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Anatomical observations on the ampullae of Lorenzini from selected skates and galeoid sharks of the Western North

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The College of William and Mary in Virginia PH.D. 1984

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ANATOMICAL OBSERVATIONS ON THE AMPULLAE OF LORENZINI FROM SELECTED SKATES AND GALEOID SHARKS OF THE WESTERN NORTH ATLANTIC

A Dissertation

Presented to

The Faculty of the School of Marine Sciences

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Doctor of Philosophy

by

William Raschi

1984

APPROVAL SHEET

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

Doctor of Philosophy

William Raschi

Approved, April 1984

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ABSTRACT

The gross structure of the ampullae of Lorenzini and its distribution on the body of 40 species of skates (Rajoidei) and 5 species of sharks (Galeomorphii) were compared in an attempt to investigate correlations within this system to feeding mechanisms. Three general lines of morphological change are observed. A larger proportion of the ampullary pores are associated with the ventral surface of the dorsoventrally flattened skates than the more conically shaped sharks. The relative proportion of ventral pores is significantly reduced on those species inhabiting aphotic waters. Secondly, the more piscivorous rajoids possess an array of ventral pores which covers the majority of the body surface whereas those species feeding predominantly on infaunal invertebrates exhibit a comparatively reduced pattern which are primarily concentrated around the mouth. The density of these pores on the adult is inversely related to the collective mobility of each species' prey items. Similarly, the relative density of pores on the sharks is reduced in both those species inhabiting pelagic waters and those exhibiting reduced prey selectivity. Lastly, the overall size of, and the number of alveoli associated with, each ampulla is directly related to the habitat depth of each skate species.

The proposed effects of each of these modifications is discussed. The overall pore distribution appears compensatory for reduced visual input whereas relative densities (resolution) further reflect major differences in feeding strategies. Increased ampullary size and complexity suggest mechanisms for increased sensitivity and signal - to - noise ratios.

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FROM SELECTED SKATES AND GALEOID SHARKS
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INTRODUCTION

The discovery and subsequent description of the ampullae of Lorenzini can be traced through a series of chronologically isolated observations. From a gross anatomical standpoint, Lorenzini (1678) initially described the whole structure, including the somatic pores, canals and ampullae. However, the isolated pores had been noted 14 years earlier by Stenonis whereas their innervation was not observed until much later (Monro, 1783). A more complete chronology of these earliest studies is found in Ewart (1891) and Lamont (1916) but as might be expected from such an intermittent history, the understanding of the functional aspects of the ampullae of Lorenzini has been slow to develop.

The ampullary system of elasmobranchs consists of a series of canals, each terminating at the skin surface as a pore and proximally, in the cranial region, as an expanded, alveolate bulb. The canal walls are composed of several layers of closely joined squamous epithelium which yield an extremely high mural resistance. The tubes themselves are filled with a gelatinous mucopolysaccharide (Doyle, 1963) with an ionic composition nearly the same as that of seawater (Murray and Potts, 1961). The outpocketings, or alveoli, characteristic of the ampulla contain both receptor and supporting cells. Receptor cells are innervated by nerve fibers originating from one of four branches of the anterior lateral line nerve (see McCready and Boord, 1976) including the superficial ophthalmic, buccal, and the external mandibular. These fibers are carried via the dorsal root to the anterior lateral line lobe of the medulla (Boord and Campbell, 1977).

Many purely descriptive anatomical studies of the whole ampullary system are available. Ewart (1891) was the first to designate the separate groups of ampullae found in both the shark, *Laemargus (=Somniosus)*, and the skate, *Raja batis* (Ewart and Mitchell, 1891). He named each group after the branch of the facial nerve which innervated it, establishing the terminology used by the majority of subsequent authors. Lamont (1916) expanded on Ewart's skate study, describing the general distribution of the ampullary canals from six additional species of European *Raja*. Unfortunately, much of this work is very generalized and therefore of only limited value. Similar studies (Metcalf, 1915 and Norris, 1929) include descriptions of the arrangement and distribution of the ampullary system in *Squalus acanthias*. In addition however, Norris also summarized the number of ampullary clusters, or points of innervation, for a large number of elasombranch taxa, including the rajoids and carcharhinoids of interest here. Two additional, anatomical surveys have recently become available. Dislers (1977) briefly described the ampullary systems from a wide variety of elasmobranch genera, including *Squalus*, *Dalatias*, *Squatina*, *Pristiurus*, *Orectolobus*, *Rhinobatus*, *Raja*, *Dasyatis*, and *Torpedo*; while Chu and Meng (1979) surveyed this system in a number of Chinese elasmobranchs, including 73 species from 46 genera. Lastly, a limited amount of additional anatomical information is also available as a byproduct of primarily physiological studies, including semidiagrammatic representations of the ampullary systems in *Raja clavata* (Murray, 1960) and *Scyliorhinus canicula* (Dijkgraff and

Kalmijn, 1963).

Information concerning isolated portions of the ampullary system is also available. The shape and structure of the somatic pores are described by Metcalf (1915) whereas their overall distribution has been taxonomically evaluated on both rajids (Aloncle, 1966; Stehmann, 1970) and sphyrnids (Gilbert, 1967). Both the canal and the ampulla have been described in terms of their general (Metcalf, 1915) and histological (Peabody, 1897; Waltman, 1966) structure. Comparative counts and measurements of selected ampullae from separate clusters, or capsules, are available for _S. acanthias_ (Metcalf, 1915; Norris, 1929), _Mustelus canis_ (Peabody, 1897) and two species of _Raja_ (Raschi, 1978). Histological considerations of ampullae innervation is presented in Peabody (1897) and Waltman (1966) while observations on the gross, peripheral nerve patterns are described by Ewart (1891), Ewart and Mitchell (1891) and Lamont (1916). Lastly, the central nervous system connections have been described in _Mustelus_ (McCready and Boord,1976) and _Raja_ (Boord and Northcutt, 1982; Koester, 1983).

Whereas the ampullary system is now widely accepted as electroreceptive by the majority of researchers, a variety of functions were previously ascribed to it. The very earliest investigators considered the ampullae to be secretory, providing the fish's skin with its characteristic coating of mucous. Following Monro's (1783) description of their innervation however, the majority of the work has focused on sensory functions. Through these efforts, a large number of sensory stimuli have been considered, including mechanoreception (Parker, 1909; Metcalf, 1915; Murray, 1957 and 1960; Lowenstein, 1960; and most recently Szabo, 1972), thermoreception (Sand, 1938; Hensel, 1955 and Murray, 1959) and chemoreception (Hensel, 1957; Murray, 1962 and Lowenstein and Ishiko, 1962). Most of these responses however, may be explained as either an artifact of electroreception (Akoev et al., 1980) or as a response to an inappropriate stimulus (Kalmijn, 1974). The evidence for the electroreceptive function of the ampullae is very extensive (see for example Fessard, 1974; Viancour, 1979) and, along with the more general physiological considerations of this sensory system, is beyond the scope and aim of this work. However, the absence of a generally accepted function significantly hampered early attempts to comparatively describe the gross anatomy of this system.

A number of biologically relevant sources of electrical information are available in the natural environment (Kalmijn, 1974). Among the most widely investigated of these sources are dipole fields which normally surround most organisms (Kalmijn, 1972) including many prey species frequently utilized by elasmobranch fish. These fields are either D.C. or low frequency A.C. and may vary considerably in strength from 1.0 uV to 500.0 uV. Of particular interest is the observation that those fields surrounding wounded crustacea are several orders of magnitude stronger than normal. Electrophysiological studies have established receptor threshold values of 0.01 uV/cm in several elasmobranch taxa including Raja (Kalmijn, 1966). Fields of comparable strengths exist within approximately 25 cm of several prey species (Kalmijn, 1974). Lastly, behavioral studies in both the laboratory (Kalmijn, 1971) and in the field (1978b) demonstrate the integral role played by bioelectric information in successful prey capture.

The purpose of the present study is to try to extend the anatomical descriptions of the ampullary system an additional step. In the absence of a functional focus, many of the intricacies of complex, anatomical systems, such as the ampullae of Lorenzini, are lost through generalization. When viewed functionally, many of these intricacies become significant in relation to specific environmental parameters. The importance of such an approach to morphological studies is too often underestimated (Disler, 1971). My aim here, is to examine the gross anatomy of the ampullary system with the intent of looking for modifications which might result from various environmental constraints on the electroreceptive system as it is utilized in prey capture.

METHODS AND MATERIALS

The primary group focused on in this study is the suborder Rajoidei and was chosen for a number of reasons. It is very speciose and therefore provides a wide variety of natural histories for comparison (for example see McEachran, 1982). Its dorsoventrally flattened body helps to isolate the mouth from, and thereby partially eliminate from consideration, visual input during the final stages of prey capture. In addition, rajoids are relatively small in size and hence probably more available from museum collections. The ampullary system was also examined in a select group of galeoid sharks. They in turn, offer an opportunity to compare any functionally related trends observed in the rajoids with a group of fishes very different in overall body plan.

