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A REVISION OF THE ELECTRIC RAY GENUS
DIPLOBATIS WITH NOTES ON THE INTERRELATIONSHIPS
OF NARCINIDAE (CHONDRICHTHYES, TORPEDINIFORMES)

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AND
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UNIVERSITY OF FLORIDA

GAINESVILLE

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A REVISION OF THE ELECTRIC RAY GENUS
DIPLOBATIS WITH NOTES ON THE
INTERRELATIONSHIPS OF NARCINIDAE
(CHONDRICHTHYES, TORPEDINIFORMES)

JANICE D. FECHHELM¹ AND JOHN D. MCEACHRAN²

ABSTRACT: We examined the morphological characters and internal anatomical features of the electric ray genus *Diplobatis* (Torpediniformes, Narcinidae) in order to determine the taxonomic status of the various forms. All specimens from the northern coast of South America (Colombia to Brazil) were found to be very variable in most morphological characteristics but to be identical in skeletal structure. Based on overlapping proportional measurements and a lack of distinguishing characters (both internal and external), *D. altenai* Boeseman 1963 is synonymized with *D. pictus* Palmer 1950, and the placement of *D. guamachensis* Martin 1957 in synonymy with *D. pictus* by Bigelow and Schroeder (1962) is verified. Three subspecies are recognized within *D. pictus*: *D. pictus pictus* Palmer, *D. pictus guamachensis* Martin, and *D. pictus colombiensis* new subspecies. *D. ommata* (Jordan and Gilbert 1890), from the Pacific coasts of Mexico and Central America, is found to be identical to *D. pictus* in skeletal anatomy and similar to its congener in most proportional measurements. *D. ommata* is distinguished from *D. pictus* by its dorsal color pattern and differing clasper morphology. The genus and species of *Diplobatis* are redefined, and the three subspecies are described. Finally, the four genera of Narcinidae (*Benthobatis*, *Diplobatis*, *Discopyge*, and *Narcine*) are compared and found to be very conservative anatomically. A phylogenetic analysis based on synapomorphic character states shows *Discopyge* and *Narcine* to be the sister group to the other narcinids.

RESUMEN: Examinamos las características morfológicas y anatomía interna de la raya eléctrica del género *Diplobatis* (Torpediniformes, Narcinidae) a fin de determinar el estatus taxonómico de sus varias formas. Todos los especímenes de la costa norte de Sudamérica (desde Colombia hasta Brasil) variaron notablemente en la mayoría de sus características morfológicas pero fueron idénticos en estructura esquelética. De acuerdo a coincidencia en medidas proporcionales y a la falta de caracteres internos y externos distinguibles, la especie *D. altenai* Boeseman 1963 se considera sinónima a *D. pictus* Palmer 1950. Asimismo, se verifica la sinonimia de *D. guamachensis* Martin 1957 con *D. pictus* por Bigelow y Schroeder (1962). Se reconocen tres subspecies pertenecientes a *D. pictus*: *D. pictus pictus* Palmer, *D. pictus guamachensis* Martin y *D. pictus colombiensis* nueva subespecie. *D. ommata*, proveniente de las costas pacíficas de México y América Central, se considera idéntica a *D. pictus* en cuanto a anatomía del esqueleto y similar a su congénere en la mayoría de sus medidas proporcionales. *D. ommata* se distingue por su patrón dorsal de color y diferente morfología de los ganchos copulatorios ("clasper"). Se redefine el género y las especies de *Diplobatis* y se describe tres subspecies. Finalmente, los cuatro géneros de Narcinidae (*Benthobatis*, *Diplobatis*, *Discopyge* y *Narcine*) se comparan y se concluye que son anatómicamente muy conservativos. El análisis filogenético basado en caracteres sinapomórficos demuestra que *Discopyge* y *Narcine* son grupos hermanos de los otros narcinidos.

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INTRODUCTION

The systematic relationships within the Torpediniformes, as with many other elasmobranch taxa, are largely unknown because of morphological conservatism and lack of comprehensive anatomical studies. Most anatomical studies of torpedinoids have been limited to a single species or were undertaken as a minor part of comparative anatomical surveys of elasmobranchs (Henle 1834; Richardson 1841; Gegenbaur 1865, 1872; De Beer 1926; Daniel 1934; Holmgren 1940). While a few workers have examined more than one genus (Haswell 1885; Howes 1890; Garman 1913; Holmgren 1941), the results of these studies were used to define structural differences between torpedinoids and other elasmobranch taxa and said nothing of the relationships within the electric rays. Recently, Compagno (1973, 1977) combined these earlier studies with additional examinations in order to determine interrelationships of the Torpediniformes. His work suggests that Torpediniformes is a monophyletic group derived from the guitarfishes (Rhinobatiformes) and distinguished by the following derived characters: huge pectoral electric organs; no supra-orbital crests on the neurocranium, anteriorly directed, fan- or antler-shaped antorbital cartilages, extending to but not articulating with propterygia of pectoral fins; and unique pectoral girdles, with a strut-supported posterior tube-like extension holding a rhinobatoid-like articular surface for the pectoral basals (Compagno 1977). Phylogenetically, the Torpediniformes are something of an enigma: while they exhibit some plesiomorphic character states and are most often allied with primitive batoid groups (Gegenbaur 1865; Daniel 1934; Bigelow and Schroeder 1953; Compagno 1977), they possess several highly derived character states that are not shared with any other orders of Batoidea (Heemstra and Smith 1980). Torpediniformes are also the last batoid group to appear in the fossil record (Romer 1966), and recent work on chromosome number and genome size suggests a more advanced phylogenetic position for this group (Donahue 1974; Stingo 1979).

Currently, four families of Torpediniformes are recognized (Compagno 1973): Hypnidae Gill 1862, a monotypic family; Torpedinidae Bonaparte 1838, with 1 genus and 14–17 species; Narkidae Fowler 1934, with 4 genera and 9 or 10 species; and Narcinidae Gill 1862, with 4 genera and 17 or 18 species.

The four genera of Narcinidae differ only slightly from each other. *Benthobatis* Alcock 1898 is distinguished by an ovoid disc, very minute, possibly non-functional eyes which may be entirely concealed by overlying integument, and no lateral fold on the tail. There are two species, one from off the coast of India and one from the western Atlantic, both found in deep water (up to 1000 m). *Narcine* Henle 1834 has a nearly

circular disc, normal, functional eyes, and a thin lateral fold on the tail. There are 11 or 12 species: 8 from the Indian and southwestern Pacific oceans, 2 or 3 from the eastern Pacific Ocean, and 1 from the western Atlantic Ocean. All are usually found in shallow water. *Discopyge* Tschudi 1864 has a circular disc, a prominent lateral fold on the tail, and pelvic fins joined across the base of the tail. The genus is monotypic and is found off the coasts of Peru, Chile, Argentina, and southern Brazil. *Diplobatis* Bigelow and Schroeder 1948 has a subcircular disc with a moderately convex anterior edge, normal functional eyes, nostrils subdivided into two apertures, and a narrow lateral fold on the tail. Representatives are found in the eastern Pacific Ocean from the Gulf of California to Colombia and in the western Atlantic Ocean from Colombia to the mouth of the Amazon River (Bigelow and Schroeder 1953).

Considerable confusion exists as to the number of distinct species within *Diplobatis*. The genus was erected by Bigelow and Schroeder (1948) for *Discopyge ommata* Jordan and Gilbert 1890 from the Gulf of California, because of the unique structure of its nasal apertures. *Diplobatis pictus* Palmer 1950 was described from the western Atlantic (Brazil to Guyana) and was distinguished from *D. ommata* by disc shape, shape and location of the pelvic fins, and dorsal coloration. Another species, *Diplobatis guamachensis* Martin 1957, was described from the coast of Venezuela. It was distinguished from *D. ommata* and *D. pictus* by proportional measurements, location of the lateral fold, and coloration. A fourth species, *Diplobatis altenai* Boeseman 1963, was described from a single specimen taken off the coast of Surinam. It was distinguished from its congeners by the size of the eyes and spiracles, lack of papillae along the spiracular margin, shape of the nasal curtain, location of the cloaca, size of the dorsal and caudal fins, and coloration.

Bigelow and Schroeder (1962) examined 24 specimens of *D. pictus* and noted considerable morphological variation, particularly in coloration, but because of the small number of specimens examined, they simply separated the specimens into freckled and non-freckled forms, based on their dorsal patterns. In 1968, after examining additional specimens of *Diplobatis* taken off the coasts of Venezuela and Brazil, Bigelow and Schroeder stated that because of the extreme color variation observed within *D. pictus*, and because proportional measurements of *D. guamachensis* fell within the ranges for *D. pictus*, *D. guamachensis* was a junior synonym of *D. pictus*.

Palacio (1974) reported four specimens of what he identified as *D. pictus* from the northwest shore of Colombia, but he gave no description of them. Heemstra (pers. comm. to Palacio 1974) expressed the view that both *D. guamachensis* and *D. altenai* were possibly juvenile forms of *D. pictus*.

The examination of a large number of specimens of *Diplobatis* indi-

cated greater morphological variation within the Atlantic forms than had been previously recognized. This study was undertaken to assess the extent of the morphological variation in order to determine the taxonomic status of the Atlantic forms. Examinations of skeletal characteristics along with morphometrics and coloration were used to determine interrelationships within the genus. Finally, anatomical examinations of the other genera of Narcinidae (*Benthobatis*, *Discopyge* and *Narcine*) were used to elucidate interrelationships within the family.

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METHODS AND MATERIALS

Specimens examined in this study are listed in Appendix I and were borrowed from the following institutions: British Museum (Natural History) (BMNH), London; Florida State Museum (UF), Gainesville; Los Angeles County Museum of Natural History (LACM), Los Angeles; Museum of Comparative Zoology (MCZ), Cambridge; National Museum of Natural History (USNM), Washington, D.C.; Rijksmuseum van Natuurlijke Historie (RMNH), Leiden; and the Texas Cooperative Wildlife Collection (TCWC), College Station.

A total of 274 specimens of *Diplobatis* were examined; 45 external measurements as well as eight morphological characters were recorded for each specimen. Methods of Bigelow and Schroeder (1953) were followed in making external measurements. Characters that have proved valuable in distinguishing and grouping other taxa of batoids, i.e. neurocranium, hyobranchial skeleton, scapulocoracoid, pelvic girdle, and claspers, were examined for all species. Anatomical descriptions are based on dissected specimens: complete dissections, involving removal of the neurocranium, jaws, hyobranchial skeleton, scapulocoracoid, and pelvic girdle, were performed on at least one specimen of each form examined. To facilitate dissection of some of the smaller specimens, the cartilage was first stained with methylene blue following the methods of Van Wijhe (1902). Clasper dissections were not possible because of their small size (less than 20 mm) and the fragile nature of the cartilage. Terminology for clasper morphology is as follows: all cartilages on the dorsal, lateral, and ventral aspects of the clasper are referred to as the dorsal terminal, lateral terminal, and ventral terminal cartilages, respectively. Other terms are from Hulley (1972). The use of these terms does not imply that these structures in torpedinoids are homologous to those in skates (Rajoidei). Terminology for all other skeletal structures is from Holmgren (1940), Compagno (1973, 1977), and McEachran and Compagno (1979).

Radiographs were examined in order to count vertebrae and pelvic radials, as well as

to confirm the dissection. The vertebral counts represent the total number of vertebrae, as differentiation between trunk and precaudal vertebrae could not be made. In the only case where dissection was not possible (i.e. *Discopyge tschudii*), the drawings were constructed from radiographs.

Programs from the Statistical Analysis System (SAS: Helwig and Council 1979) were used to perform Student's *t*-tests as well as to compute the mean, range, standard deviation, and standard error of the mean for variables separated into various subsets of the data. In these analyses, external measurements were expressed as percent of total length to account for differences in size.

Specimens separated into various groups based on geographical distribution were examined in order to determine if there were any significant differences between two groups using Student's *t*-tests. For those that showed a significant difference, levels of significance are given in the text.

Multivariate analyses were performed using the Cluster and Principal Component Analyses of the Numerical Taxonomy System (NT-SYS; Rohlf and Kispauh 1972). Of the 45 variables measured for each specimen, only those that could be measured with good accuracy ($n = 21$) were used. Damaged specimens on which it was impossible to take complete measurements were not used in the multivariate analyses. Data from the specimens were first standardized using an arcsine transformation. In the analyses, no assumptions were made regarding the taxonomic status of any specimen nor were any *a priori* groups formed.

Presumably owing to the extreme morphometric variation exhibited by the specimens, these multivariate tests gave inconclusive results in that they failed to separate the specimens into any discrete groups. Since none of the results of this study were based solely on morphometric differences, the results of these tests are not presented.

RESULTS AND DISCUSSION

The Atlantic forms of *Diplobatis* can be divided into three geographically distinct color morphs. Group A is found from the mouth of the Amazon River to Trinidad (Fig. 1) and is characterized by a polytypic color pattern (Fig. 2) ranging from tan with no markings (morph #1) to tan with a few indistinct brown or white spots or both (morph #2) (the non-freckled type of Bigelow and Schroeder, 1962); tan with well defined, fairly symmetrical brown spots (morph #3) (as described for *D. altenai*); tan with well defined, fairly symmetrical brown and white spots (morph #4) (as described for the holotype of *D. pictus*); and tan with numerous, asymmetrical, very small brown and white spots (morph #5). While all specimens examined from this region can be roughly classified under one of the above morphs, it should be stressed that a complete gradation exists between all color patterns. The polytypic nature of this group is also evidenced by a mature female (157 mm TL) taken off Surinam, which contained four nearly full term young. While the female has a non-freckled dorsal color pattern (morph #2), two of the embryos have very distinct markings similar to the holotype of *D. pictus* (morph #4), while the remaining two exhibit the color pattern of *D. altenai* (morph #3).

