in 93 mm TL posssessing teeth in both jaws); number of teeth in upper jaw 29 to 35 ($\bar{x}$=33) (35 in embryo).

Distance between first gill slits 1.66 to 1.71 times ($\bar{x}$=1.69) distance between nostrils; distance between fifth gill slits 1.32 to 1.67 times ($\bar{x}$=1.52) distance between nostrils. Number of vertebral centra 83 to 86 ($\bar{x}$=86).

Coloration.-- After preservation in formalin and storage in alcohol, dorsal disc, pelvic fins, and tail uniformly dark grayish brown, narrowly edged with yellowish white. Ventral surface uniformly yellowish white, with relatively broad brownish margin along edge of disc and pelvic fins. A brownish band running longitudinally on ventral surface of tail between level of posterior tip of pelvic fins and origin of tail spine.

Range.-- Punta Paitille, Bay of Panama.

Urotrygon aspidura (Jordan and Gilbert, 1881)

Urolophus aspidurus Jordan and Gilbert, 1881:307; Jordan, 1885:364; Jordan and Evermann, 1896:81-82; Gilbert and Starks, 1904:16-17; Kendall and Radcliffe, 1912:80.

Urotrygon aspidurus: Garman, 1913:405-406; Meek and Hildebrand, 1923:85; Jordan, Evermann, and Clark, 1930:30; Fowler, 1930:23; Beebe and Tee-Van, 1941:264-265; ? Castro Aguirre, 1965b: 226-227 (or U. rogersi according to the description and figure); ? Castro Aguirre et al., 1970:120 (or either U. rogersi or U. chilensis according to locality, Gulf of California); Chirichigno, 1974:66; Ramirez Hernandez and Gonzalez Pages, 1976:65; Miyake and McEachran, 1986: 291-302.

Syntypes.-- USNM 29454, male (294 mm), Panama, Feb.- Mar. 1881, collected by C. H. Gilbert; USNM 29410, female (225 mm), Panama, Feb.- Mar. 1881, collected by C. H. Gilbert; USNM 29307.

Other material.-- CAS 51834, 3 males (126 to 284 mm), 2 females (295 to 317 mm), Panama, Bay of Panama, Isla Tobago, 1-2 July 1953; CAS 51835, 7 males (168 to 250 mm), 7 females (145 to 428 mm), Panama, Punta Chame and Punta Auton, 6-9 Sept. 1958, collected by E. S. Reese; MCZ 1011S, 1 female (98 mm), Panama; MCZ 1095, 1 female (317 mm), Panama, Thayer Expedition, 1865, MCZ 1096S, 1 male (101 mm), 1 female, (349 mm), Panama; MCZ 1097S, 1 female, (367 mm), Panama, 1865, collected by W. W. Brown; MCZ 1098S, 2 females (217 and 248 mm), Panama, Thayer Expedition, 1865, MCZ 1099S, 1 female (251 mm), Panama; MCZ 1100S, 1 female (248 mm), Panama, Thayer Expedition, 1865; MCZ 1102S, 1 female (106 mm), Panama, Thayer Expedition, 1865; SIO 64-764, 1 male (190 mm), Panama; SIO 64-965, 2 males (150 and 196 mm), Panama; SU 6810, 4 females (139 to 302 mm), Panama, collected by C. H. Gilbert; SU 58-402, 1 male (303 mm), Panama, Canal Zone, 08° 59'N, 79° 35.5'W, 7 Jan. 1958, collected by J. G. Simpson and P. W. Johnson.

Diagnosis.-- Eyes relatively small, diameter 2.66 to 4.47 % ($\bar{x}$=3.56 %) of distance from snout to cloaca. Midline of tail ornamented with thorns having an elongated, sharp-edged crown set on an oval basal plate. Caudal fin relatively slender and long: length of dorsal lobe of caudal fin 10.37 to 18.90 % ($\bar{x}$=14.24 %) of total length.