A total of 87 specimens, from 40 species belonging to five genera of rajoids were examined. For convenience, these are broken into two groups. The first (Table 1), including *Bathyraja richardsoni*, *Malacoraja senta*, *Raja bigelowi*, *R. eglanteria*, *R. garmani*, *R. laevis* and *R. radiata* constitutes the principal group while the second (Table 2), includes all additional specimens and constitutes the ancillary group. Members of both groups were chosen in order to examine a wide variety of bathymetric and food habit characteristics. Five to 7 specimens from each species of the principal group were included in an attempt to incorporate both sexual and ontogenetic differences. The actual size of the specimens covered from 21% (in *R. laevis*) to 72% (in *R. bigelowi*) of each species' recorded total length (Table 3) and, with the exception of B. richardsoni and R. radiata, accounted for a large portion of each species' bathymetric and geographic range (compare Tables 1 and 4). Specimens in the ancillary group were also chosen in order to include depth and food preferences from a wide variety of geographical locations. Unfortunately, only a few specimens at most, could be examined from each species. In addition to the rajoids, the ampullary system was also examined in 31 specimens from five species of galeoid sharks (Table 5). A similar attempt was made to include specimens from both sexes and covering as wide a range of total lengths as possible.

The ampullary system in the rajoids was examined by means of gross dissection of one specimen from each of the principal species. The pores were located on a diagram by initially placing the specimen beneath a monofilament grid, of approximately square centimeter dimensions, and transferring their location to graph paper. Each canal was then traced from the pore to the ampulla by hand dissection, occasionally using methylene blue to enhance the contrast of the canal from the surrounding tissue. The ampullary system of the sharks was also examined through gross dissection of one specimen from each species. Pores locations were determined by drawing a grid, of approximately square centimeter dimensions, on the surface of the specimen along the frontal plane. Their locations were then transferred to a proportionally arranged drawing. The position of the lateral line in all dissection specimens was also established through gross dissection, following its injection with methylene blue. Lastly, the relative position of the anterior lateral line nerves was traced from the ampullary capsules or clusters to the cranial wall.

The drawings that resulted from these dissections were placed within an outline for each species adapted from the previously published works listed in Table 3 for the skates or as presented in Bigelow and Schroeder (1948) for the sharks, and are superimposed on a generalized skull drawing, adjusted for each species, to provide appropriate landmarks. These skull drawings, and subsequent nomenclature are adapted from Hulley (1972) and Parker (1878) for the rajoids and from Compagno (1979) for the galeoids. Additional nomenclature used in subsequent descriptions includes that of Marion (1905) for the musculature and Garman (1888) for the lateralis system. My intent is that these drawings accurately represent the relative position and abundance of the ampullae of Lorenzini, with respect to both the lateral line and more generally, to the chondocranium.

The structure of the ampulla itself was examined by removing the tissue containing each ampullary capsule in the case of the rajoids, or clusters of ampullae in the case of the galeoid sharks, from either the left or right side of each specimen. All ampullae were removed from the rajoid capsules and counted beneath a dissecting scope. Since this was not possible in the majority of the shark species due to the diffuse arrangement of the ampullae, their numbers were inferred from the corresponding number of pores. Five ampullae from each capsule, or group, were stained with eosin and mounted on a glass slide through standard histological techniques. Any shrinkage that might have occurred was considered to be consistent among all specimens. The length, from the proximal end of each ampullary canal to the point of innervation on the ampulla, and the width across the widest portion of the ampulla, normal to the length, were measured by means of a calibrated occular micrometer.

Ventral somatic pore densities were calculated for all rajoid species from corresponding ventral pore counts. Drawings of each species were enlarged to the maximum total lengths listed in the literature (Table 3 and 6). Surface areas were then measured by means of a digital planimeter (Electronic Graphics Calculator 1224, Numonics Corp.) or graphics tablet (Apple IIe).

Five ampullae were removed from the left superficial ophthalmic capsule from an additional 27 specimens (12 female, 15 male) of *Raja eglanteria* and were included along with the material from the original six specimens (Table 1) in order to further examine structural differences through a more complete ontogenetic series. This material was prepared as above with the number of alveoli, length and width being measured. All statistical methods follow Snedecor and Cochran (1967) unless otherwise noted.

RESULTS

The general arrangement and distribution of the ampullae of Lorenzini in the rajids differs little among the principal species and is relatively consistent with previous descriptions. A brief delineation of this system in the single species, Raja eglanteria (figure 1), will suffice to provide a basis for further comparisons. In this species, the ampullae of Lorenzini are grouped into four pairs of bilaterally located, connective tissue capsules (figures 2 and 3). However, as previously noted by Lamont (1916), those ampullae innervated by the inner buccal as well as by the superficial ophthalmic branches of the anterior lateral line nerve are often located within close proximity of each other, or as in some of the species discussed here, actually united within a single capsule. In such instances, the two capsules are considered jointly as the superficial ophthalmic. Each capsule contains ampullae with canals running beneath the dermis to pores located over various areas of the skin surface. Appropriate branches of the anterior lateral line nerve enter these capsules and innervate the individual ampullae, with the remaining trunk continuing to specific sections of the lateral line. A more thorough description follows (figures 2 and 3).

SUPERFICIAL OPHTHALMIC

This capsule pair is located along either side of the rostral cartilage (figure 4A and B), situated beneath its dorsal shelf and

Figure 1. Semidiagrammatic representation of the ampullary system from a 550 mm TL female specimen of *R. eglanteria*. The ampullary system is shown in green, the lateralis system in blue and the cranial nerves in red.

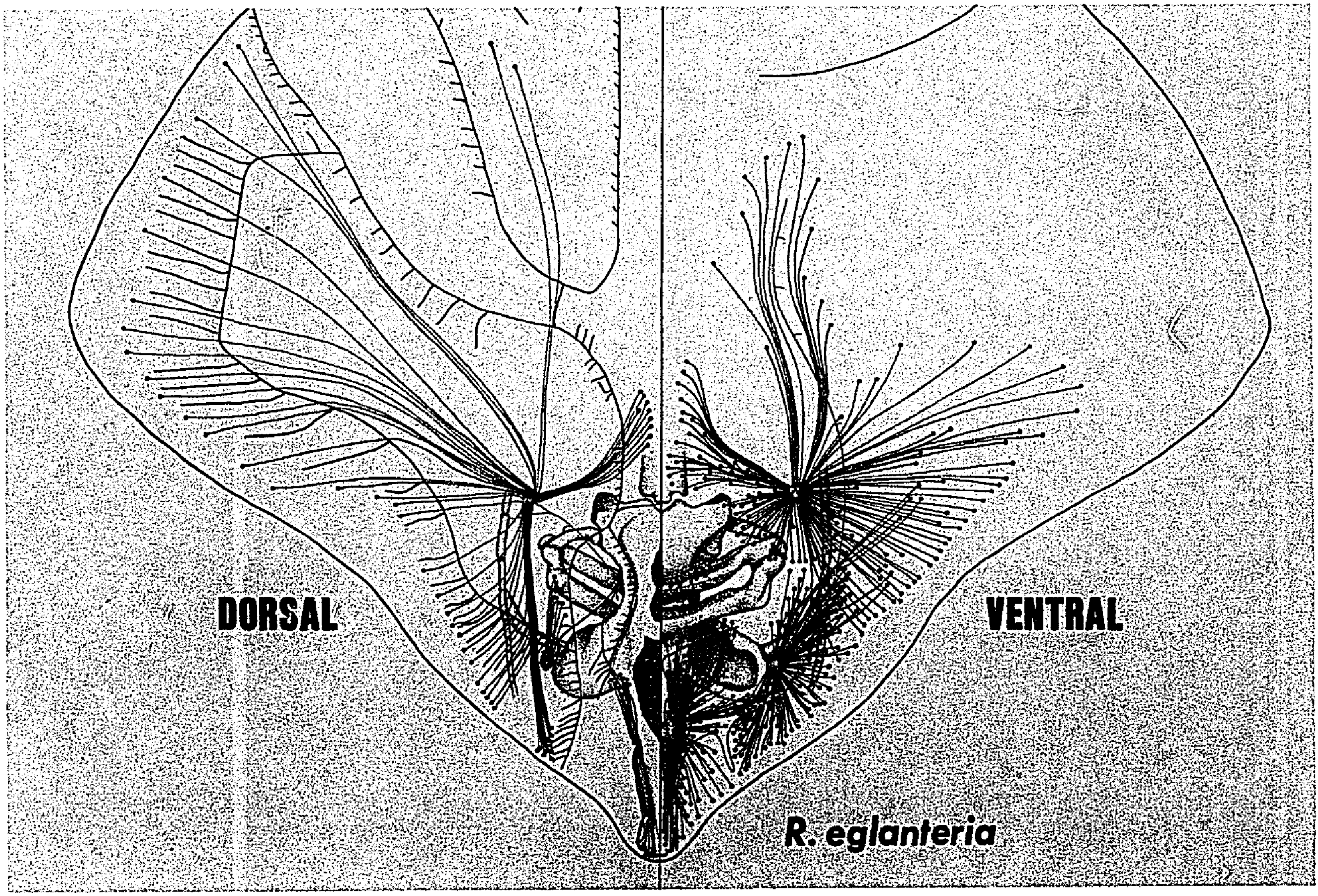

DORSAL
VENTRAL
R. eglanteria

Figure 2. Superficial dissection of R. eglanteria (ca. 600 mm TL female); dorsal view on the right side, ventral view on the left side. Abbreviations as follows: "A", ampullary canals from pores of subsection "A"; Aml, adductor mandibularis lateralis; Dr, depressor rostri; "E", ampullary canals from pores of subsection "E"; "F", ampullary canals from the pores of subsection "F"; Hyo, hyomandibular cartilage; "I", ampullary canals from the pores of subsection "I"; Lls, levatores labiales superioris; Lr, levator rostri tendon; Nas, nasal capsule; Pro, propterygium.