Group B is found from Trinidad to just west of the Gulf of Venezuela

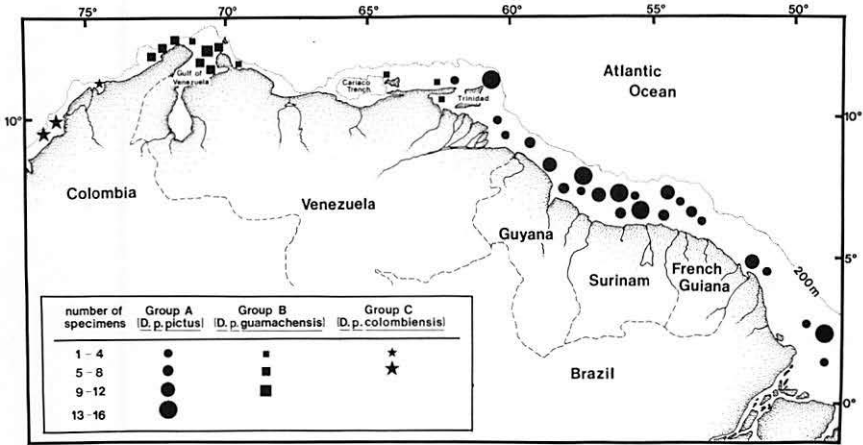


Figure 1. Map of northern South America showing the distribution of the Atlantic forms of *Diplobatis* examined in this study. Some locations represent multiple lots.

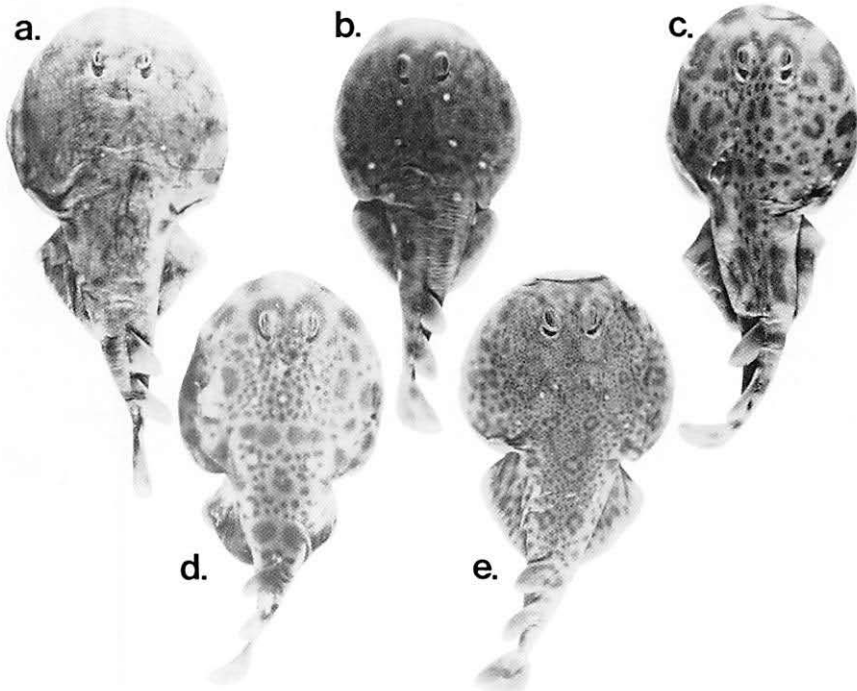


Figure 2. Dorsal color patterns found in Group A: (a) morph #1, USNM 226775, female, 162 mm TL; (b) morph #2, UF 29894, female, 138 mm TL; (c) morph #3, USNM 186422, male, 133 mm TL; (d) morph #4, TCWC 1905.1, female, 101 mm TL; (e) morph #5, BMNH 1961.8.31, female, 145 mm TL.

(Fig. 1) and is characterized by the dorsal color pattern described for *D. guamachensis* (Fig. 3a), i. e. golden tan with brown bands running longitudinally on the edges of the disc and the pelvic fins and transversely on the body and tail. The thickness of the bands varies but never exceeds 0.5 times the diameter of the eye, and while indistinct in some specimens, the bands are always arranged in the characteristic pattern.

Group C is found off the coast of northwestern Colombia (Fig. 1), and its dorsal color pattern (Fig. 3b) is golden tan with brown spots of various sizes. The spots also vary in number and at times are somewhat symmetrical.

The three groups varied little in body shape and morphometrics (Table 1). All characteristics examined (including both proportional measurements and morphological features) showed broad overlap among the three groups. However Group B has a somewhat shorter snout length (preocular and prebuccal) than either Group A ($P < 0.01$) or Group C ($P < 0.01$) (Fig. 4a,b), and Group C has a relatively narrower disc than either Group A ($P < 0.01$) or Group B ($P < 0.01$) (Fig. 4c). External clasper morphology of all three groups is identical, as is the internal skeletal structure of the neurocranium, hyobranchial skeleton, scapulocoracoid, and pelvic girdle.

The areas inhabited by the three groups are contiguous but do show some substrate and salinity differences. Within the range of Group A the substrate is mainly soft mud with virtually no coral reef formation; salinity levels fluctuate dramatically from the large amounts of freshwater runoff from the numerous river systems, in particular the Amazon and Orinoco river systems (Mitchell 1959; Lowe-McConnell 1962; Bullis and Thompson 1965; U.S. Naval Oceanographic Office 1965; Gines and Cervigon 1968; Gorshkov 1978). The fluvial outflow also exerts a noticeable influence on the coastal morphology of the region in the form of extensive tidal mud flats in some areas (Lowe-McConnell 1962). The substrate in the range of Group B is mostly hard sand with extensive coral reef development in some areas; there is little fluctuation in salinity, and the coastline is very eroded and embayed owing to the action of strong tidal currents (Bullis and Thompson 1956; U.S. Naval Oceanographic Office 1965; Gorshkov 1978). The area inhabited by Group C shows similarities to both of the preceding areas: the substrate is mostly hard sand, but there are areas of soft mud, and while there is coral reef development, it is much less than in the preceding region (Bullis and Thompson 1965; U.S. Naval Oceanographic Office 1965; Gorshkov 1978).

The Atlantic forms of *Diplobatis* and the Pacific *D. ommata* differ mainly in coloration and clasper structure. The dorsal coloration of *D. ommata* is strikingly distinct from its congeners and consists of a brown background irregularly mottled and spotted with lighter and darker markings which are more pronounced on the disc and absent on the snout. Most

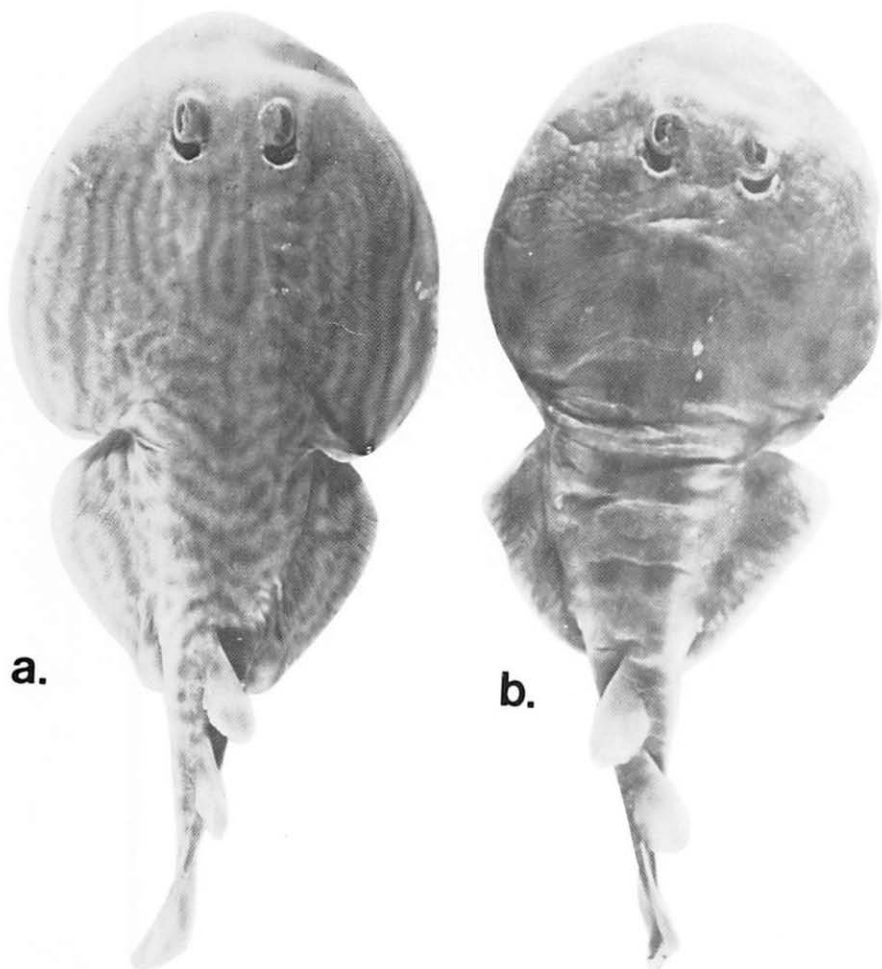


Figure 3. Dorsal color patterns of: (a) Group B, UF 19886, male, 128 mm TL; and (b) Group C, USNM 226773, male, 129.5 mm TL.

noticeable is the large blackish and yellowish ocellated spot in the center of the disc. Both Atlantic and Pacific specimens of *Diplobatis* have very short and stout claspers, but the claspers of the Atlantic forms are constricted at mid-length and taper distally to a blunt point, while the clasper of *D. ommata* is stout its entire length (not constricted at mid-length), with a broadly rounded distal tip. The ventro-lateral slit (= pseudosiphon?) of the Atlantic forms extends from the lateral edge onto the ventral surface, while that of *D. ommata* is confined to the lateral edge. In the Atlantic forms, the dorsal terminal cartilage does not form the dorsal wall of the clasper groove, but in *D. ommata* the dorsal terminal cartilage

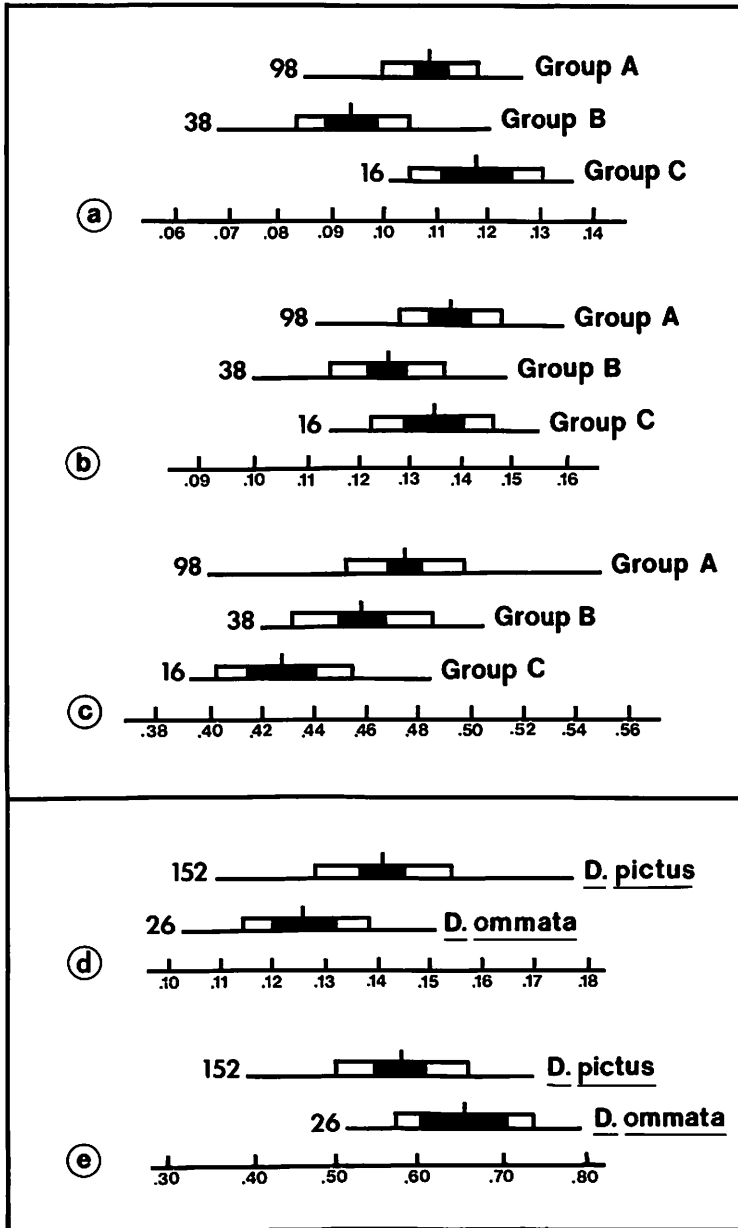


Figure 4. Variation in (a), preocular snout length; (b), prebuccal snout length; and (c) disc width among the Atlantic forms of *Diplobatis* (Group A, Group B, and Group C). Variation in (d), length of dorsal lobe of caudal fin; and (e), interorbital distance between *D. pictus* and *D. ommata*. In each diagram the horizontal line represents the mean, the open rectangle equals one standard deviation and the closed rectangle represents two standard errors of the mean. Numbers on the vertical scale are percent of total length; the number to the left of each diagram is the sample size.

is distally folded 180° to overlie the lateral terminal cartilage, thereby forming the dorsal wall of the clasper groove.