Description.-- Proportional dimensions of embryos are not included. Disc nearly rhomboid in shape, 1.05 to 1.16 times ($\bar{x}$=1.09)

long; disc length to maximum width of disc 42.6 to 54.7 % ($\bar{x}$=47.9 %) of disc width; antero-lateral margin of disc, convex in females and strongly concave in males, broadly expanded laterally to level of behind spiracles, but abruptly rounded toward insertion of pectoral fin; angle of snout 102°to 115°($\bar{x}$=109) in males and 113°to 121°($\bar{x}$=116°) in females; tip of snout in adults forming a narrow projection. Pelvic fins forming a right-angled triangle, lateral margin slightly concave and posterior margin broadly rounded; width of pelvic fins 1.03 to 1.91 times ($\bar{x}$=1.29) long. Tail slender and dorso-ventrally flattened, width at axil of pelvic fins 4.88 to 6.90 % ($\bar{x}$=5.54 %) of distance from cloaca to tip of caudal fin; tail rarely with weak keels on sides; distance from cloaca to origin of tail spine 39.34 to 53.68 % ($\bar{x}$=42.99 %) of distance from cloaca to tip of caudal fin; distance from cloaca to tip of caudal fin 48.92 to 57.43 % ($\bar{x}$=54.59 %) of total length. Caudal fin very slender and elongated, dorsal lobe much shorter than lower lobe; tip of caudal fin usually pointed; distance from cloaca to origin of dorsal lobe of caudal fin 16.69 to 24.72 % ($\bar{x}$=19.81 %) of total length; height of dorsal lobe of caudal fin 10.37 to 18.90 % ($\bar{x}$=14.24 %) of length.

Preorbital length 3.39 to 5.38 times ($\bar{x}$=4.48) orbit diameter; preoral length 2.48 to 3.18 times ($\bar{x}$=2.59) distance between nostrils; interorbital width 0.41 to 1.84 times ($\bar{x}$=1.56) orbit diameter; eye small and oriented almost dorsally, diameter 2.66 to 4.47 % ($\bar{x}$=3.50 %) of distance from snout to cloaca. Length of spiralces 0.67 to 2.78 times (x=0.86) interorbital width. Nasal curtain moderately long, posterior margin broadly concave and fringed; length of nasal curtain 39.81 to 57.28 % ($\bar{x}$=49.23 %) of its width. Lobe-like expansion of

posterior margin of nostrils well developed inwardly and accommodating expansion of nasal curtain; one to five papillae on proximal margin of lobe-like expansion. Teeth in both jaws, arranged in quincunx, with sharply pointed cusp in males larger than about 200 mm TL; 28 to 46 ($\bar{x}$=35) rows of teeth in upper jaw.

Distance between first gill slits 1.99 to 2.48 times ($\bar{x}$=2.27) distance between nostrils; distance between fifth gill slits 1.12 to 1.95 times ($\bar{x}$=1.35) distance between nostrils. Number of vertebral centra 84 to 94 ($\bar{x}$=90).

Coloration.-- After preservation in formalin and storage in alcohol, dorsal surface whitish to yellowish tan. Ventral surface yellowish or white. Several specimens possess a few small brownish spots on dorsal disc.

Range.-- Panama Bay and Pacific side of Canal Zone, Panama, with one record from the coast of Peru.

KEY TO THE SPECIES OF UROTRYGON

1a Velvet-like denticles present on dorsal disc and both dorsal and ventral surface of tail. Long snout; preorbital length 16.61 to 19.86 % of total lenght.

-------- U. daviesi.

1b Denticles absent on ventral surface of tail. Relatively short snout; preorbital length 12.37 to 18.47 % ($\bar{x}$=12.57 %) of total length. -------- 2.

2a Brownish vermiculation pattern on entire dorsal disc.