Figure 3. Deeper dissection of R. eglanteria (same specimen as Fig. 2); dorsal view on the right side, ventral view on the left side. Abbreviations as follows: H, hyoid branch of the ALLN; Hc, hyoid capsule; IB, inner buccal branch of the ALLN; OB, outer buccal branch of the ALLN; OBc, outer buccal capsule; SO, superficial ophthalmic branch of the ALLN; SOc, superficial ophthalmic capsule.

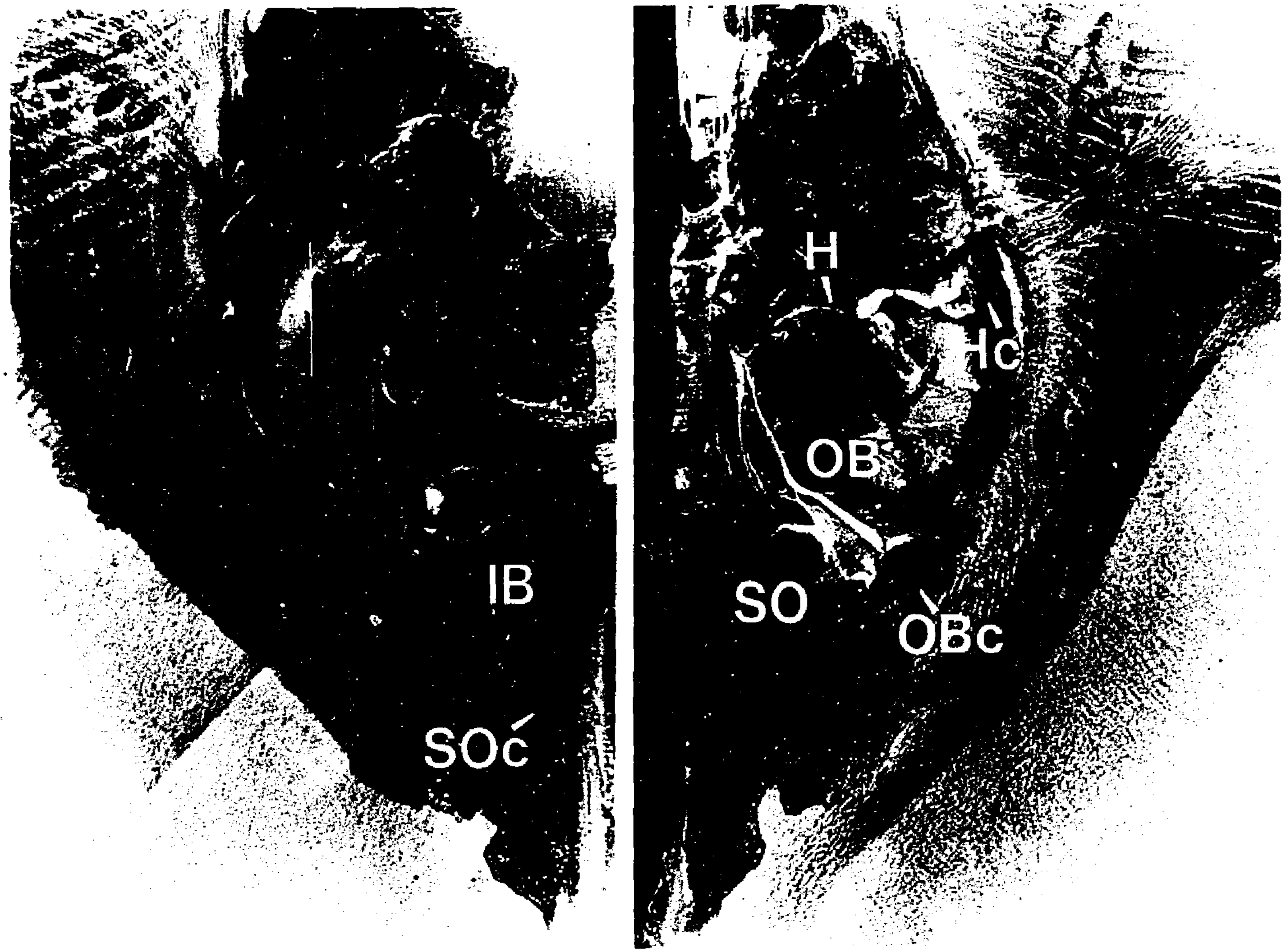

IB
SOc
H
Hc
OB
SO
OBc

Figure 4. The ampullary capsules, indicated by arrows, of *R. eglanteria* (ca. 600 mm TL female): A. Ventral view, superficial ophthalmic capsule. B. Dorsal view, superficial ophthalmic capsule. C. Dorsal view, outer buccal capsule. D. Dorsal view, hyoid capsule.


A
B
C
D

slightly anterior to the nasal capsule. On the ventral surface, pores from the superficial ophthalmic ampullae are generally distributed from the mouth and the tip of the rostrum, their density increasing somewhat posteriorly. One or two loosely arranged rows are located along the length of the rostral cartilage. Pores are evenly distributed in the space between these rows and the medial loop of the subrostral branch of the lateral line. Numerous pores are also located posteriorly between the subrostral branch and the nares. Pores from the superficial ophthalmic ampullae are clustered in two areas on the dorsal surface; one containing from 3 to 6 pores overlying the rostral appendix (subarea "K" in Raschi, 1978) and a second consisting of from 7 to 11 pores associated with the cranial branch of the lateral line adjacent to the anterior fontanelle (subarea "D"). Canals from both of these dorsal groups run parallel to the rostral cartilage. This capsule, being the amalgamation of two clusters of ampullae, is innervated by both the inner buccal and the superficial ophthalmic branches of the anterior lateral line nerve. Both exit the chondocranium jointly through the pro-otic foramen. The first runs anteroventrally along the subethmoidal depression and ventral surface of the rostral cartilage; whereas the second runs beneath the crista supraorbitalis, through the ophthalmic foramen and along the dorsal border of the rostral cartilage.

OUTER BUCCAL

This capsule pair is located along the anterior margin of the antorbital cartilage between the nasal capsule and the propterygium (figure 4C). Ventrally, pores from outer buccal ampullae are fairly evenly distributed laterally from the medial loop of the subrostral branch of the lateral line to the margin of the pectoral fin. Additional pores are located in two groups. The first is distributed posteriorly along the medial side of the angular branch of the lateral line from the position of the antorbital cartilage to a point even with the corner of the mouth overlying the adductores mandibularis lateralis; whereas the second is found along the lateral side of the angular branch of the lateral line from a position along the fin margin opposite the nasal branch to one approximately even with the location of the hyoid ampullary capsule. Substantial overlap occurs between these canals and those belonging to both the hyoid and superficial ophthalmic ampullae. Dorsally, 5 to 10 pores from outer buccal ampullae form a group anterolateral to the eye (subsection "C" in Raschi, 1978) overlying portions of the levatores labialis superioris (2) and adductor mandibularis lateralis (2) muscle masses. The outer buccal branch of the anterior lateral line nerve also exits the chondocranium via the pro-otic foramen and traverses anteriorly along the orbital wall, passing beneath the eyeball and through the center of the antorbital cartilage to the capsule.