While the two groups are similar in proportional measurements (Table 2), *D. ommata* has a shorter dorsal lobe of the caudal fin ($P < 0.01$) which results in a more rounded caudal fin when compared to the Atlantic forms, which have a more triangular caudal fin (Fig. 4d). Also, *D. ommata* has a slightly greater interorbital distance than the Atlantic forms ($P < 0.01$) (Fig. 4e).

TAXONOMIC CONCLUSIONS

THE STATUS OF *Diplobatis altenai* BOESEMAN 1963

Morphological comparisons of the holotype of *D. altenai* with specimens of *D. pictus* failed to reveal any concrete morphological differences. The characters used to differentiate *D. altenai* from *D. pictus*, i. e. vent before half total length, smaller eyes and orbits, lack of papillae along the spiracular margins, smooth free edge of the nasal curtain, smaller gill openings, lower and shorter dorsal fins, and larger caudal fin (Boeseman 1963), are also found in many specimens of *D. pictus*. The dorsal coloration of *D. altenai* (light brownish with numerous dark spots of various size) does not represent a distinct type but rather is part of a continuum that ranges in Group A from specimens with no markings to those with very ornate patterns. Also, proportional measurements of the holotype of *D. altenai* fall well within the ranges of *D. pictus* examined (Table 3), and the clasper morphology of *D. altenai* is identical with that of *D. pictus*. The lack of differences between these two species was previously noted by Gines and Cervigon (1968). After examining specimens of *D. pictus* taken off the coasts of the Guianas and Surinam, they stated that they did not identify any specimens of *D. altenai* (which had been described from this area) because of their inability to differentiate between *D. pictus* and *D. altenai*. Heemstra (pers. comm. to Palacio 1974) also noted the similarities between *D. altenai* and *D. pictus* and stated that the two species were possibly synonymous. As no morphological or morphometrical differences are discernible between the two species, we consider *D. altenai* a junior synonym of *D. pictus*.

THE STATUS OF *Diplobatis pictus* PALMER 1950

The various Atlantic forms of *Diplobatis* are very similar with the exception of their differing dorsal color patterns, which are possibly related to their benthic existence. Living in close association with the substrate,

it is likely that the various types of sediment found in the three areas could result in differing selection pressures which may enhance the development of the various color patterns. If the selection pressures remain relatively constant, genetic reinforcement of the differences could occur (Barlow 1961). The parapatric and allopatric distributions of the three groups suggests a possible lack of or reduction in gene flow between the populations, and enforces the idea that the between-group color differences are at least partially genetic. While the vagility of *Diplobatis* is not known, there appear to be no absolute physical or biotic barriers that would prevent movement of individuals from one area to another. This, along with the absence of any differences in both internal structure and clasper morphology of the three groups, suggests that the groups have not attained levels of specific distinction. The similarity of the clasper morphology among the specimens is even more striking when we consider the differentiation this structure has undergone between the Atlantic *Diplobatis* and the Pacific *D. ommata*.

Therefore, while the three Atlantic groups of *Diplobatis* do not appear distinct enough to warrant recognition as separate species, they do seem sufficiently heterogeneous to justify subspecific designation. *D. pictus pictus* (= Group A) consists of specimens formerly identified as *D. pictus* and *D. altenai*; *D. pictus guamachensis* (= Group B) consists of specimens formerly identified as *D. guamachensis*; and *D. pictus colombiense* subs. nov. (= Group C) which is described herein.

THE STATUS OF *Diplobatis ommata* (JORDAN AND GILBERT 1890)

While *D. ommata* is similar to *D. pictus*, the distinctions between the two warrant their continued recognition as separate species. The fact that these two species are identical in internal anatomy and similar in proportional measurements is not surprising when one considers the conservative nature of electric rays. Within the genus *Narcine* few, if any, anatomical or proportional differences exist between the species *N. brasiliensis*, *N. entemedor*, and *N. vermiculatus* (pers. obs.). In fact, there are very few anatomical differences between the four genera of Narcinidae. Concerning clasper structure, it is important to note that the other three genera (*Narcine*, *Benthobatis*, and *Discopyge*) are virtually identical in their external clasper morphology. This emphasizes the importance of the morphological differentiation this structure has undergone between *D. pictus* and *D. ommata*. (While the claspers were not examined internally [as previously discussed], it is reasonable to assume that the gross differences in external morphology reflect differing internal anatomy.) Also, there is absolutely no intergradation of either clasper structure or dorsal color pattern between the two species.

SYSTEMATIC ACCOUNTS

Diplobatis BIGELOW AND SCHROEDER

Diplobatis Bigelow and Schroeder 1948:562–565. Type species: *Discopyge ommata* Jordan and Gilbert 1890; by monotypy.

DIAGNOSIS.—*Diplobatis* is distinguished from all other genera of Narcinidae by nostrils that are subdivided into two apertures and by clasper morphology. Other important characters are as follows: disc sub-circular, slightly broader than long to slightly longer than broad; anterior edge of disc slightly to moderately convex; pelvic fins not joined across base of tail; claspers not continuous with inner edge of pelvic fin; moderately stout tail with two dorsal fins and well developed, subtriangular caudal fin; narrow lateral fold on tail; snout to cloaca length 43–65% of total length. *Diplobatis* is also the smallest genus of Torpediniformes, ranging from 50 to 60 mm TL at birth to a maximum size of 250 mm TL.

INTERNAL DESCRIPTION.—Neurocranium (Fig. 5) has a very long and broad rostrum, its length 40–60% of total cranial length; antorbital cartilages variable in shape and extent of branching, joining indistinctly with tip of rostrum; precerebral fossa rectangular, occupying nearly all of rostrum; basonasal fenestrae sub-rectangular, length approximately 30% precerebral fossa length; frontoparietal fenestrae slightly smaller than basonasal fenestra and elliptical in shape; area between antorbital cartilages and rostrum interlaced with strong bands of fibrous tissue; condyles for antorbital cartilages triangular, located on lateral surface of nasal capsule; nasal capsule very variable in extent of cartilaginous development. Anterior foramen for preorbital canal very small and located on dorsal aspect of nasal capsule, near junction of nasal capsule and rostral base; posterior foramen for preorbital canal extremely small and located dorsolaterally at junction of nasal capsule and orbit; interorbital region broad; anterior fontanelle irregular in shape, narrowing posteriorly; foramen for orbitonasal canal just ventral to posterior foramen of preorbital canal; optic nerve foramen of moderate size and situated anterior to midline of orbit; oculomotor nerve foramen very small and located posterior to optic nerve foramen and dorsal to optic pedicle; orbital fissure very large, situated on posterior aspect of orbit, anterior to foramen for hyomandibular branch of facial nerve; glossopharyngeal nerve foramen located posterodorsally to hyomandibular facet; vagus nerve foramen located posterodorsally to glossopharyngeal nerve foramen. Basal plate extremely narrow, particularly at level of orbits.

Hyomandibula (Fig. 6a) very stout and anterolaterally oriented to cranium; jaws stout, lower jaw much longer than upper jaw and with strong attachment to hyomandibula; labial cartilages at corners of jaw,

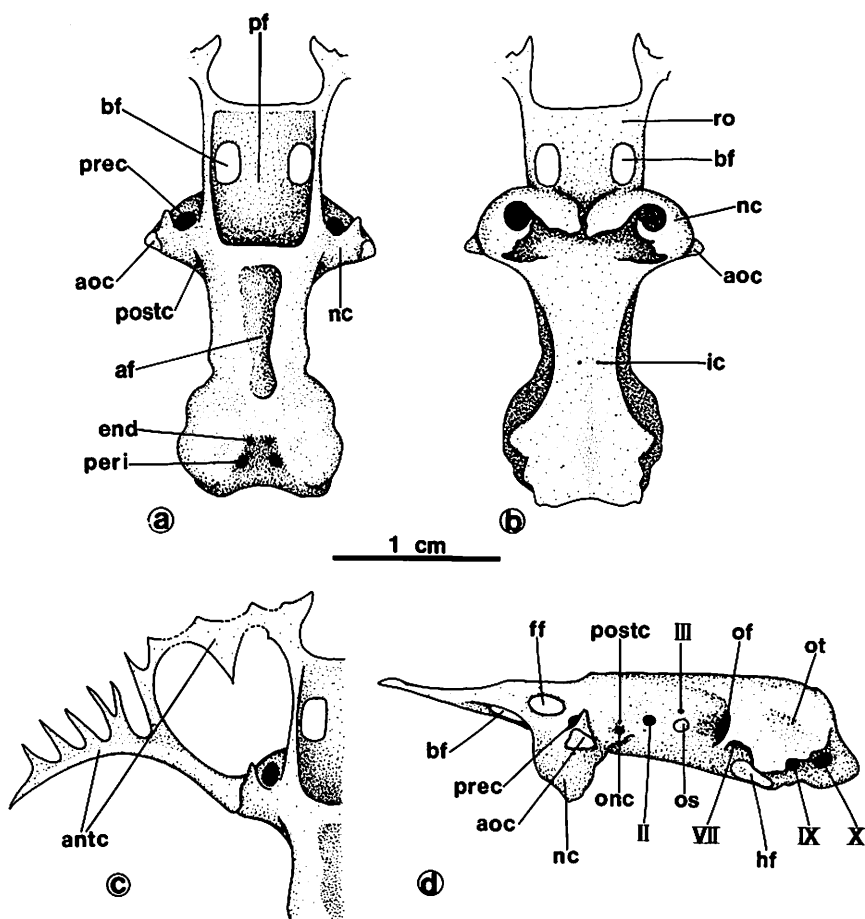


Figure 5. Neurocranium of *Diplobatis* (TCWC 1900.1). (a) dorsal view; (b) ventral view; (c) partial dorsal view showing antorbital cartilages; (d) lateral view: af, anterior fontanelle; antc, antorbital cartilages; aoc, antorbital condyle; bf, basonasal fenestrae; end, endolymphatic foramen; ff, frontoparietal fenestrae; hf, hyomandibular facet; ic, internal carotid artery foramen; nc, nasal capsule; of, orbital fissure; onc, orbital nasal canal; or, orbit; os, optic stalk; ot, otic capsule; peri, perilymphatic foramen; pf, precerebral fossa; postc, postorbital canal foramen; prec, preorbital canal foramen; ro, rostrum; II, optic nerve foramen; III, oculomotor nerve foramen; VII, hyomandibular branch of facial nerve foramen; IX, glossopharyngeal nerve foramen; X, vagus nerve foramen. Dashed lines indicate areas of indistinct calcification.

not calcified at midsection. Ceratohyal (Fig. 6b) very long and slender, attached to hyomandibula by weak ligamentous connection; ventral pseudohyoid flattened anteroposteriorly, its lateral end articulating with dorsal pseudohyoid; first hypobranchials dorsal to medial end of ceratohyal and ventral to first ceratobranchial, second hypobranchials very large and rectangular in shape; ceratobranchials well developed, 1 through 3

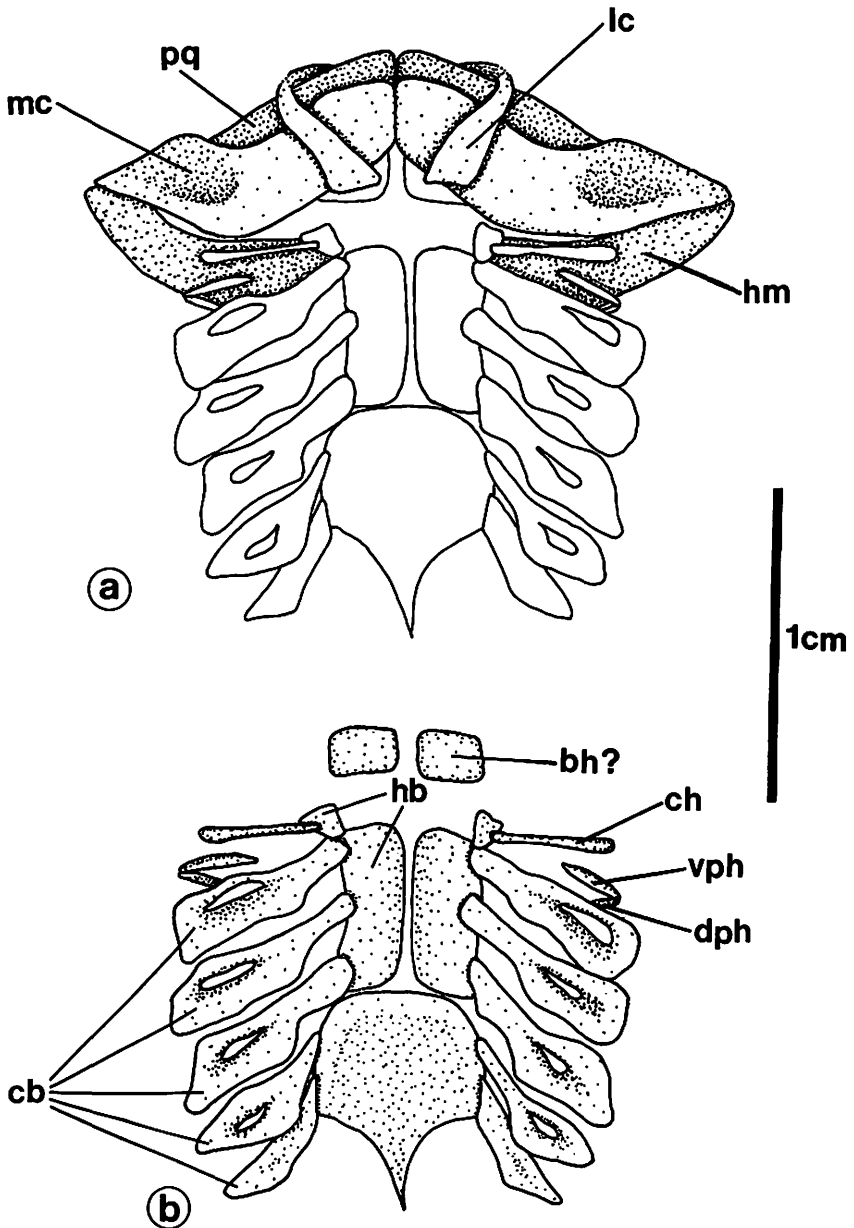


Figure 6. Jaws and hyobranchial skeleton of *Diplobatis* (TCWC 1900.1). (a) ventral view of jaws and hyomandibula showing placement in relation to hyobranchial skeleton; (b) ventral view of hyobranchial skeleton: bh, basihyoid; cb, ceratobranchial; ch, ceratohyal; dph, dorsal pseudohyoid; hb, hypobranchial; hm, hyomandibula; lc, labial cartilage; mc, Meckel's cartilage (lower jaw); pq, platoquadrate (upper jaw); vph, ventral pseudohyoid.

articulating with second hypobranchial; ceratobranchials 4 and 5 articulating with basibranchial copula; fifth ceratobranchials somewhat reduced and articulating distally with anterior ascending process of scapulocoracoid; basibranchial copula triangular with pronounced posterior projection. In addition to these elements, a pair of moderately large, rectangular-shaped cartilages are located ventral to the cranium. The identity of these cartilages is unclear. Compagno (1977) tentatively identified them as basihyoids, which appears incorrect as these elements are not associated with the hyobranchial skeleton, but lie directly below the cranium and dorsal to the esophagus.