-------- U. sp (2)

2b Dorsal aspect of disc generally uniformly brownish to tan; dark brownish markings present in some individuals of two species (U. asterias and U. rogersi). -------- 3.

3a Short and robust caudal fin; length of dorsal lobe of caudal fin 9.49 to 17.61 % ($\bar{x}$=12.99 %) of total length. Small but strong recurved denticles covering entire dorsal disc and tail.

-------- U. munda.

3b Slender caudal fin with or without tapered tip; length of dorsal lobe of caudal fin 12.44 to 23.53 % ($\bar{x}$=16.62 %) of total length. Denticles small and not strongly recurved, except for those of U. sp (3). -------- 4.

4a Eyes small; eye diameter 1.57 to 3.76 % ($\bar{x}$=2.54 %) of length of snout to center of cloaca. Thorns absent on dorsal disc and tail. -------- 5.

4b Eyes relatively large; eye diameter 2.66 to 6.58 % ($\bar{x}$=4.49 %) of length of snout to center of cloaca. Thorns or enlarged denticles present on midline of dorsal disc and/or tail.

-------- 6.

5a Narrow disc width; disc width 44.23 to 56.34 % ($\bar{x}$=48.17 %) of total length. Slender and tapered caudal fin; length of dorsal lobe of caudal fin 15.07 to 23.53 % ($\bar{x}$=19.24 %) of total length. -------- U. microphthalmum.

5b Relatively wide disc; disc width 54.70 to 67.90 % ($\bar{x}$=60.90 %) of total length. Caudal fin slender but not tapered; length of dorsal lobe of caudal fin 12.44 to 19.93 % ($\bar{x}$=15.28 %) of total length. -------- U. sp (1).

6a Orbit diameter 2.39 to 2.73 % ($\bar{x}$=2.56 %) of total length. Angle of snout 138°to 148°($\bar{x}$=144°) in females. Small denticles uniformly present on dorsal disc, except narrow naked area along margin. -------- U. venezuelae.

6b Orbit diameter 2.52 to 4.74 % ($\bar{x}$=3.59 %) of total length. Angle of snout 113°to 140°($\bar{x}$=130°) in females. Denticles present on entire dorsal disc, sparsely or densely.

-------- 7.

7a Thorns present only on midline of dorsal tail. Eye diameter 2.66 to 4.47 % ($\bar{x}$=3.50 %) of length of snout to center of cloaca. Preorbital length 11.76 to 15.61 % ($\bar{x}$=13.92 %) of total length. Tail height 2.45 to 3.57 % ($\bar{x}$=3.00 %) of total length. -------- U. apsidura.

7b Thorns present on midline of both dorsal disc and tail, in a continuous or discontinuous row. Eye diameter 3.13 to 6.18 %

($\bar{x}$=4.61 %) of length of snout to center of cloaca. Preorbital length 9.82 to 13.59 % ($\bar{x}$=11.90 %) of total length. Tail height 3.03 to 4.97 % ($\bar{x}$=4.09 %) of total length.

-------- 8.

8a Small denticles arranged in several parallel rows on midline region of visceral cavity; each pectoral radial in marginal area of disc from level of eyes to posterior corner of pectoral fin bearing small denticles; the same denticles sparsely present on the other areas of dorsal disc. Tail width 2.49 to 4.00 % ($\bar{x}$=3.00 %) of total length. -------- U. rogersi.

8b Denticles sparsely or densely distributed without any special arrangements on disc. Tail width 3.03 to 4.97 % ($\bar{x}$=4.11 %) of total length. -------- 9.

9a Different shape of thorns from that of denticles. Thorns with oval basal plates on midline of dorsal disc and tail, arranged in a continuous or discontinuous row; in some individuals, thorns present only on nuchal to scapular region.

-------- U. chilensis.

9b Both denticles and thorns similar in shape; high cone-shaped and recurved with stelliform basal. Thorns arranged on midline of dorsal disc and tail continuously.

-------- U. sp (3).