HYOID

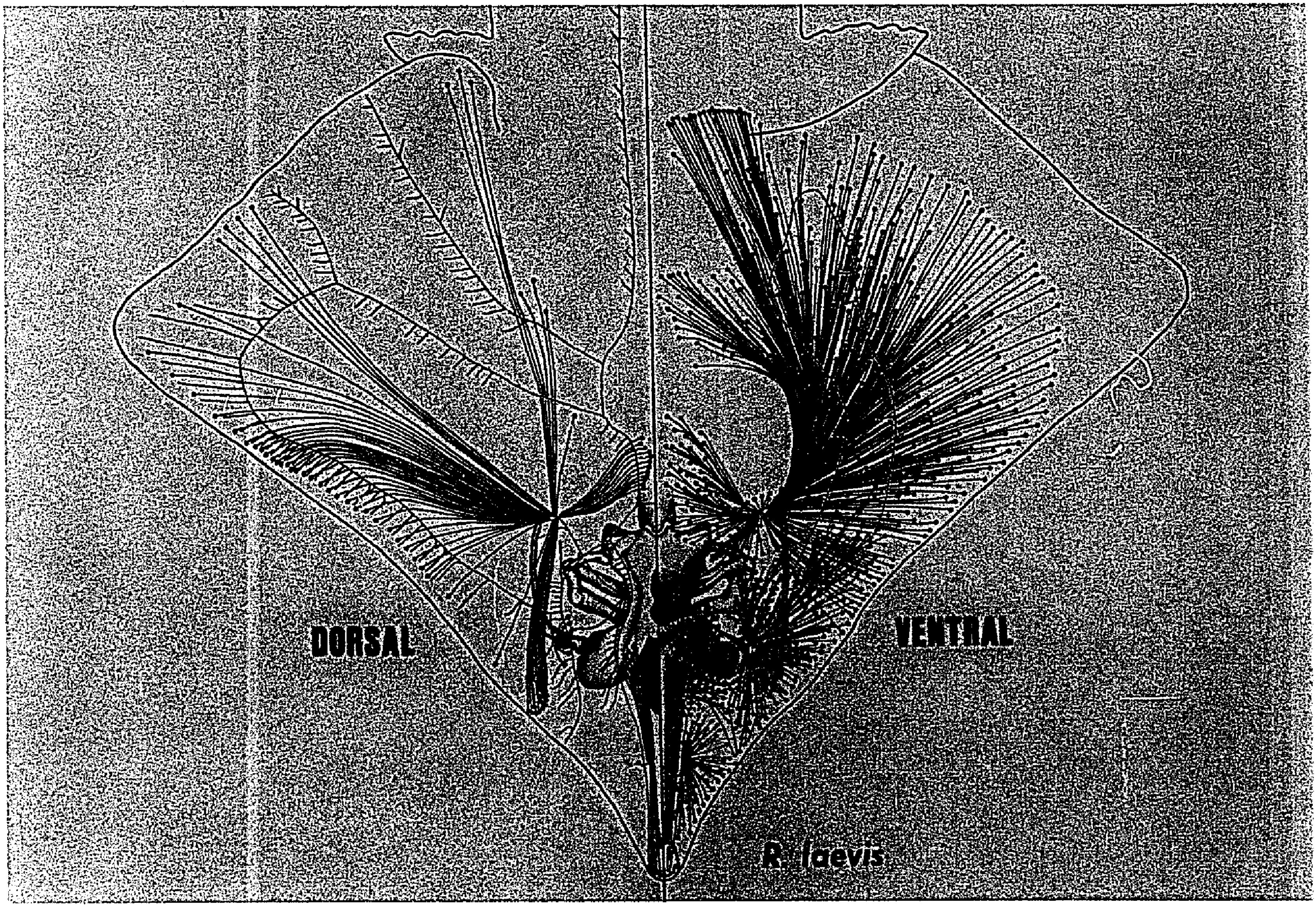
The hyoid capsule is located between the hyomandibular and propterygial cartilages (figure 4D), anterior to the branchial region. On the ventral surface, pores from these ampullae are distributed in a line along the fin margin from opposite the origin of the nasal branch of the lateral line to nearly the posterior angle of the pectoral fin, at which point they gently curve medially (in part subarea "I"). A few randomly distributed pores are found between this line and the angular and jugular branches of the lateral line. Medially, a number of pores are arranged in an arc from even with the angle of the mouth to near the midline of the abdomen overlying the coracomandibularis and depressor rostri. A group of pores are distributed posteriorly along either side of the jugular branch of the lateral line to its point of termination. Dorsally, pores from the hyoid capsule are located in three general areas. The first, is a cluster of 6 to 11 near the anterolateral margin of the fin. The pores are located near the levator rostri tendon, interspersed among the pores of the anterior pleural branch of the lateral line (subarea "B" in Raschi, 1978). The second is a group of 24 to 31 pores running along the pectoral fin margin, often in association with the pleural branch of the lateral line (in part subarea "A"). The third group forms an arc of 6 to 9 pores (subarea "E") along the midline of the scapular region. The hyoid branch of the anterior lateral line nerve exits the chondocranium through a second foramen separated from the pro-otic foramen by the prefacial commissure. It runs posteriolaterally to the capsule, having previously given off the mandibular branch.

MANDIBULAR

The mandibular capsule pair is situated on the outer concave surface of the mandible. The canals radiate medially to between 15 and 26 pores arranged in several rows. These pores are located along the posterior margin of the mouth, anterior to the oral section of the lateral line (subarea "J" in Raschi, 1978). The mandibular branch of the anterior lateral line nerve originates from the hyomandibular branch and runs ventromedially, passing between the mandible and the adductores mandibularis lateralis muscle to the capsule.

Of the remaining principal species, R. laevis (figure 5) shows the greatest amount of variation from this general pattern, those differences involving the distribution of somatic pores being particularly noticeable due to the dark pigmentation of the distal ends of the ampullary canals. The proportionally longer rostrum is reflected in a more complete separation of the inner buccal and superficial ophthalmic capsules, each innervated by a separate branch of the anterior lateral line nerve, as well as in a general increase in the number of pores on the ventral surface of the snout. The generally larger body size of this species (Table 3) is accompanied by an increased number of ampullae (Table 7), ranging from an additional 78% (in R. radiata) to 304% (in M. senta) as compared with the other principal species. Whereas the distribution of the pores is nearly the same as on R. eglanteria, with 89% (as compared with 84%) being ventrally located (Table 8), significant differences in the general arrangement of the ventral pores are apparent. These include pores extending further caudally, covering a significantly greater proportion of the body surface, as well as the presence of isolated clusters of pores associated with the vent, and to a lesser extent, the mid-abdominal region. Lastly, as described by Garman (1888), the ventral portion of the lateralis system exhibits a complete pleural loop in conjunction with the jugular branch. As a result, there is a slight increase in the number of lateral line tubules on the ventral surface. All of these differences are characteristic of the majority of

Figure 5. Semidiagrammatic representation of the ampullary system from a 700 mm TL female specimen of *R. laevis*. The ampullary system is shown in green, the lateralis system in blue and the cranial nerves in red.


DORSAL
VENTRAL
R. laevis

other species in the subgenus *dipturus* examined here.

The general arrangement of the ampullary system in the remaining principal species differs from *R. eglanteria* in only a few minor aspects, the first of which involves the relative amount of overlap of canals from adjacent ampullary capsules. *M. senta*, for example, exhibits a conspicuous near-absence of any overlap, probably due to a reduction in the number of hyoid ampullae by almost 50% as compared with *R. eglanteria* (Table 7). *R. garmani*, on the other hand, exhibits a slight increase in overlap resulting from the more lateral position in many of the ventrally located superficial ophthalmic canals. Both *R. bigelowi* (figure 6) and *B. richardsoni* (figure 7) exhibit a similar increase due to the increased number of ventral hyoid canals extending rostrally. Secondly, slight differences are also apparent in the relative abundance and distribution of lateral line canals. In *M. senta*, the anterior portion of the pleural branch appears to have fewer tubules while the lateral subrostral and nasal branches have more. Both *R. radiata* and *R. garmani* exhibit fewer tubules on the ventral surface. Similarly, an additional section of the pleural branch is present on the ventrum of *R. bigelowi*. The outer buccal branch of the anterior lateral line nerve passes over the antorbital cartilage in both *B. richardsoni* and *R. laevis* instead of through it as it does in the remaining species. All of these observations however, are based on only a single dissection specimen from each species and therefore provide no information on intraspecific variation.

The ampullae of galeoid sharks are more widely scattered throughout the cranial region than they are in the rajoids. Major innervation points consist of loosely aggregated clusters, often occupying large

Figure 6. Semidiagrammatic representation of the ampullary system from a 445 mm TL male specimen of R. *bigelowi*. The ampullary system is shown in green, the lateralis system in blue and the cranial nerves in red.