Scapulocoracoid (Fig. 7a, b) with sub-rectangular lateral face; scapular process inclined posteromedially; posterior corner of scapulocoracoid extends as a tube-like structure which holds articular surfaces for pectoral basals; anteroventral corner extends below vertebral column as coracoid; anterior fenestrae of moderate size, its height approximately 50% of the total height and its length approximately 30% of the total length of the scapulocoracoid. There are four nerve foramina; postdorsal nerve foramen and postventral nerve foramen are located on either side of both the procondyle and the mesocondyle.

Pelvic girdle (Fig. 7c) consists of a relatively short puboischiadic bar with lateral extremes curved dorsally; prepelvic processes well developed, though lightly calcified anteriorly, their length nearly equal to the width of the girdle; iliac processes stout, slightly curved and directed posterolaterally. Three obturator foramina are located at the junction of the iliac and prepelvic regions.

REMARKS.—The subdivided nostrils of this genus set it apart not only from other Narcinidae but from all batoids as well. This condition was originally described by Bigelow and Schroeder (1953) as “. . . nostril subdivided about midway of its length into two separate apertures by a cross bridge of stiff tissue,” and is illustrated as such in Bigelow and Schroeder (1953) and Palmer (1950). As Tucker (1954) pointed out, this description is not wholly accurate, for rather than being divided by a bridge of tissue, the division of the nasal apertures is the result of fusion between the dorsal side of the nasal curtain (anterior nasal flaps) and the ventral side of the posterior nasal flap. This connection can be broken if the nasal curtain is forceably lifted. Once the two are separated, it is difficult to determine if the connection ever existed. For this reason, Tucker (1954) felt that this character was of questionable use taxonomically. We disagree with Tucker (1954) and consider this character very useful, for in none of the specimens of *Diplobatis* we examined was this connection broken on both sides of the nasal curtain.

Morphometrics are of little value in the systematics of *Diplobatis* owing to the great amount of morphological variability. Every characteristic

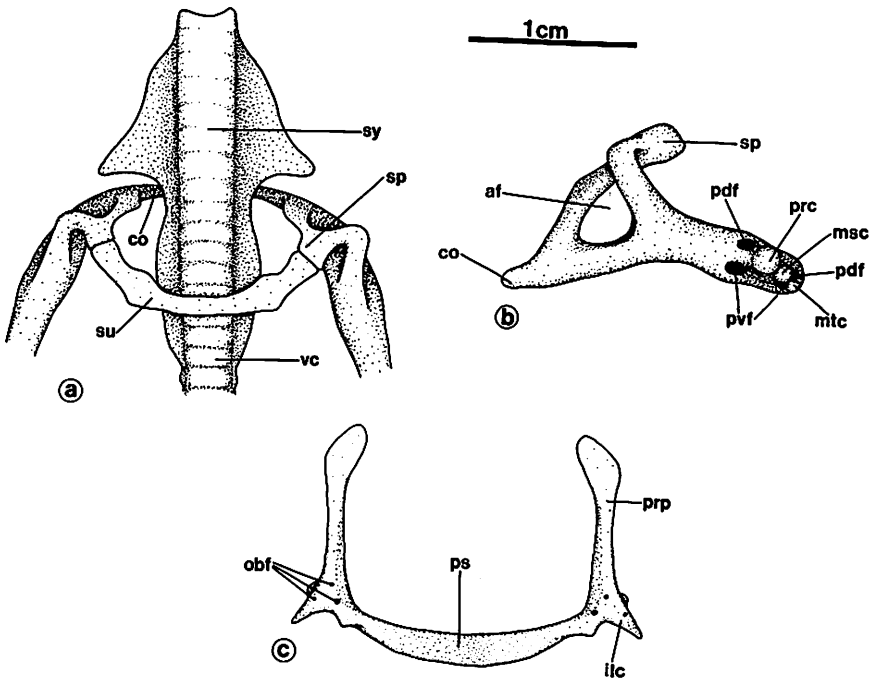


Figure 7. Scapulocoracoid and pelvic girdle of *Diplobatis* (TCWC 1900.1). (a) lateral view of scapulocoracoid; (b) dorsal view of scapulocoracoid and vertebral column; (c) dorsal view of pelvic girdle: af, anterior fontanelle; co, coracoid; msc, mesocondyle; mtc, metacondyle; obf, obturator foramina; pdf, postdorsal nerve foramina; prc, precondyle; prp, prepelvic processes; ps, puboischiadic bar; pvc, postventral nerve foramina; sp, scapular process; su, suprascapula; sy, synarcual; vc, vertebral column.

examined, including all measurements recorded, illustrated this. Many specimens appear very wrinkled, with folds of loose skin all over the body, particularly on the ventral side, making measurements difficult. We have also examined several deformed specimens ($n = 17$) of *Diplobatis*. In these cases, the cloaca and gill slits are stretched into circular openings, the mouth protrudes, the nasal curtain is pulled anteriorly, the spiracles are pulled open making the papillae along their margins barely evident, the pelvic fins are pulled very close to the body, the back is humped, and in most cases the skin on the disc is torn and shredded; the overall appearance of these specimens gives one the impression that the skin has somehow shrunk. The reasons for this condition are unknown. Improper preservation techniques could be the cause, but we examined one single lot that contained both deformed and normal specimens. Two species of *Torpedo*, described as having "teratological deformities," were discussed by Palmer and Wheeler (1958). Their teratological specimens are described as showing many of the features we noted

in the deformed specimens, i.e. humped back, pelvic fins pulled ventrally, and small nasal flap. While it seems somewhat unlikely that all the deformed specimens we examined exhibited teratological abnormalities, this possibility should not be ignored.

The measurements of these deformed specimens were not used in this study in any way. They are of importance, however, for they emphasize the fact that because of the variable morphological nature of electric rays, care should be taken with all taxa of Torpediniformes before basing taxonomic conclusions solely on morphometrics.

Diplobatis pictus PALMER

Diplobatis pictus Palmer 1950: 480–484.

Diplobatis guamachensis Martin 1957: 1–3.

Diplobatis altenai Boeseman 1963: 296–299.

DIAGNOSIS.—*Diplobatis pictus* is distinguished by its dorsal coloration, clasper morphology and range. Other useful characteristics are a relatively narrow interorbital distance; a subrectangular caudal fin usually with a distinct upper corner; and a very small total length, not exceeding 200 mm.

DESCRIPTION.—External morphology (Figs. 2, 3): Proportional measurements are given in Table 1. Measurements reported here represent the mean value, followed by the minimum and maximum values in parentheses. Disc round- to spade-shaped, 0.99 (0.82–1.21) times as broad as long; anterior margin of disc evenly rounded to slightly angular; axis of greatest width 68.2% (55.1–82.9%) of distance from tip of snout to axil of pectoral fins. Pelvic fins originate at or anteroventrally to axil of pectoral fins; anterior margin of pelvic fin short, 0.36 (0.27–0.49) times breadth of pelvic fins and 0.5 times or less length of posterior margin of pelvic fin; angle of anterior margin of pelvic fin from 45° to 90° to long axis of body; posterior margin of pelvic fin straight to slightly convex when fully spread; pelvic fins usually broadly rounded but at times with distinct lateral points; inner margins of pelvic fins free from or connected to sides of tail for a short distance. Tail moderately stout, convex dorsally, and slightly flattened ventrally, its width midway between posterior tips of pelvic fins and distal tip 0.49 (0.30–0.75) times as wide as interorbital distance; tail with a narrow lateral fold along lateral surfaces, originating from opposite midpoint of first dorsal fin to origin of second dorsal fin and ending at origin of, or slightly posterior to origin of caudal fin; length of tail from center of cloaca to distal tip to 0.91 (0.79–1.11) times distance from tip of snout to center of cloaca. Two dorsal fins on tail; upper corner of both dorsal fins from broadly rounded to acute; first dorsal fin located from entirely over to entirely posterior to pelvic fins; interspace between first and second dorsals 0.64 (0.41–0.98) times as long as base of first dorsal fin; second dorsal fin usually slightly higher than first; distance

between second dorsal fin and caudal fin 0.73 (0.41–1.28) times as long as base of second dorsal fin. Caudal fin sub-triangular, with distinct upper corner; base of caudal fin 0.86 (0.65–1.10) times as long, and its height 0.92 (0.67–1.17) times as great as dorsal lobe of caudal fin.

Preocular length 2.32 (1.53–3.41) times as long as orbit-spiracle distance; preoral length 2.07 (1.47–2.70) times internarial distance; eyes well developed, diameter of orbit equal to or slightly less than interorbital distance in smaller specimens (< 130 mm), and approximately 0.5 times interorbital distance in larger specimens (> 130 mm); orbit length greater than spiracle length in most cases; spiracle ringed with 5–10 low, rounded papillae (papillae barely evident or absent in a few cases). Nasal curtain very variable in size, much wider than long, free edge of nasal curtain either smooth or slightly crenulate and often projecting slightly at midline; nasal curtain often extending posteriorly to overlap upper and reaching lower jaw when mouth is fully closed; mouth approximately as wide as nasal curtain. Teeth in both jaws in a triangular patch, arranged in quincunx, about 14–16 rows counting inward at center of jaw, outermost row with one or two teeth and each succeeding row increasing, resulting in 16–20 teeth in innermost rows; anterior few teeth usually without cusps, the succeeding teeth with small triangular cusps which become increasingly long and narrow on the posterior teeth, all cusps pointing inward; teeth usually concealed when mouth is closed, however, two to seven rows of teeth may be exposed on the lower jaw even when mouth is closed.

The clasper of *D. pictus* (Fig. 8) is very short and stout, not continuous

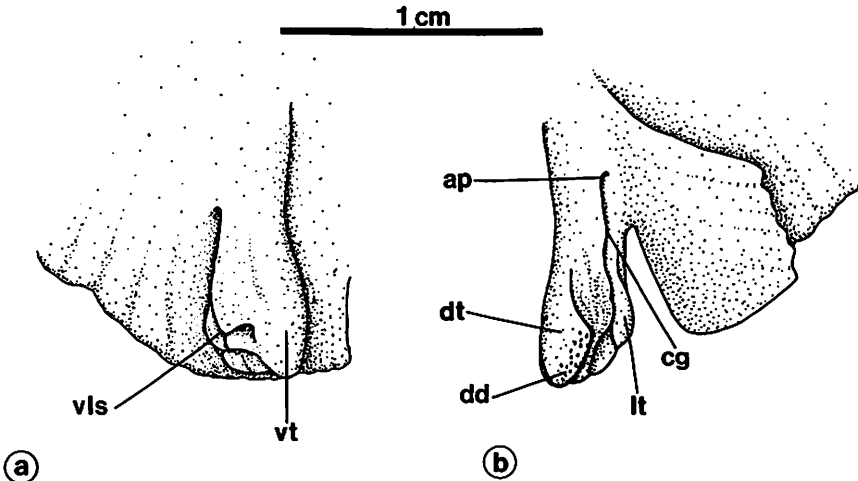


Figure 8. External clasper morphology of *Diplobatis pictus* (USNM 226775). (a) ventral view; (b) dorsal view: ap, apophyle; cg, clasper groove; dd, dermal denticles; dt, dorsal terminal cartilage; lt, lateral terminal cartilage; vls, ventrolateral slit; vt, ventral terminal cartilage.

with inner edge of pelvic fin and extending posterior to or just beyond posterior tip of pelvic fin; clasper constricted approximately at midpoint, widening distally, then tapering to a blunt point; ventrolateral slit (= pseudosiphon?) extending from lateral edge well onto ventral surface; dorsal surface with dermal denticles on dorsal terminal cartilage; dorsal terminal cartilage not forming dorsal wall of clasper groove.