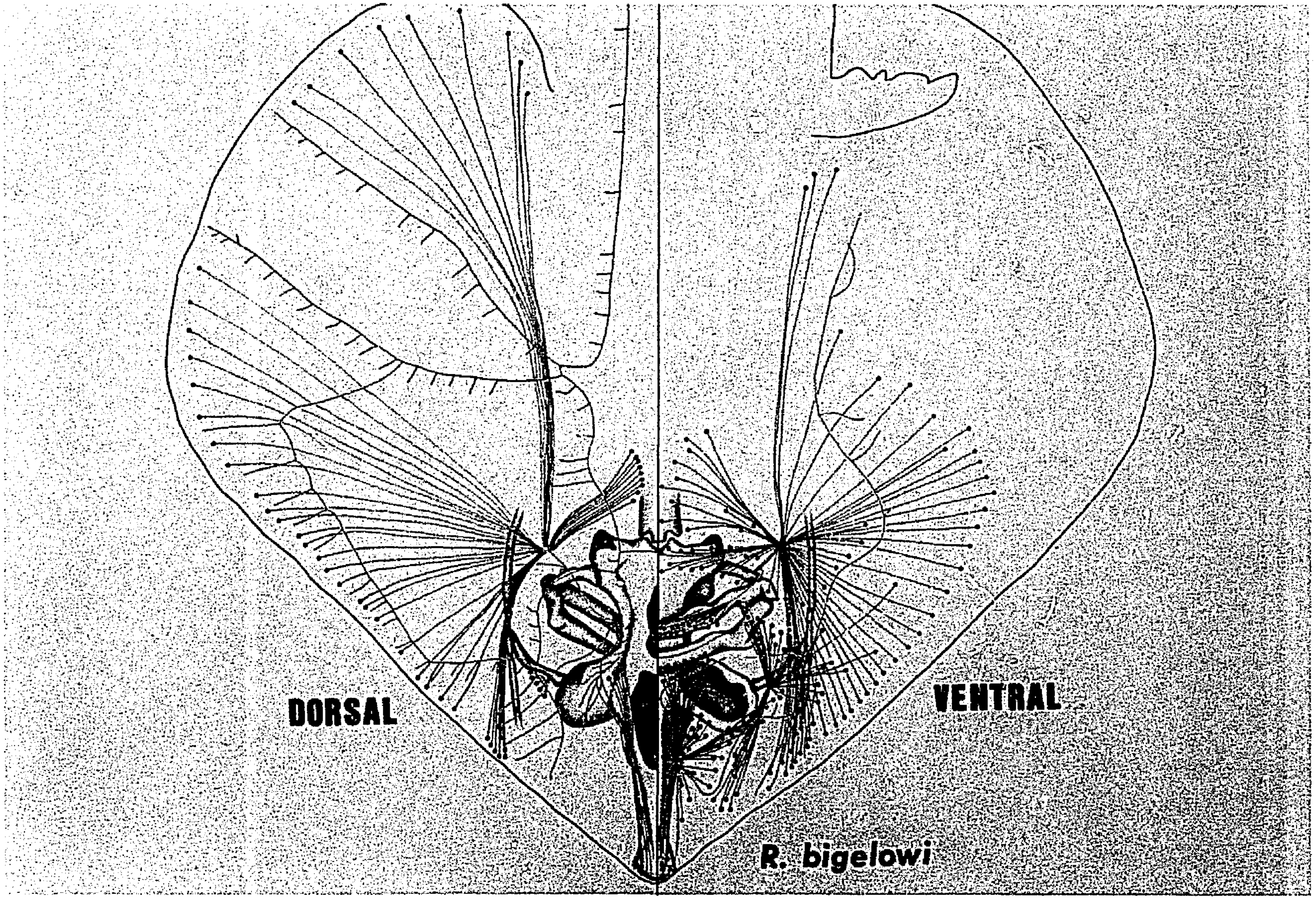
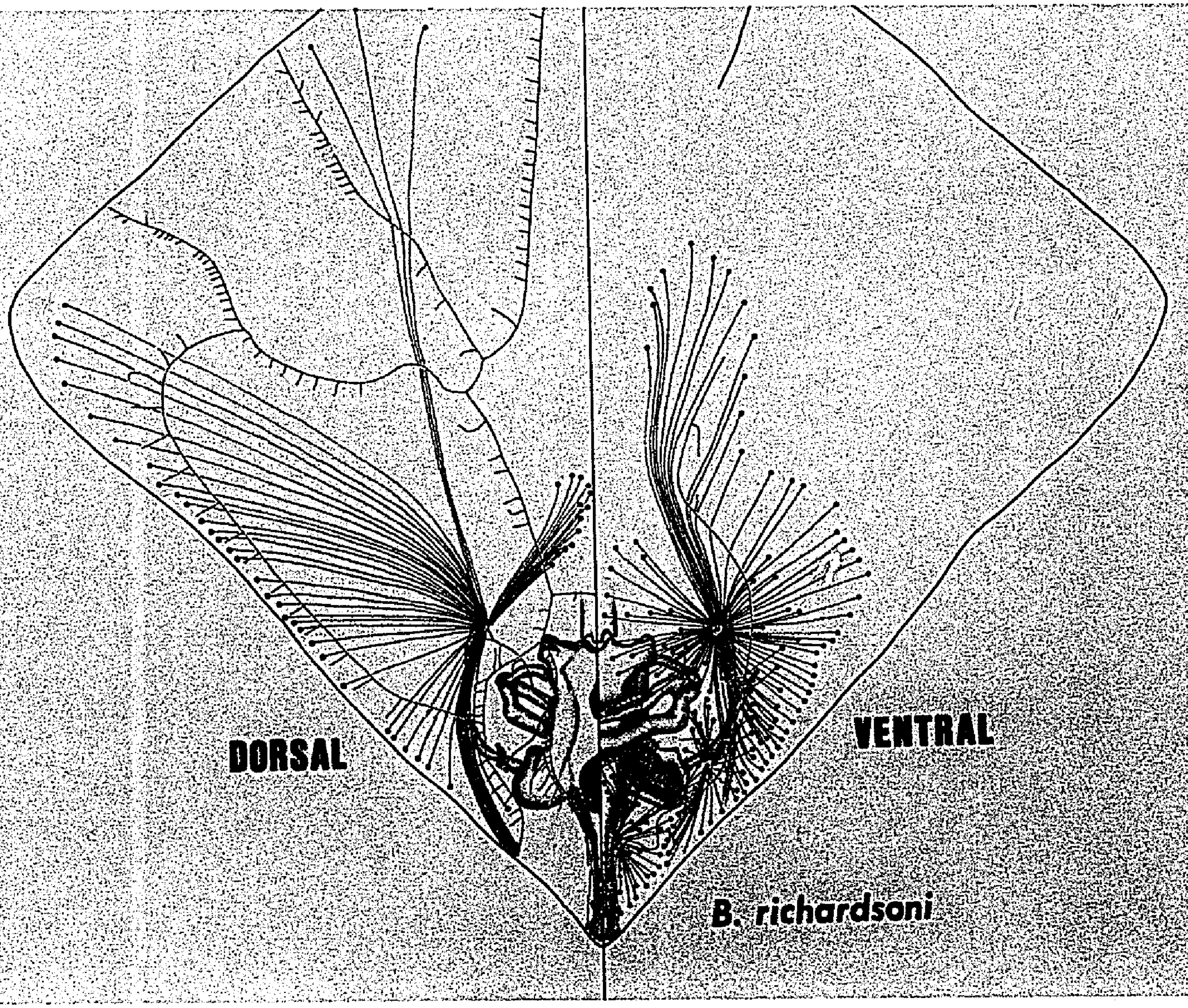

DORSAL
VENTRAL
R. bigelowi

Figure 7. Semidiagrammatic representation of the ampullary system from a 752 mm TL female specimen of *B. richardsoni*. The ampullary system is shown in green, the lateralis system in blue and the cranial nerves in red.


DORSAL
VENTRAL
B. richardsoni

areas, within the head region. This occasionally necessitates careful scrutiny of the individual nerve fibers associated with each ampulla in order to determine from which branch of the anterior lateral line nerve they originate. All five shark species exhibit the three major innervation areas characteristic of the carcharhinoids (Norris, 1929). While the relative extent of these areas may vary considerably, their relative location remains constant within the species examined and thereby allows the following description of the single species, _Carcharhinus_ _plumbeus_ (figure 8), to serve as a basis for further comparisons.

SUPERFICIAL OPHTHALMIC

This (supra-orbital of Norris, 1929) is the most extensive group, including all of the ampullae innervated by the superficial ophthalmic branch of the anterior lateral line nerve. In _C_. _plumbeus_, these ampullae are numerous enough to warrant the establishment of the following smaller subdivisions. SUBDIVISION I consists of ampullae located along the lateral wall of the anterior fontanelle above the base of the lateral rostral cartilage. The corresponding pores are distributed over a region posterior to the eye on the dorsolateral surface of the head (figure 9, subsections I and A, in part) and in a second region overlying the depression between the posterior wall of the nasal capsule and the preorbital process extending onto the ventrum as part of an arc of pores in front of the eye (figure 9, in part subareas D, C and C'). This group of ampullae is innervated by the medial-most branch of the superficial ophthalmic. SUBDIVISION II includes the ampullae lying along the proximal 2/3 to 3/4 of the

Figure 8. Semidiagrammatic representation of the ampullary system from a 211 cm TL female specimen of *C. plumbeus*. The cranial nerves are shown in red, the lateralis system in blue and the ampullary system as follows (see text): superficial ophthalmic - DIVISION I in dark green, DIVISION II in light green, DIVISION III in brown, outer buccal in orange and mandibular in black.

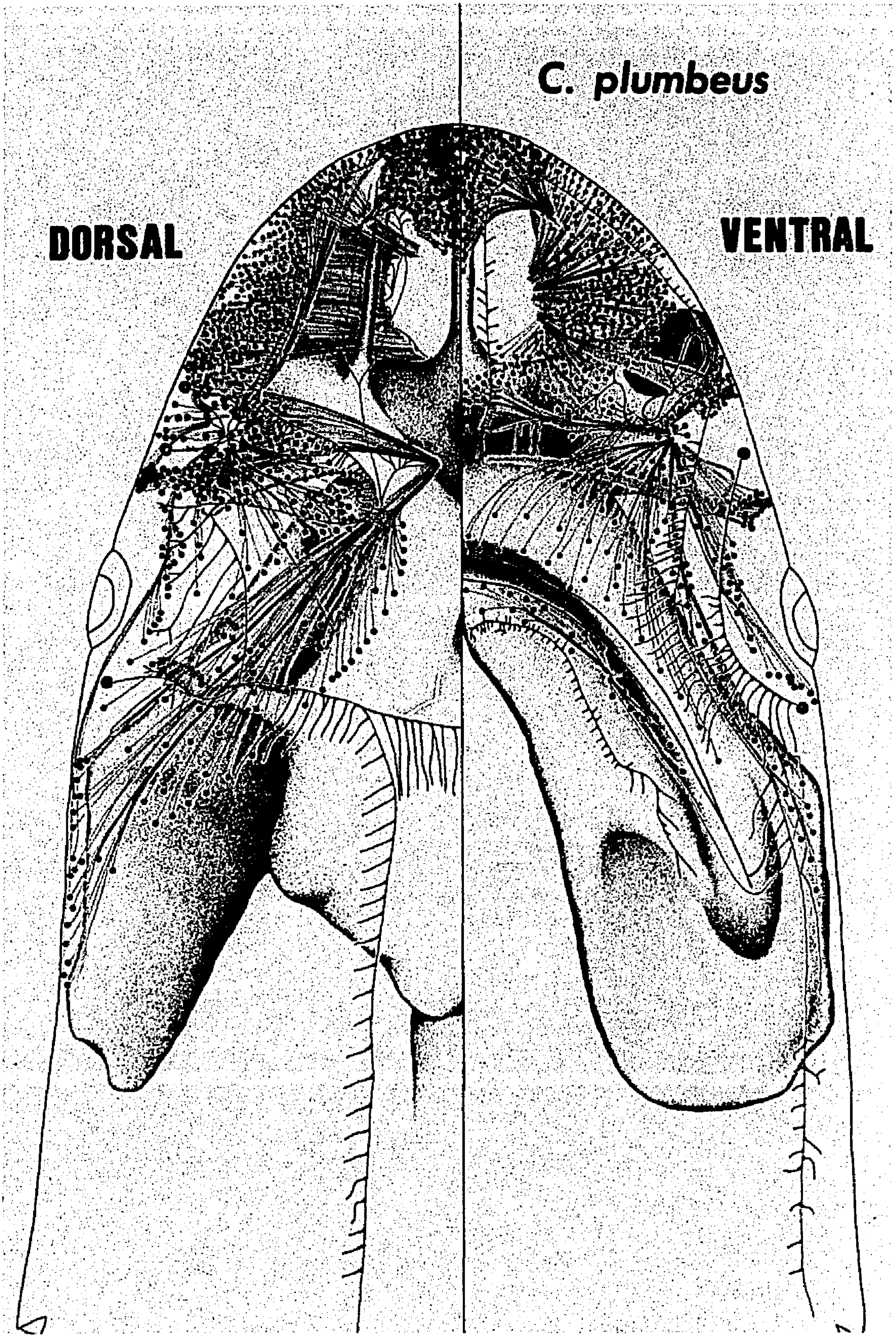
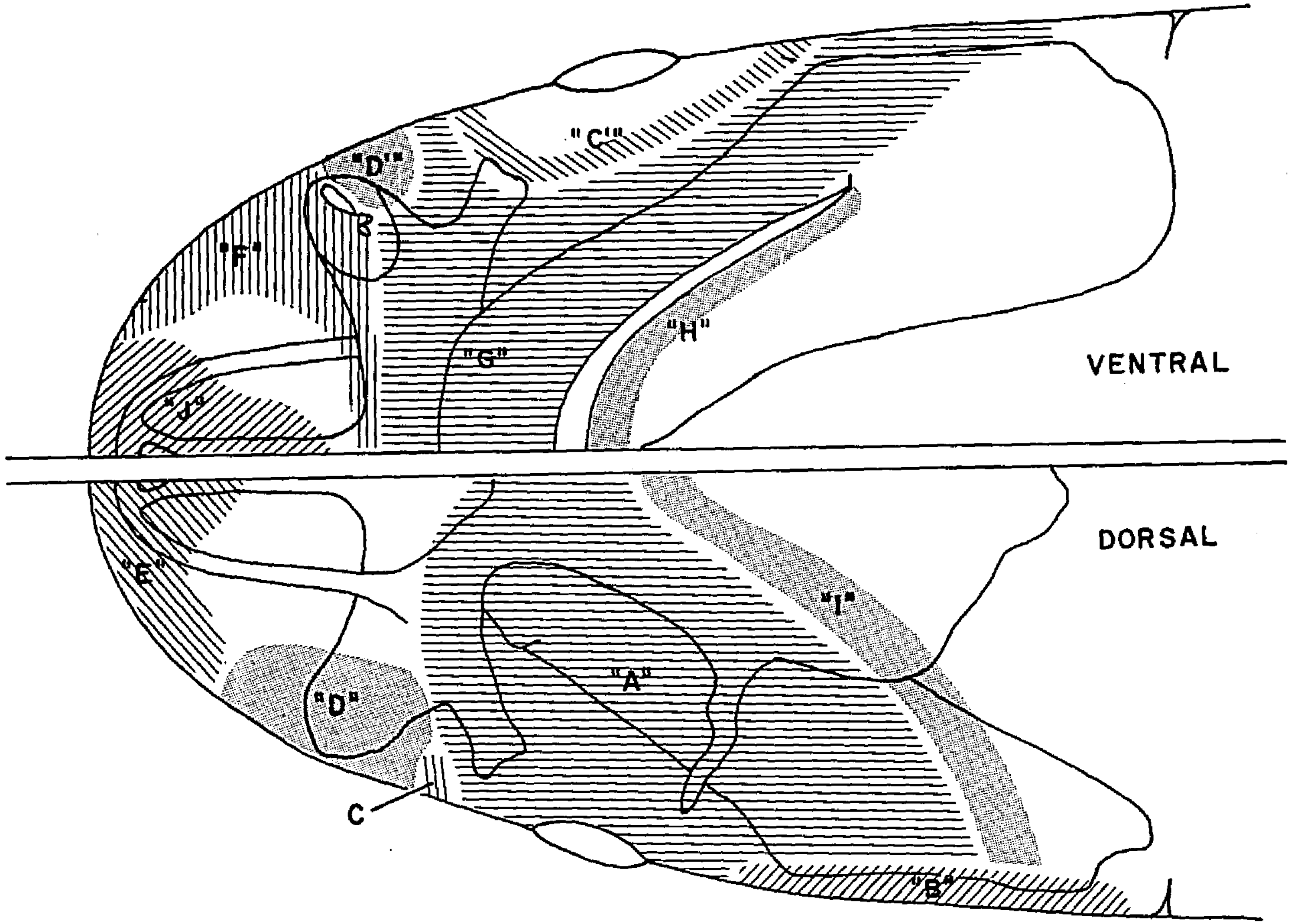

C. plumbeus
DORSAL
VENTRAL

Figure 9. Location of the subareas (A-I) used in counting the ampullary pores on the five species of galeoid sharks.


"C'"
"D'"
"F"
"H"
"G"
"J"
VENTRAL
DORSAL
"E"
"I"
"A"
"D"
C
"B"

lateral rostral cartilage, the pores from which are located in a band along the dorsolateral margin of the rostrum from the posterior margin of the nasal capsule to a point roughly parallel with the rostral node (figure 9, in part subareas C and D). The majority of these pores are bordered medially by the rostral-cranial branch and caudally by a posterior loop of the subrostral branch of the lateral line and are interspersed marginally with pores from outer buccal ampullae (see below). On the ventral surface, pores originating from this subdivision occupy the space between the lateral margin of the rostral node and the nasal aperture, these pores extending medially to the prenasal branch of the lateral line in the region overlying the cranial margin of the inter-nasal cartilage (figure 9, subsection F). A second, smaller group lies directly behind the nasal aperture and is interspersed among a series of outer buccal pores (figure 9, in part subarea D'). This branch of the superficial ophthalmic runs along the outer base of the lateral rostral cartilage before dividing into three sections, one remaining along the lateral side of the rostral cartilage, the other two passing beneath it and continuing to medially located groups. The ampullae of SUBDIVISION III occupy the distal end of the rostrum, their pores forming the cranial-most groups on both the dorsal and ventral surfaces (figure 9, subareas E and J). This last section of nerve separates from the main superficial ophthalmic branch and runs medial to the lateral rostral cartilage to its point of innervation.