The dorsal color pattern of *D. pictus* is very variable, with individuals ranging from tan with no markings to tan with either small brown or white spots or both; golden tan with wavy brown bands; and golden tan with brown spots of various size. Detailed descriptions of the coloration of all forms are included in the subspecies descriptions.

RANGE.—*D. pictus* is known only in the Atlantic Ocean, from the coasts of Brazil (north of the Amazon River basin), French Guiana, Surinam, Guyana, and Colombia (Fig. 1). Most specimens are taken in depths of less than 40 m, although a few specimens have been taken as deep as 183 m.

Diplobatis pictus pictus PALMER 1950
FIGURE 9

MATERIAL EXAMINED.—182 specimens, listed in Appendix I. Proportional measurements are given in Table 1.

DIAGNOSIS.—*Diplobatis pictus pictus* is distinguished from the other subspecies of *Diplobatis* by its dorsal color pattern and range.

DESCRIPTION.—The dorsal color pattern of this subspecies is extremely variable and consists of a tan or light brown background which is usually overlaid with a variety of brown or white spots, or both. Specimens can be divided into five somewhat arbitrary color morphs (Fig. 2). Morph #1: tan with no markings except for a few dark scratch-like marks on some specimens. Morph #2: tan with two to six small white spots, 1/4 the size of the orbits, irregularly scattered on the disc, or a few larger, indistinct and irregularly scattered dark blotches, or both. Morph #3: tan with fairly symmetrical dark brown spots, ranging from 1/4 to 1/2 the size of the orbits, well defined and smaller on the central part of the disc and increasing to one to four times the size of the orbits towards the margins of the disc and pelvic fins; usually with a dark blotch in front of and/or aside each dorsal fin and one or more dark spots on the dorsal and caudal fins. Morph #4: tan with dark brown spots, 1/4 to 1/2 the size of the orbits and larger brown blotches arranged fairly symmetrically; also four to eight (usually five) moderately sized white spots symmetrically arranged on the central part of the disc and usually four or more white

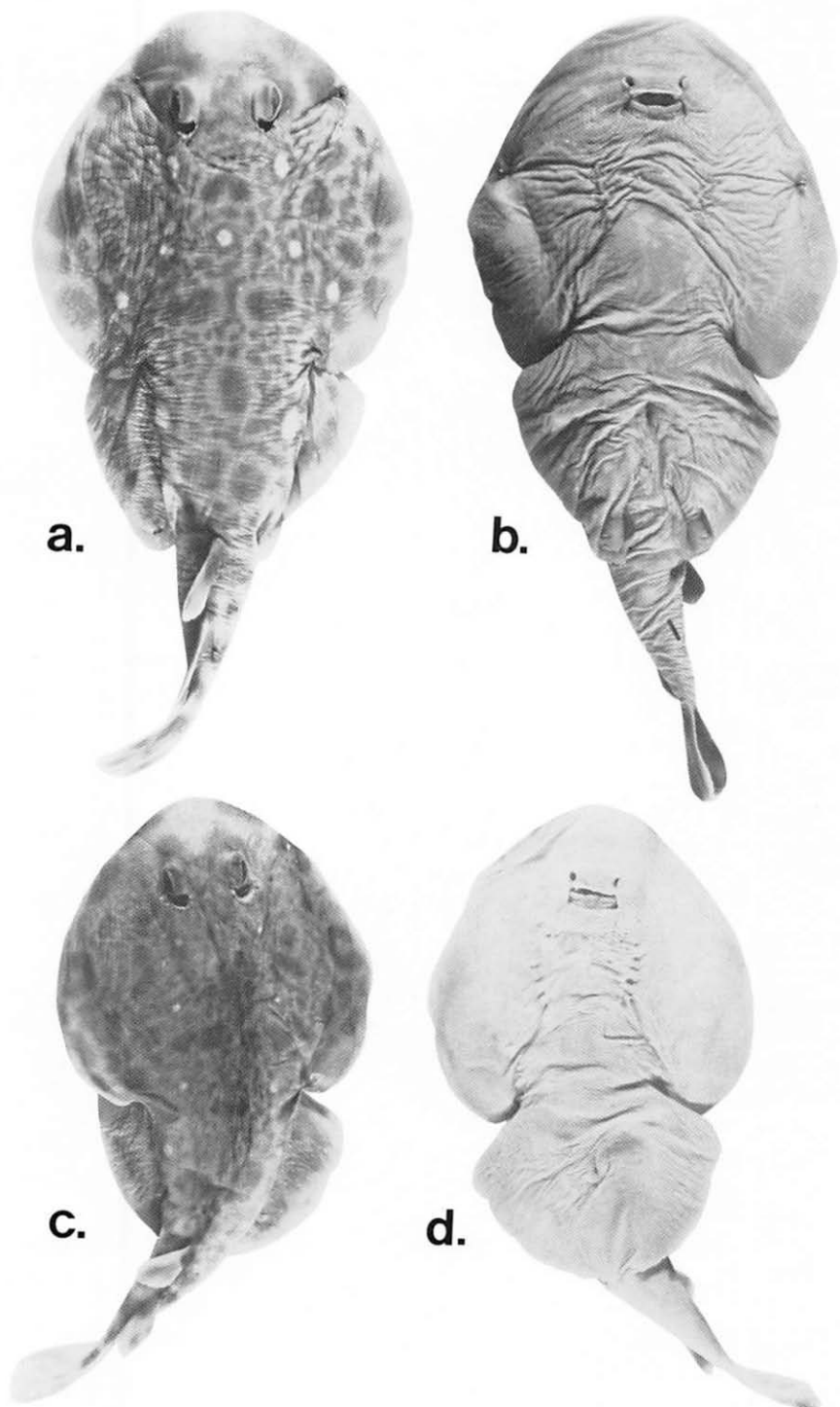


Figure 9. *Diplobatis pictus pictus*: (a, b) UF 19882, mature male, 134.8 mm TL, dorsal and ventral views; (c, d) UF 29893, female, 102.7 mm TL, dorsal and ventral views.

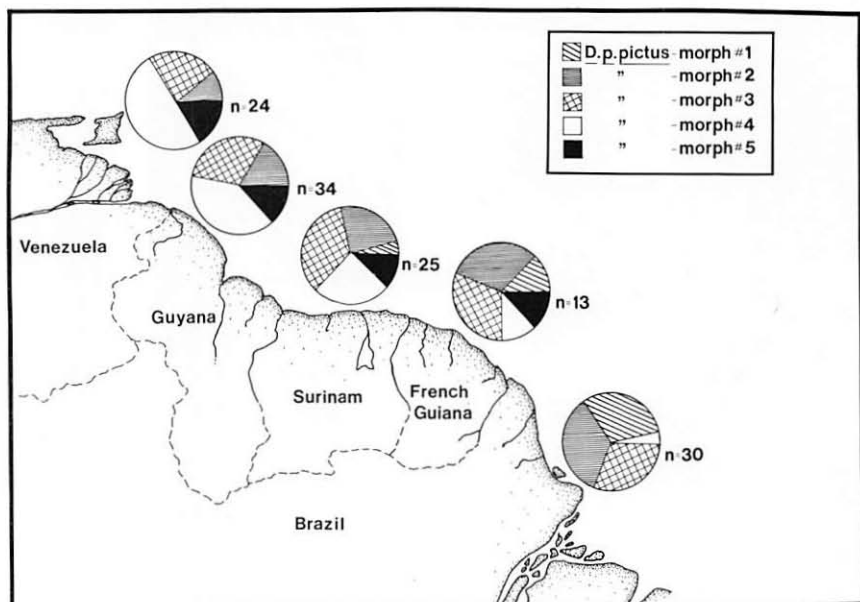


Figure 10. Coastline of northeastern South America showing the distribution of the five color morphs observed within *Diplobatis pictus pictus*. Sample sizes are indicated. Refer to Fig. 2 for photographs of the various color morphs.

spots, two each at the axils of the pectoral fins and on the pelvic fins; both the white spots and the dark blotches often appear ringed by a series of very small brown spots; there is usually a dark blotch in front of and/or aside each dorsal fin and several dark spots may be present on the dorsal and caudal fins. Morph #5: tan with numerous small to very tiny brown and white spots densely scattered over the surface, at times symmetrical, and usually larger on the margins of the disc and pelvic fins; at times the brown spots form indistinct circles; there is usually a dark blotch present in front of and/or aside each dorsal fin and several dark spots may be present on the dorsal and caudal fins. In all morphs, two dark, crescent-shaped blotches may be present surrounding the anterior edge of the orbits, and anterior to this (i.e. on the tip of the snout) there may be no coloration at all. The ventral surface of all morphs is white to cream colored with no markings.

RANGE.—*D. p. pictus* is found off Brazil from the mouth of the Amazon River northward along the coasts of French Guiana, Surinam, Guyana, and southeastern Venezuela to the Orinoco River delta and Trinidad. It is most common on muddy or sand bottoms and ranges in depth from 2 to 130 m.

REMARKS.—The five color morphs of *D. p. pictus* are distributed in a

southeast to northwest cline (Fig. 10). Specimens with a few or no markings (morphs #1 and #2) are more prevalent in the southern part of the range while specimens with a variety of white and brown markings (morphs #4 and #5) are more common in the northern part of the range. Intermediate types (morph #3) occur throughout the entire area. This morphocline again suggests that some extrinsic factor such as sediment composition or salinity influences the development of the differing dorsal color patterns. Most noticeable in this case is the fact that specimens in morph #1, i.e. those with no distinct markings, are most common off the Amazon River delta, a region of very turbid waters and muddy, silt-covered bottoms. The remaining morphs do not appear to be directly related to any particular ecological conditions. Again, more information on the natural history of these fish is necessary before further conclusions can be reached.

Diplobatis pictus guamachensis MARTIN 1957

FIGURE 11

MATERIAL EXAMINED.—51 specimens, listed in Appendix I. Proportional measurements are given in Table 1.

DIAGNOSIS.—*Diplobatis pictus guamachensis* is distinguished from the other subspecies of *D. pictus* by its dorsal color pattern and range. In addition to this, *D. p. guamachensis* has a relatively short snout length (preocular and prebuccal).

DESCRIPTION.—The dorsal color pattern of *D. p. guamachensis* consists of a tan to golden-tan background with darker brown wavy bands running longitudinally on the edges of the disc and pelvic fins and transversely on the tail, and ranging in thickness from very thin to approximately 1/2 the diameter of the orbits. There is an elongated U-shaped brown band located just posterior to the eyes and often continuing anteriorly to form dark, crescent-shaped areas in front of the orbits, usually appearing as an M- or Y-shaped design. In some specimens the bands form indistinct circles, particularly on the tail. There are usually a few to several dark brown spots on the dorsal and caudal fins. The ventral surface color is white to cream with no markings.

RANGE.—*D. p. guamachensis* is distributed from just west of Trinidad to slightly west of the Gulf of Venezuela (eastern Colombia) (Fig. 1). However, this species is most common in the area near the Gulf of Venezuela (69°W to 73°W long). It ranges in depth from 30 m to 183 m.

REMARKS.—*D. p. guamachensis* exhibits little of the variation seen in the preceding subspecies. The dorsal color pattern of this subspecies is very distinctive, and although some specimens appear faded or faint, the distinctive markings are always visible.

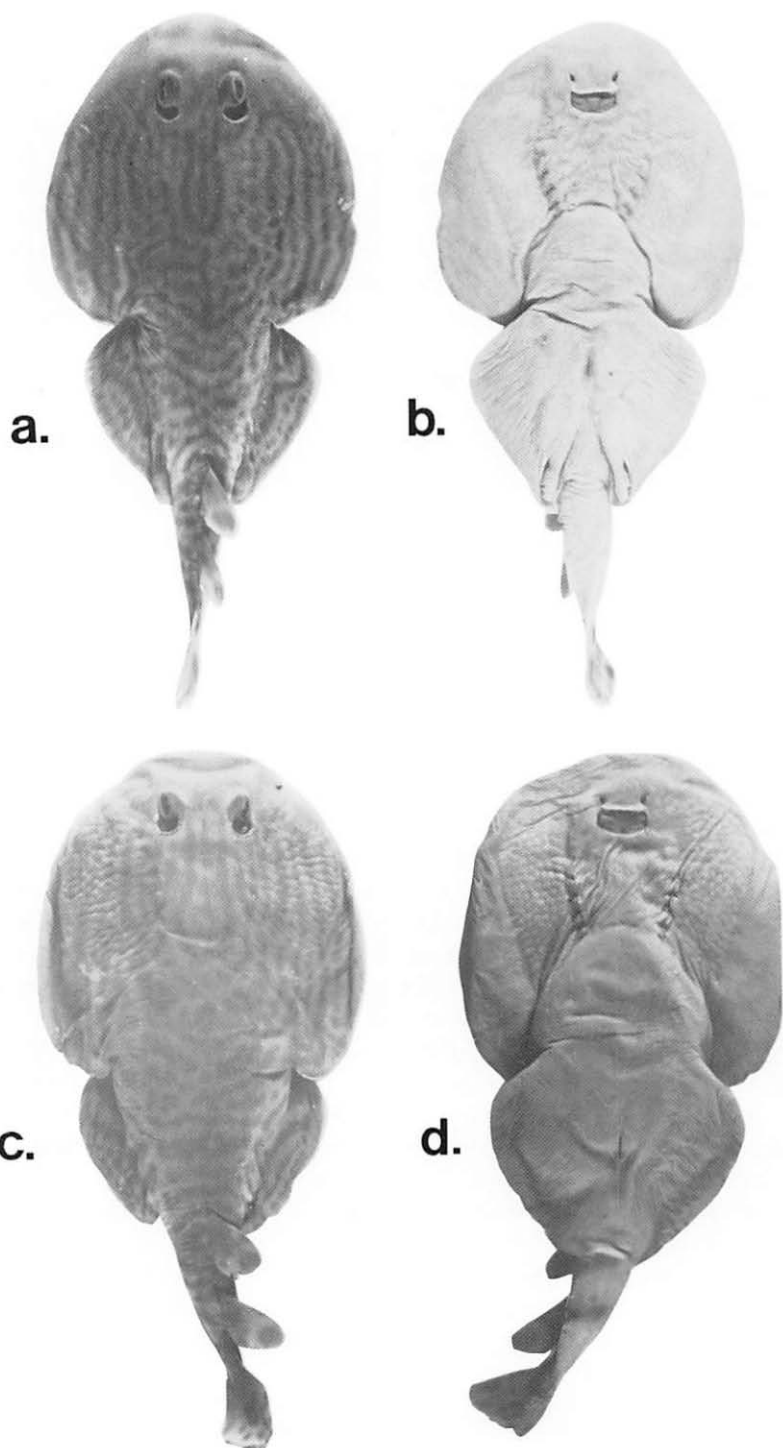


Figure 11. *Diplobatis pictus guamachensis*: (a, b) UF 29886, male, 128 mm TL, dorsal and ventral views; (c, d) USNM 226777, female, 120 mm TL, dorsal and ventral views.

While this species is known from Trinidad to eastern Colombia, only a few specimens have been recorded from eastern Venezuela (Fig. 1; see also Cervigon 1966). The Cariaco Trench, situated between Trinidad and the Gulf of Venezuela (Fig. 1), ranges from 900 m to 1400 m in depth. As these benthic fish have never been taken deeper than 183 m, this area could serve as a partial barrier to this subspecies' eastward migration. Those specimens taken east of the Cariaco Trench are possibly stragglers from the main population, although this cannot be verified without additional sampling.

D. guamachensis Martin 1957, described from the area and later synonymized with *D. pictus* (Bigelow and Schroeder 1962), represents the type of this subspecies, hence the subspecific designation of *guamachensis*.

Diplobatis pictus colombiensis new subspecies

FIGURE 12

HOLOTYPE.—USNM 232494, female, 149.2 mm TL, 9°51' N. lat., 76°09' W. long., off northwestern Columbia, at a depth of 98 m, 42 XI 68.

PARATYPES.—USNM 232929, male, 129.5 mm TL; male, 134.7 mm TL, 9°51' N. lat., 76°09' W. long., off northwestern Colombia, at a depth of 98 m, 24 X 68.

MATERIAL EXAMINED.—16 specimens, listed in Appendix I. Proportional measurements are given in Table 1.

DIAGNOSIS.—*Diplobatis pictus colombiensis* is distinguished from the other subspecies of *D. pictus* by its dorsal color pattern and range. In addition to this, *D. p. colombiensis* has a relatively narrow disc.

DESCRIPTION.—The dorsal color pattern of *D. p. colombiensis* consists of a golden tan background with brown spots ranging from 1/4 to 1 times the size of the orbits, arranged fairly symmetrically on the disc, pectoral fins and tail. The spots range in number from 6 to approximately 50 and are indistinct in some specimens. The disc anterior to the orbits is usually without markings and is often lacking in all coloration except for dark, crescent-shaped areas directly in front of the orbits in some specimens. There are usually from one to three indistinct spots on the dorsal fins and several spots on the caudal fin. The ventral surface color is white to cream with no markings.

RANGE.—*D. p. colombiensis* is known only from the coast of northern Colombia and ranges in depth from 30 m to 100 m.

REMARKS.—While the dorsal color pattern of *D. p. colombiensis* vaguely recalls that of *D. p. pictus*, several important distinctions separate the two. In *D. p. pictus* the background color of the dorsal surface is tan or

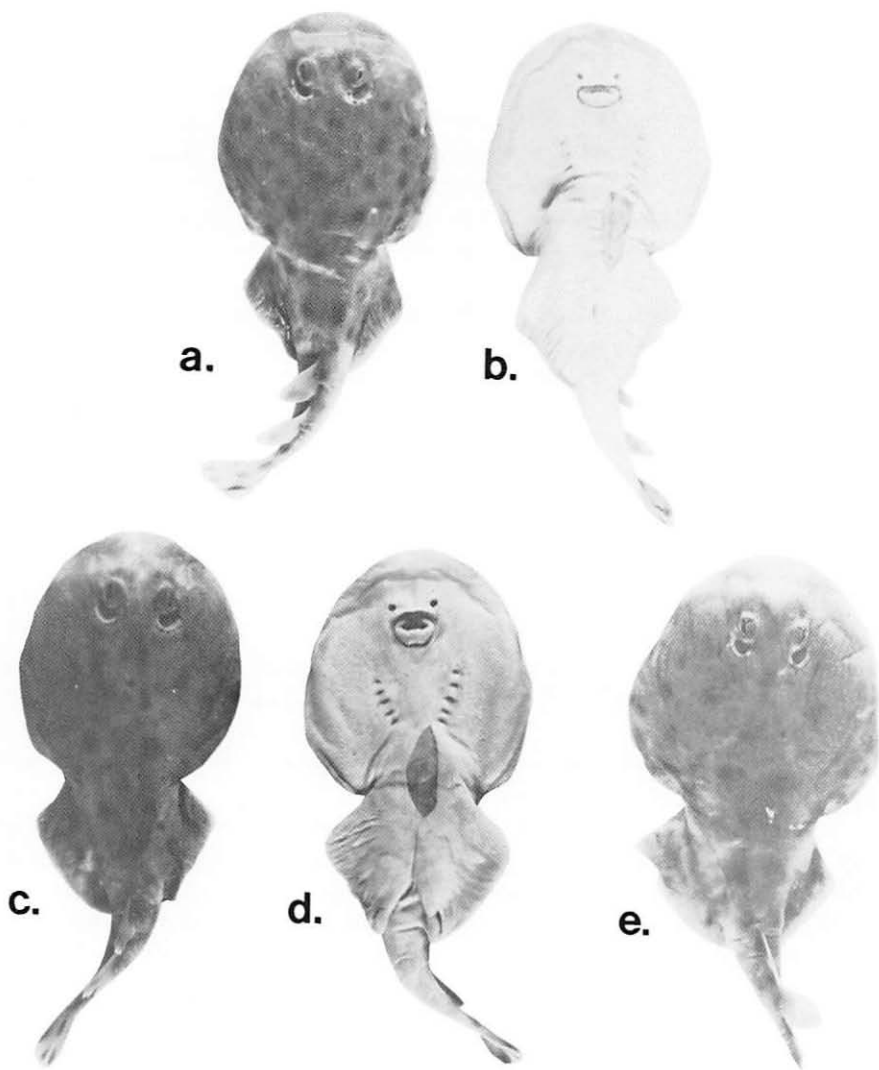


Figure 12. *Diplobatis pictus colombiensis*: (a, b) Holotype, USNM 226773, female, 149 mm TL, dorsal and ventral views; (c, d) Paratype, USNM 26773, male, 135 mm TL, dorsal and ventral views; (e) Paratype, USNM 226773, male, 130 mm TL, dorsal view.

light brown with distinctly darker brown spots, but in *D. p. colombiensis* the background color is golden tan with only slightly darker brown spots; in *D. p. pictus* the spots increase in size toward the edges of the disc compared with *D. p. colombiensis* where they do not increase in size; and *D. p. pictus* usually has a dark brown blotch beside each dorsal fin which is lacking in *D. p. colombiensis*.

ETYMOLOGY.—The subspecific epithet *colombiensis* is in reference to the known range for this subspecies.

Diplobatis ommata (JORDAN AND GILBERT 1890)

Discopyge ommata Jordan and Gilbert in Jordan and Bollman 1890:151.

Narcine ommata Clark 1936:383–384.

Diplobatis ommata Bigelow and Schroeder 1948:562–565. MATERIAL EXAMINED.—24 specimens, listed in Appendix I. Proportional measurements given in Table 2.

DIAGNOSIS.—*Diplobatis ommata* is distinguished by its dorsal coloration, clasper morphology and range. *D. ommata* also has a relatively great interorbital distance; a sub-triangular caudal fin usually without a distinct upper corner; and attains a relatively large size, reaching 250 mm TL.

DESCRIPTION.—External morphology (Fig. 13). Measurements reported here represent the mean value followed by the minimum and maximum values in parentheses. Disc round- to spade-shaped, 1.02 (0.93–1.09) times as broad as long; anterior margin of disc evenly rounded to slightly angular; axis of greatest width 64.2% (60.1–77.0%) of distance from tip of snout to axils of pectoral fins. Pelvic fins originate anteroventrally to or occasionally at axils of pectoral fins; anterior margins of pelvic fins short, 0.29 (0.23–0.35) times breadth of pelvic fins and 0.5 times or less the length of the posterior margin of the pelvic fins; angle of anterior margin of pelvic fins from 45° to 90° to long axis of body; posterior margin of pelvic fins slightly convex when fully spread; pelvic fins anterior to rear tips free from or connected to sides of tail for a short distance. Tail stout, convex dorsally and nearly flattened ventrally, its width midway between posterior tips of pelvic fins and distal tip of tail 0.51 (0.39–0.64) times as wide as interorbital distance; tail with a narrow lateral fold along lateral surface, beginning from opposite midpoint of first dorsal fin to origin of second dorsal fin and ending at or slightly posterior to origin of caudal fin; length of tail from center of cloaca to distal tip 0.90 (0.83–1.00) times distance from tip of snout to center of cloaca. Two dorsal fins on tail; upper corner of both dorsal fins usually rounded but occasionally acute; first dorsal fin located entirely over to entirely posterior to pelvic fins; interspace between first and second dorsal fins 0.61 (0.38–0.83) times as long as base of first dorsal fin; second dorsal fin usually slightly taller than first, distance between second dorsal fin and caudal fin 0.73 (0.48–1.02) times as long as base of second dorsal fin. Caudal fin sub-triangular, usually without a distinct upper corner; base of caudal fin 0.97 (0.88–1.06) times as long, and its height 1.08 (0.86–1.19) times as great as dorsal lobe of caudal fin.

Preocular length 2.40 (1.90–2.88) times as long as orbit-spiracle dis-

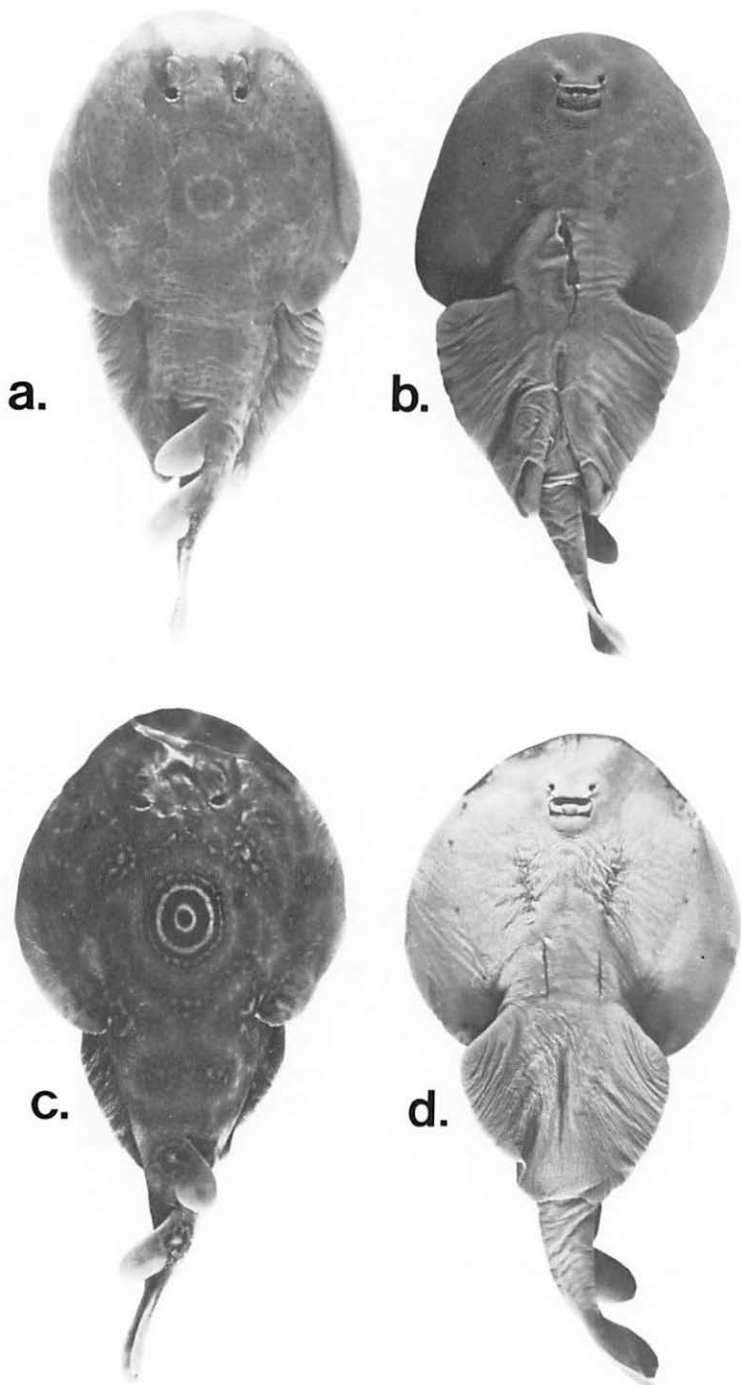


Figure 13. *Diplobatis ommata*. (a, b) LACM W60-11, male, 139 mm TL, dorsal and ventral views; (c, d) LACM 6971-1, female, 193 mm TL, dorsal and ventral views.

tance; preoral length 2.00 (1.63–2.19) times internarial distance; eyes well developed, diameter of orbit 0.5 times or slightly less interorbital distance; length of orbit greater than length of spiracle; spiracle ringed with 7–10 low, rounded papillae. Nasal curtain smooth or slightly crenulate, often projecting slightly at midline; nasal curtain often extending posteriorly to overlap upper jaw and reaching lower jaw when mouth is fully closed; mouth approximately as wide as nasal curtain. Teeth in both jaws in a triangular patch, arranged in quincunx, in about 14–16 rows counting inward at center of jaw, outermost row with one or two teeth and each succeeding row increasing, making a series of 16–22 teeth in innermost rows; anterior few rows of teeth usually without cusps, the succeeding teeth with small, triangular cusps which become increasingly long and narrow on the posterior teeth, all cusps pointing inward; teeth completely concealed when mouth is closed, except in a few cases where two to four rows of teeth may be exposed on lower jaw even when mouth is closed.