OUTER BUCCAL

This cluster of ampullae is situated within the cavity formed between the posterior wall of the nasal capsule and the preorbital process. Four isolated clusters of pores associated with this group are located on the dorsal surface of the head. The first consists of only a few pores that are interspersed with those from the superficial ophthalmic (SUBDIVISION I) and that run along the lateral margin of the head from near the orbital branch of the lateral line to the distal corner of the palatoquadrate (figure 9, in part subarea B). The second occupies a large region between the cranial and caudal pore groups of SUBDIVISION I (superficial ophthalmic) in association with the cranial branch of the lateral line (figure 9, in part subarea A). The third is located along the caudolateral margin of the SUBDIVISION II (superficial ophthalmic) pores. The fourth runs along the anteriomedial margin of this same group and connects SUBDIVISIONS II and III. Ventrally, outer buccal pores are also located in four distinct groups, the largest of which is located between the nasal branch of the lateral line and the mouth (figure 9, in part subarea G). The second begins in association with the ventral extension of SUBDIVISION I (superficial ophthalmic) and continues as a semicircle around the eye (figure 9, in part subarea C'). The third group extends posteriorly from the lateral margin of the first ventral group as a condensed line bounded on either side by the orbital and angular branches of the lateral line. The fourth ventral group consists of a small cluster of pores lying along the cranial margin of the more posterior SUBDIVISION II (superficial ophthalmic) group (figure 9, in part subarea D'). Following its exit from the orbit wall, the outer buccal branch of the anterior lateral line nerve passes beneath the eyeball and runs anterolateral to the ampullary cluster.

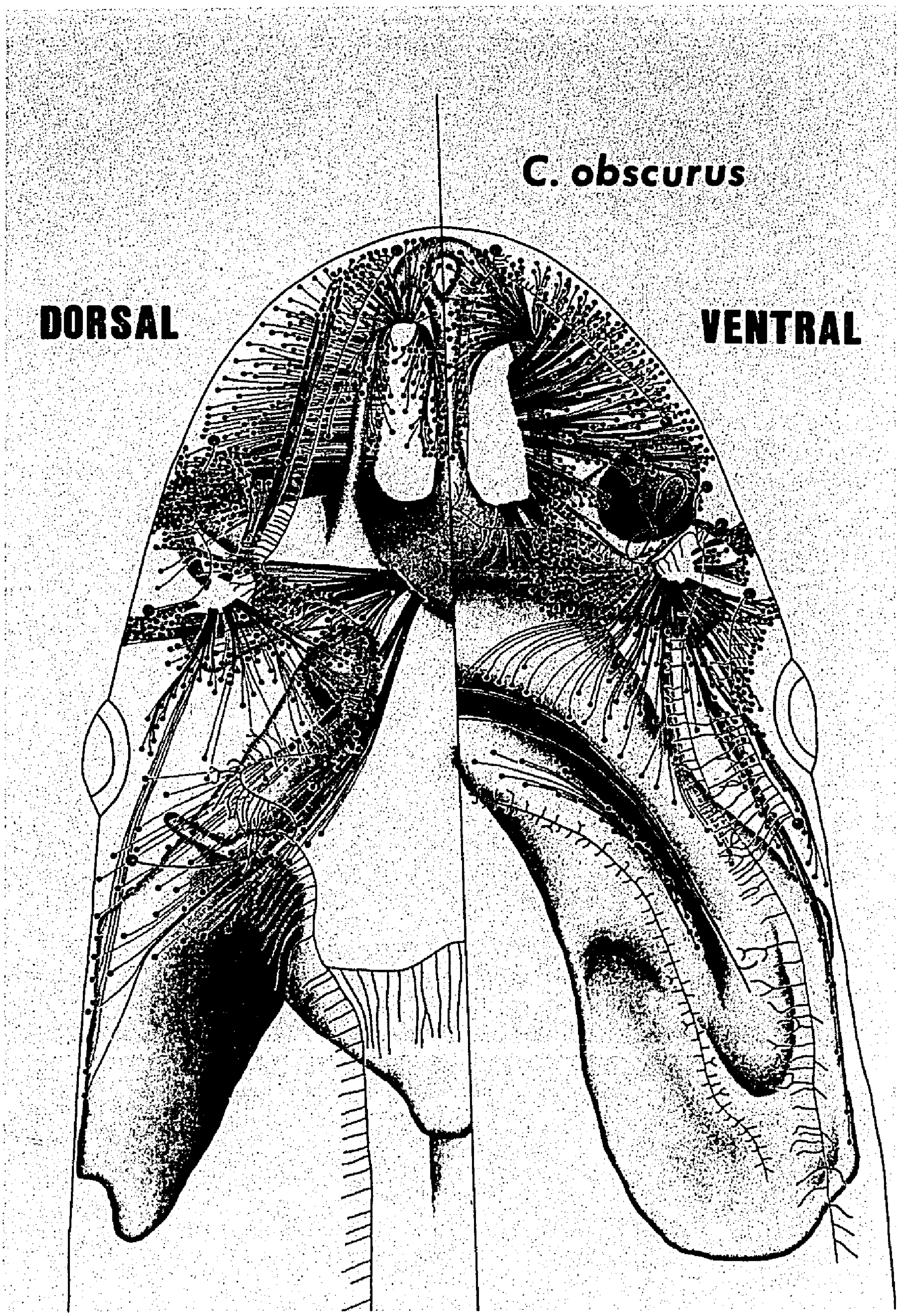
MANDIBULAR

This is the smallest group and is located in a small connective tissue capsule approximately midway along each side of the lower jaw. From 18 to 24 pores (Table 19) pores are located between the angle of the mouth and the midline and lie cranial to the oral section of the lateral line. The mandibular branch of the anterior lateral line nerve runs posteriolaterally from the orbit, over the dorsolateral edge of the palatoquadrate, and directly to the capsule.

The ampullary systems in the remaining four species of sharks are remarkably similar to that just described. With only a few exceptions, differences that do exist either reflect reductions in the overall numbers of ampullae or in the relative development of the lateralis system. For example, a reduction in the number of superficial ophthalmic, DIVISION I ampullae (Table 9) result in a less distinct and generally abbreviated subarea "I". In addition, _G. cuvieri_, _O. taurus_ and _P. glauca_ exhibit a limited number of pores extending rostrally from their normal point of innervation. Variations in the general arrangement of DIVISION II ampullae include a noticeable separation of the cluster into nearly equal cranial and caudal subdivisions in _P. glauca_ as well as shifts in the arrangement of somatic pores caudally (on _G. cuvieri_) and/or laterally (on _O. taurus_). Differences in the arrangement of outer buccal ampullae include reductions in their relative contribution to subarea "A" (_G. cuvieri_ and _P. glauca_), and a somewhat unusual expansion of numerous pores into the area caudal to the eye on _O. taurus_, possibly compensating for the reduction in the number of pores originating from SUBDIVISION I (superficial ophthalmic) ampullae. Minor differences are also apparent in the distribution of the ventrally located outer buccal, particularly in the area in front of the mouth (subarea "G"). Variations in the relative extent of the lateralis system range from a slight increase on both the dorsal and ventral surfaces in *C. obscurus* (figure 10) to decreases, slight on the dorsal and ventral surfaces of *G. cuvieri* to extreme on the ventral surface of *P. glauca*.

While the overall arrangement of somatic pores on the surface of the rajoids exhibits many interspecific similarities, differences in actual numbers exist. Pore counts from previously established subareas (Raschi, 1978) are presented for both the principal (Table 10) and ancillary (Table 11) species. These artificial subareas are of only limited use, particularly in those species with modified pore distributions such as the subgenus *dipturus* or *A. longirostris*, in which subareas "H" and "I" are not sufficiently distinct to permit their separation (see figure 5). Comparisons of these subareas yield no noticeable trends, but are useful in calculating total counts. Table 8 summarizes the pore distributions on the principal species. Total numbers of pores generally reflect the overall size of each species (Table 3), ranging from 380 on *R. garmani*, to 1691 on *R. laevis*. The majority of these pores are on the ventral surface of each species and range from 64% of the total in *B. richardsoni* to 89% in *R. laevis*. Pore densities are therefore greater on the ventral surface, with values ranging from 0.05 pores/sq. cm on *B. richardsoni* to 0.96 pores/sq. cm on *R. bigelowi*. Species in the ancillary group exhibit total pore counts (Table 12) which are comparable to the principal species, with

Figure 10. Semidiagrammatic representation of the ampullary system from a 160 cm TL male specimen of C. obscurus. The cranial nerves are not included. The lateralis system is shown in blue and the ampullary system as follows (see text): superficial ophthalmic - DIVISION I in dark green, DIVISION II in light green, DIVISION III in brown, outer buccal in orange and mandibular in black.


C. obscurus
DORSAL
VENTRAL

the exception of the reduced numbers of pores on the comparatively smaller sized Gurgesiella ishiyamai and G. plutonia (compare Tables 6 and 3). As seen in the principal species, the majority of these pores are also associated with the ventrum, with the single exception of R. clarkii, on which 52% of the pores are located on the dorsum. The percentage of the total pores located on the ventrum of the ancillary species are similar to the principal group except for the two previously mentioned gurgesiellids, which have fewer ventral pores, and Anacanthobatis longirostris which exhibits a greater value. The ventral pore densities on the ancillary species range from 0.04 pores/sq. cm on R. alba to 2.73 pores/sq. cm on Gurgesiella atripinna.