The clasper of *D. ommata* (Fig. 14) is very short and stout, its diameter the same the entire length; clasper not tapering posteriorly but broadly rounded; ventrolateral slit (= pseudosiphon?) running along lateral edge and not extending onto ventral surface; dorsal terminal cartilage folded 180° to overlie marginals; dermal denticles on rotated surface of dorsal terminal cartilage; dorsal terminal cartilage forming dorsal wall of clasper groove, but separated from groove by a fleshy, membranous fold resembling a rhipidon.

D. ommata exhibits a polytypic color pattern with the most common pattern consisting of a light grayish-brown dorsal background, covered with small, well-defined dark dots. In the center of the disc there is a very distinct ocellus with a black or yellow-ochre core, surrounded by a succession of solid or broken rings of alternating black and pale brown. Other ocelli consisting of dark brown and ochre spots are scattered on the disc; some of the spots are darker along the periphery of the ocellus thereby giving it a ringed appearance and some ocelli are almost solid. These smaller ocelli are most common at the axils of the pectoral fins, a pair midway between the central ocellus and the first dorsal fin and one at the base of each dorsal fin. The preorbital area is usually grayish-brown with no dark dots, but there may be up to five large dark blotches present on the anterior edges of the disc. This area may also have brown and ochre crescent-shaped areas in front of the orbits, often in the shape of an M or Y. Other color patterns consist of a very light grayish-brown background with numerous tiny brown spots and indistinct brown blotches replacing the smaller ocelli, resulting in a faded, delicate appearance. Still other specimens may be dark brown with few or no visible markings except a very darkened central ocellus. The ventral surface is white to

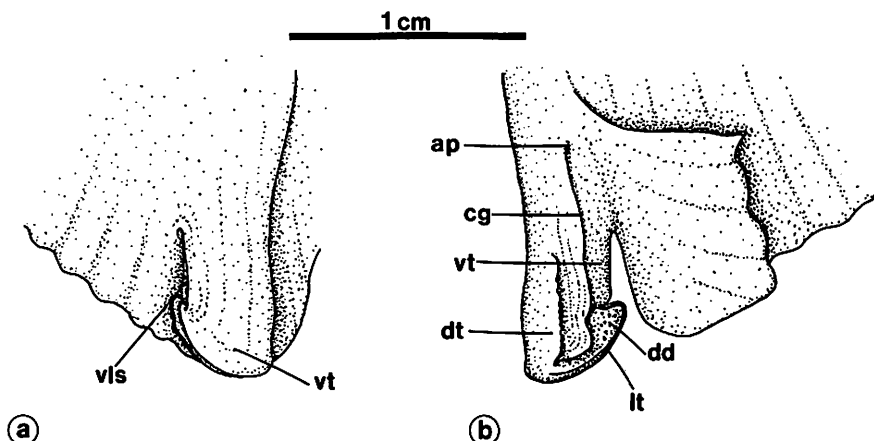


Figure 14. External clasper morphology of *Diplobatis ommata* (LACM W60-11). (a) ventral view; (b) dorsal view: ap, apophyle; cg, clasper groove; dd, dermal denticles; dt, dorsal terminal cartilage; lt, lateral terminal cartilage; vls, ventrolateral slit; vt, ventral terminal cartilage.

cream colored, and brown blotches on the anterior dorsal edge of the disc and pectoral fins frequently continue onto the ventral surface. There may also be a few dusky areas at the axils of the pectoral and pelvic fins.

RANGE.—*D. ommata* occurs in the tropical eastern Pacific along the southwest coast of Baha California, in the Gulf of California and south along Central America to Panama (Fig. 15). It is very common in inshore areas (Breder 1928; pers. obs.) and has been reported as deep as 64 m (Jordan and Bollman 1890).

REMARKS.—As with its congener *D. pictus*, *D. ommata* is very variable in its dorsal color pattern, but again there is no correlation between the various color patterns and sex, location or any other variable. The suggestion of Breder (1928) that young specimens of *D. ommata* have very intricate, distinct patterns that darken and become indistinct with age does not appear to be correct. We have seen small specimens of this species that were very dark with few markings, save the central ocellus, as well as larger specimens with very intricate and distinct patterns. Despite the variation in the color pattern of *D. ommata*, the central ocellus is present at all times.

INTERRELATIONSHIPS WITHIN THE FAMILY NARCINIDAE

The four genera of Narcinidae (*Benthobatis*, *Diplobatis*, *Discopyge*, and *Narcine*) form a monophyletic group clearly separated from other genera of Torpediniformes and distinguished by the following characters:

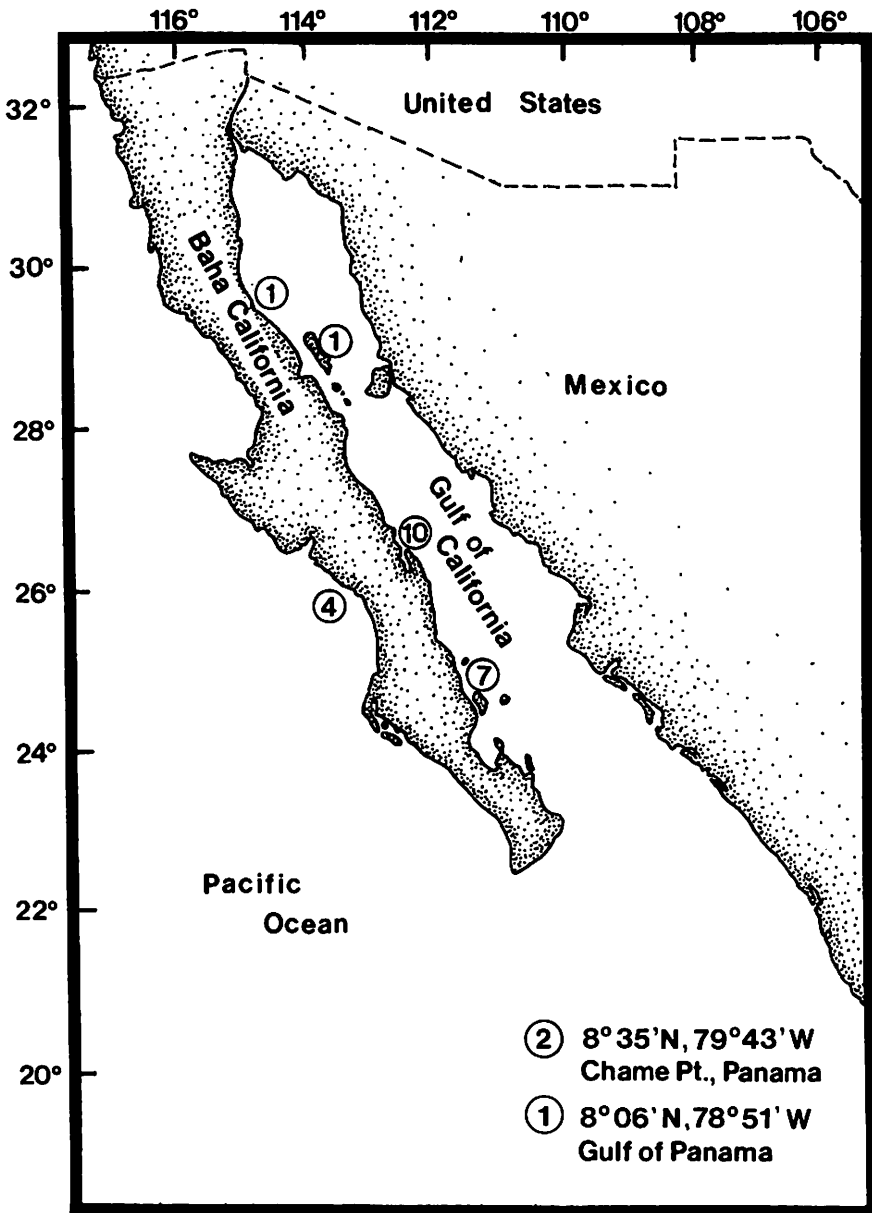


Figure 15. Map of Baha California and northwestern Mexico showing the distribution of *Diplobatis ommata* specimens examined in this study. Circled numbers indicate the number of specimens examined from that locality. Some locations represent multiple lots.

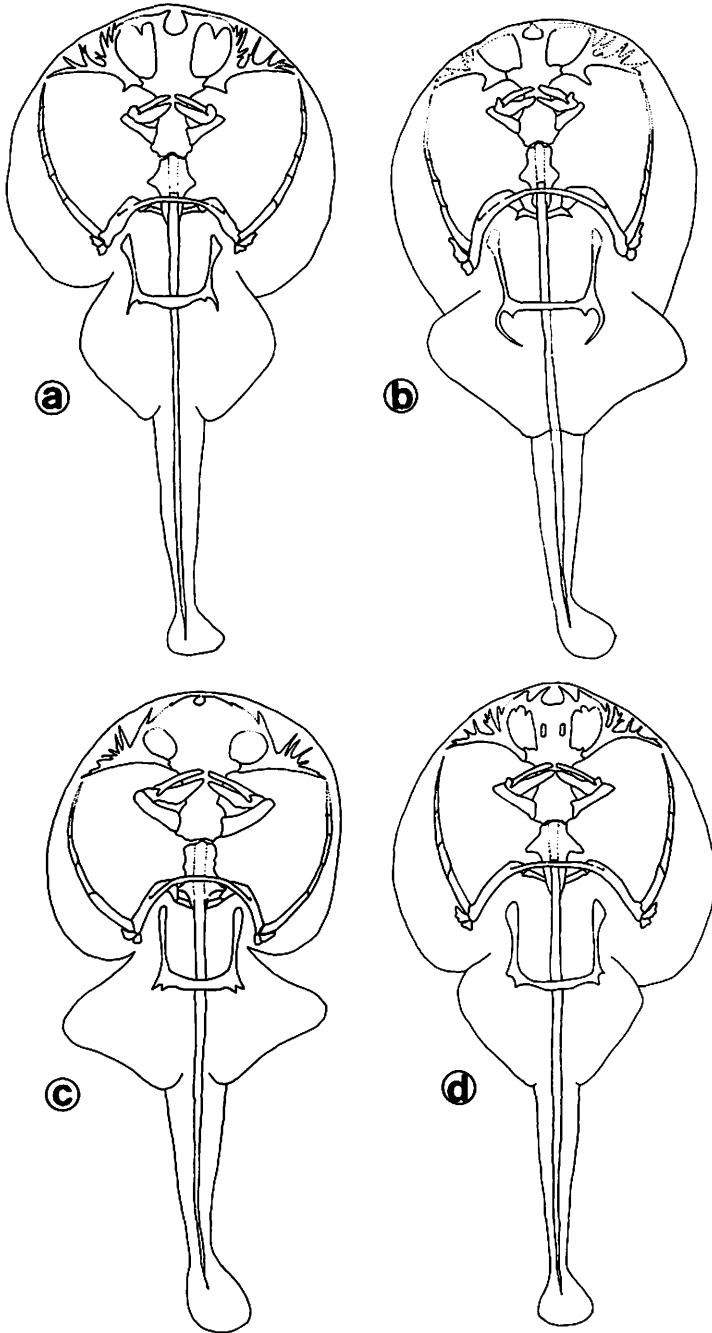


Figure 16. Schematic illustrations showing the major skeletal elements of the four genera of Narcinidae. (a) *Narcine*; (b) *Discopyge*; (c) *Benthobatis*; (d) *Diplobatis*. All illustrations represent a ventral view of a mature female.

broad, trough- or shovel-shaped rostrum; ventrolaterally directed nasal capsules; forked, antler-shaped antorbital cartilages; large precerebral fossa; transverse mouth with well developed labial cartilages; anterior hypobranchial elements large and nearly meeting mid-ventrally; and a large basibranchial copula (Compagno 1973).

Phylogenetic analysis of the relationships between the four narcinid genera is difficult for two reasons. First, the polarity of many character states used in batoid systematics is difficult to define due to a very poor fossil record, many instances of parallel evolution, and a lack of understanding of the character states of pleisomorphic taxa (out-groups) (Compagno 1977). Secondly, while each of the four genera exhibit several unique characteristics (autapomorphies), synapomorphic character states (i.e. shared, derived characters) are scarce. Only the latter can be used to determine phylogenetic relationships, i.e. taxa sharing an immediate common ancestor (Hennig 1966; Wiley 1979).

The four genera are very conservative in their internal anatomy (Fig. 16). However, *Discopyge* and *Narcine* share two characters that are considered to be synapomorphic. The iliac processes on the pelvic girdle of *Narcine* and *Discopyge* are very well developed (when compared to those of *Diplobatis* and *Benthobatis*) and represent the derived condition, as primitive batoids (*Pristiophorus* and *Rhinobatos*) have very poorly developed iliac processes (Garman 1913). The posterolateral processes on the antorbital cartilages of these two genera also seem to be derived, as it is a more complex structure than the antorbital cartilages of other narcinids and of primitive batoids. Based on these two characters and on the lack of any other synapomorphic character states within the family, *Discopyge* and *Narcine* are considered to be sister groups, and they in turn form the sister group of *Benthobatis* and *Diplobatis* (Fig. 17). The trichotomy of *Narcine-Discopyge*, *Benthobatis*, and *Diplobatis* cannot be resolved with our present state of knowledge.

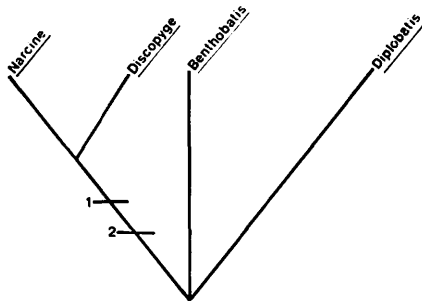


Figure 17. Cladogram illustrating possible phylogenetic relationships within Narcinidae. Numbers refer to the following synapomorphies. (1) relatively well developed iliac processes on the pelvic girdle; (2) postlateral processes on the antorbital cartilages.

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APPENDIX I

MATERIAL EXAMINED¹*Diplobatis pictus pictus*

BRAZIL: MCZ 40373 (7:110-162); MCZ 40411 (2:74-102); MCZ 42466 (3:81-*); USNM 156775 (6:131-172); USNM uncat., Oreg. II 17688 (3:124-132); Oreg. II 17626 (2:103-127); Oreg. II 17694 (1:131).

FRENCH GUIANA: MCZ 40213 (2:88-130); MCZ 42455 (2:138-140); USNM 159882 (1:140); USNM uncat., Oreg. II 10530 (1:81*); Oreg. II 10577 (1:109); Oreg. II 10599 (1:105); Oreg. II 17622, 17623 (3:131-173); Oreg. II 17626 (2:145-158).

SURINAM: MCZ 40397 (2:101-116*); USNM 156771 (1:127); USNM 156784 (1:103); USNM 159232 (2:97-132); USNM 186422 (2:97-136); USNM 186423 (2:120-134); USNM 226774 (4:75-137); USNM uncat., UNDP/FAO Calamar (5:157*); RMNH 24706 [Holotype, *D. altenai*] (1:140); RMNH uncat., (57:48-130); TCWC 1901.1 (1:98); TCWC 1904.1 (1:112); TCWC 1905.1 (1:110); TCWC 1906.1 (1:86).

GUYANA: BMNH 1961.8.31:24-28 (5:105-145); MCZ 40234 (1:130); MCZ 40378 (2:86-118*); USNM 156786 (1:95); USNM 19711 (2:*); USNM uncat., Oreg. II 10499 (2:89-112*); Oreg. II 10505 (1:104); Oreg. II 10515 (1:117-128*); Oreg. II 10516 (1:125); UNDP/FAO Calamar 651 (3:*); UNDP/FAO Calamar 675 (5:*).

VENEZUELA: UF 29893 (8:60-146); UF 29894 (2:104-138); UF 29883 (1:115*); UF 29882 (1:135); MCZ 40377 (4:99-117*); MCZ 40404 (1:125); MCZ 40410 (2:94-107); USNM uncat., UNDP/FAO Calamar 660 (3:*); TCWC 1900.1 (1:119).

Diplobatis pictus guamachensis

EASTERN VENEZUELA: UF 29884 (1:120); USNM uncat., Oreg. I 4476 (2:150-151*).

GULF OF VENEZUELA: UF 29869 (1:*); UF 29870 (1:119); UF 29871 (7:99-130); UF 29872 (3:89-105); UF 29876 (4:104-132*); UF 29879 (3:*); UF 29880 (1:174); UF 19881 (3:141-170); UF 19885 (1:158); UF 29890 (1:148); UF 19891 (1:*); MCZ 48721 (1:196); MCZ 51052 (2:151-156); USNM 226776 (2:138-149*); USNM 226777 (3:100-147); USNM uncat., Oreg. I 4392 (4:*); Oreg. I 4467 (2:*).

Diplobatis pictus colombiensis

COLOMBIA: UF 29877 (2:107-126*); UF 29878 (2:73-125*); USNM 226773 (4:107-166); USNM 232494 [Holotype, *D. p. colombiensis*] (1:150); USNM 232929 [Paratypes, *D. p. colombiensis*] (2:130-135).

¹Lots marked with an asterick(*) contained damaged specimens, some of which were not measured.

²Sample contained one female that contained four embryos. Because of their underdeveloped state, measurements were not taken on the embryos.

Diplobatis ommata

GULF OF CALIFORNIA: LACM W55-85 (1:203); LACM W59-12 (1:187); LACM W60-11 (1:139); LACM 31759-1 (4:128-192); LACM 6962-23 (10:193-246); LACM 6971-7 (5:144-226); USNM 46723 (1:159).

PANAMA-COLOMBIA: LACM W53-310 (2:115-126); USNM 41133 [Holotype, *D. ommata*] (1:158).

Table 1.

Proportional measurements of Group A (*Diplobatis pictus pictus*), Group B (*D. p. guamachensis*) and Group C (*D. p. colombiensis*). Proportions in percent of total length.

	Group A (n=98)		Group B (n=38)		Group C (n=16)	
	\bar{x}	Range	\bar{x}	Range	\bar{x}	Range
Total length (mm)	125.2	60.5-173.0	133.1	97.6-195.9	130.2	103.2-165.8
Disc width	47.6	40.0-55.1	46.1	42.2-50.6	43.3	39.4-48.7
Disc length	47.0	43.0-55.4	46.4	41.1-51.6	44.0	33.6-47.2
Snout length:						
Preocular	10.9	8.4-12.6	9.4	6.8-12.0	11.8	10.2-13.6
Preoral	13.1	10.5-15.2	12.6	10.0-14.9	13.5	11.5-15.8
Snout to maximum disc width	29.5	21.5-37.1	29.6	19.4-36.3	29.8	25.2-37.6
Snout to axil of pectoral fins	44.9	30.9-55.3	44.3	39.7-48.3	43.9	41.1-48.3
Jaw width	6.6	4.9-7.8	6.9	6.3-8.0	7.1	6.6-8.6
Nasal curtain:						
Width	6.5	3.6-8.1	6.4	5.4-7.1	6.7	5.8-7.7
Length	1.8	0.8-3.1	1.9	1.4-2.5	1.6	1.1-2.1
Distance between:						
1st gill openings	14.1	12.2-16.3	13.3	11.6-14.8	13.4	12.2-14.8
5th gill openings	10.1	7.6-12.2	9.6	7.9-10.9	9.3	7.2-11.0
Orbits	5.6	3.9-7.3	5.5	4.3-6.7	5.7	4.7-7.3
Orbit and spiracle length	6.7	5.1-8.8	7.2	5.9-8.0	5.7	4.7-7.3
Pelvic fin:						
Anterior lobe	12.4	8.9-15.7	12.4	9.4-15.1	12.5	10.1-15.6
Posterior lobe	21.9	15.3-31.7	24.8	20.5-29.0	21.3	17.7-24.0
Breadth of pelvic fins	34.7	27.9-43.2	34.6	31.8-38.6	33.6	30.2-37.4
Tail width at axil of pectoral fins	9.1	6.4-12.3	8.4	6.5-10.2	7.7	6.1-10.8
Height:						
1st dorsal fin	6.9	5.0-9.1	7.4	4.6-9.5	6.6	5.1-8.8
2nd dorsal fin	7.4	4.6-9.7	7.7	4.6-9.5	6.8	4.7-7.3
Length:						
1st dorsal fin	5.8	3.9-7.5	6.2	5.0-7.7	5.3	4.3-6.6
2nd dorsal fin	6.0	4.2-7.7	6.5	5.1-7.5	5.8	4.7-7.3
Caudal fin:						
dorsal lobe length	14.1	9.7-17.7	13.8	12.0-16.4	14.4	13.2-16.3
ventral lobe length	12.4	10.0-15.4	11.7	10.0-15.4	11.7	10.1-14.9
height	12.6	9.3-16.4	13.3	11.7-15.5	11.4	9.6-13.6
Snout to cloaca length	52.3	43.1-59.0	53.0	42.7-69.3	53.1	50.1-58.5
Cloaca to origin of caudal fin	32.6	20.0-48.2	33.6	27.0-38.2	33.0	30.3-35.6

Table 2.
Proportional measurements and meristics of the Atlantic forms of *Diplobatis* and
Diplobatis ommata. Proportions in percent of total length.

	<i>Diplobatis</i> (Atlantic forms) n=152		<i>D. ommata</i> n=26	
	\bar{x}	Range	\bar{x}	Range
Total length (mm)	128.9	60.5-195.9	180.2	114.5-245.6
Disc width	46.4	39.4-55.1	47.7	41.9-52.5
Disc length	45.9	33.6-55.4	46.9	42.8-52.3
Snout length (preocular)	10.7	6.8-13.6	10.6	9.3-14.4
Snout length (preoral)	12.9	10.0-15.8	11.9	10.2-17.0
Snout to maximum disc width	29.7	19.4-37.6	29.1	25.9-35.7
Snout to axil of pectoral fins	44.7	30.9-55.3	45.4	41.6-50.2
Jaw width	6.8	4.9-8.6	6.5	5.7-7.4
Nasal curtain width	6.5	3.6-8.1	5.9	5.1-6.7
Nasal curtain length	1.8	0.8-3.1	1.6	1.1-2.4
Distance between				
1st gill openings	13.9	11.6-16.3	13.2	11.9-15.2
5th gill openings	9.5	7.2-12.2	9.9	8.1-13.0
orbits	5.7	3.9-7.3	6.5	5.1-7.9
Orbit and spiracle length	6.9	4.7-8.8	6.2	5.7-7.0
Pelvic fin (anterior lobe)	12.4	8.9-15.7	11.3	8.4-12.6
Pelvic fin (posterior lobe)	22.4	15.3-31.7	24.2	16.9-31.8
Breadth of pelvic fins	34.5	27.9-43.2	35.6	30.1-39.9
Tail width at axil of pectoral fins	8.8	6.1-12.3	8.0	6.5-11.4
Height of 1st dorsal fin	6.9	5.0-9.7	7.2	6.2-8.5
Length of 1st dorsal fin	5.8	3.9-7.7	6.2	4.2-7.8
Height of 2nd dorsal fin	7.4	4.6-9.7	7.8	6.1-8.3
Length of 2nd dorsal fin	6.1	4.2-7.7	6.7	5.5-7.7
Caudal fin				
dorsal lobe length	14.2	9.7-17.7	12.5	10.2-15.1
ventral lobe length	12.4	7.8-18.2	12.0	9.1-14.7
height	12.7	9.3-16.4	13.1	10.9-14.5
Snout to cloaca length	52.5	42.7-69.3	52.6	49.8-54.9
Cloaca to origin of caudal fin	32.9	20.0-48.2	33.0	23.6-36.5
Number of tooth rows (upper jaw)	18 (n=3)		18-19 (n=2)	
Number of vertebrae	103	98-109 (n=10)	104	97-112 (n=50)
Number of pelvic radials	18	16-21 (n=10)	19	17-20 (n=5)

Table 3.
Proportional measurements of *Diplobatis altenai* compared with *Diplobatis pictus*.
Proportions in percent of total length. The measurements of *D. altenai* are those
of the holotype.

	<i>D. pictus</i> (n=152)		<i>D. altenai</i>
	\bar{x}	Range	
Total length (mm)	128.9	60.5–195.9	140.0
Disc width	46.4	39.4–55.1	41.4
Disc length	45.9	36.0–55.4	44.3
Snout length (preocular)	10.7	6.8–13.6	11.4
Snout length (preoral)	12.9	10.0–15.8	13.9
Snout to maximum disc width	29.7	19.4–37.6	28.1
Snout to axil of pectoral fins	44.7	30.9–55.3	43.8
Distance between orbits	5.7	3.9–7.3	6.0
Distance between spiracles	6.9	4.7–7.9	6.1
Mouth width	6.8	4.9–8.6	6.2
Nasal curtain width	6.5	3.6–8.1	6.5
Nasal curtain length	1.8	0.8–3.1	0.9
Distance between nostrils	6.3	4.9–8.3	5.7
1st gill openings	13.9	11.6–16.3	11.7
5th gill openings	9.5	7.2–12.2	7.9
Pelvic fin (anterior lobe)	12.4	8.9–15.7	12.9
Pelvic fin (posterior lobe)	22.4	15.3–31.7	21.5
Breadth of pelvic fins	34.5	27.9–43.2	29.4
Tail width at axil of pectoral fins	8.8	6.1–12.3	7.3
Height of 1st dorsal fin	6.9	5.0–9.7	6.8
Length of 1st dorsal fin	5.8	3.9–7.7	6.1
Height of 2nd dorsal fin	128.9	4.6–9.7	7.5
Length of 2nd dorsal fin	46.1	4.2–7.7	5.7
Caudal fin			
dorsal lobe length	14.2	9.7–16.4	15.7
ventral lobe length	12.4	7.8–18.2	11.4
height	12.7	9.3–16.4	14.1
Distance between dorsal fins	3.3	2.0–5.1	2.5
Snout to cloaca length	52.5	42.7–69.3	47.9