The total numbers of ampullae contained in each of the connective tissue capsules from the principal species is presented in Table 7. These totalled counts compare favorably with those for the pores (Tables 8 and 12), ranging from an increase of 10.8% (R. bigelowi) to a decrease by 14.3% (R. laevis). Generally, the the hyoid capsule contains the greatest numbers of ampullae and range from between 37.5% of the total in R. eglanteria to 51.2% in B. richardsoni. With the exception of R. laevis, the second largest capsule is the superficial ophthalmic accounting for between 26.3% (in R. bigelowi) and 30.2% (in B. richardsoni) of the total. In R. laevis however, this capsule is spatially separated from the inner buccal and therefore contains relatively fewer ampullae. When combined however, these two capsules still encompass fewer ampullae than does the outer buccal capsule, a feature different from the other principal species. The mandibular capsule contains the fewest ampullae, accounting for between only 4.0% in B. richardsoni and 9.9% in M. senta. The relative distribution of the ampullae in the ancillary species is similar to that of the principal species (Table 13). Exceptions to this include a significant reduction in the number of ampullae of the hyoid capsules from *A. longirostris* and *R. texana*; a similar reduction in the number of ampullae in the superficial ophthalmic capsule of *B. spinacauda* as well as in the combined superficial ophthalmic and inner buccal capsules of *R. rhina*; and a decrease in outer buccal ampullae in *G. ishiyamai*. Interestingly, those remaining species of the subgenus *dipturus* which possess a separate inner buccal capsule, contained more ampullae in this and the superficial ophthalmic then are present in the outer buccal capsule alone.

By comparison, the general distribution of both the ampullae (Table 9) and the corresponding pores (Table 19) of the galeoid sharks are significantly different from that of the rajoids. Total numbers of pores are greater, ranging from 941 on *P. glauca* to 2382 on *C. plumbeus* and appear to bear no relationship to the overall size of the species. These pores exhibit a much more even distribution over the surface of the head, with between only 50.3% (*C. plumbeus*) and 61.8% (*P. glauca*) of the total number being associated with the ventral region. The average, total counts of ampullae are slightly less, with reductions amounting to from 2.3% (*C. plumbeus*) to 25.0% (*P. glauca*) of the corresponding pore counts. Such large deviations probably reflect the difficulty often encountered in differentiating ampullary pores from the lateral line pores. In the absence of the hyoid capsule found in the rajoids, the majority of ampullae, from 74.3% (*C. plumbeus*) to 49.2% (*G. cuvieri*) of the total, are located in the superficial ophthalmic region. Similarly, the mandibular capsules contain the fewest ampullae, accounting for only between 1.8% (*C. plumbeus*) and 5.8% (*G. cuvieri*).

Variation is present in the number of alveoli on ampullae from the principal species of rajoids (Table 14). Counts of alveoli vary considerably among ampullae within the same capsule and are most variable in the hyoid and least variable in the mandibular capsule. Furthermore, average numbers of alveoli differ between capsules within the same specimen; from a high value of 20.5 (in *B. richardsoni*) to 8.3 (in *R. laevis*) on ampullae from the hyoid capsule, and lows from 9.6 (in *B. richardsoni*) to 3.8 (in *R. leavis*) on ampullae from the mandibular capsule. The average number of alveoli do not appear to exhibit any ontogenetic variation, as indicated by the superficial ophthalmic ampullae from *R. eglanteria* (figure 11). Finally however, considerable intraspecific variation does exists in the average number of alveoli within the same capsule (figure 12 and 13), with *B. richardsoni* exhibiting consistently greater values for each capsule and *R. laevis*, or in one instance *M. senta*, exhibiting the lowest.

Both the number and arrangement of alveoli are similar in the ancillary group (Table 15). Ampullae from the hyoid capsule exhibited the largest variation in the number of alveoli, with the exception of six species; *A. longirostris*, *G. ishiyamai*, *R. clarkii*, *R. doutrei*, *R. mirelatus* and *R. ocellata*. An additional five species (*G. plutonia*, *R. alba*, *R. erinacea*, *R. rhina* and *R. teevani*), exhibit ampullae in either the superficial ophthalmic, inner buccal or outer buccal capsules with less variation in alveoli counts than the mandibular. Total averaged numbers of alveoli exceed the 20.5 of *B. richardsoni* in six species (*R. bathyphila*, *R. binoculata*, *M. fuliginea*, *R. fyllae*, *R. jenseni* and *M.*

Figure 11. Relationship between the number of alveoli and the total length of the individual in *R. eglanteria*. Each data point represents an averaged count from five ampullae removed from the superficial ophthalmic capsule of each specimen. Statistical analysis was performed on separate counts.

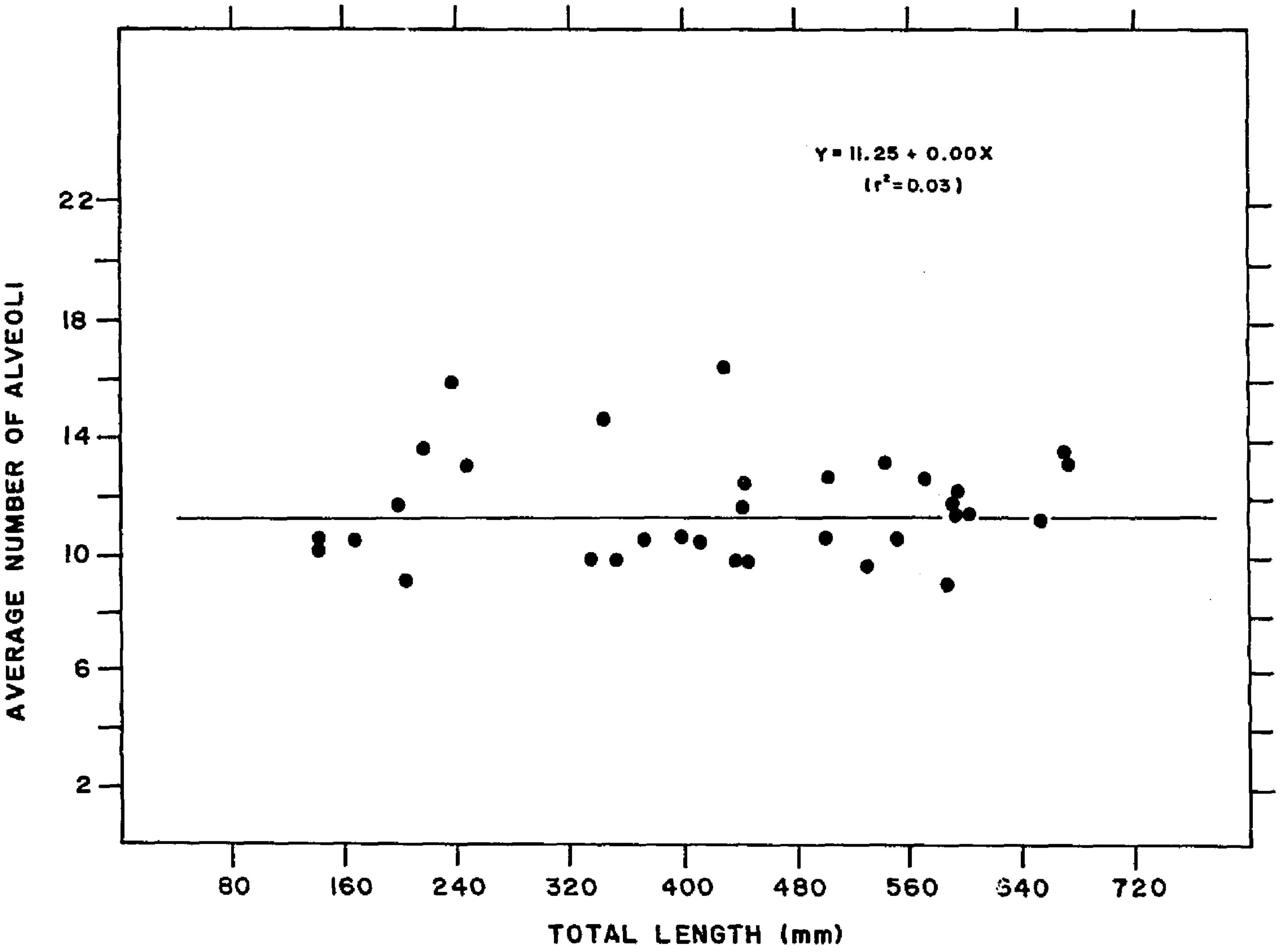

Y = 11.25 + 0.00X
(r^2 = 0.03)
AVERAGE NUMBER OF ALVEOLI
22
18
14
10
6
2
80
160
240
320
400
480
560
640
720
TOTAL LENGTH (mm)

Figure 12. Isolated ampullae from the superficial ophthalmic capsule of the following species: A. *R. laevis* (Disc 490, female). B. *R. eglanteria* (Disc 395, female). C. *M. senta* (Disc 173, female).

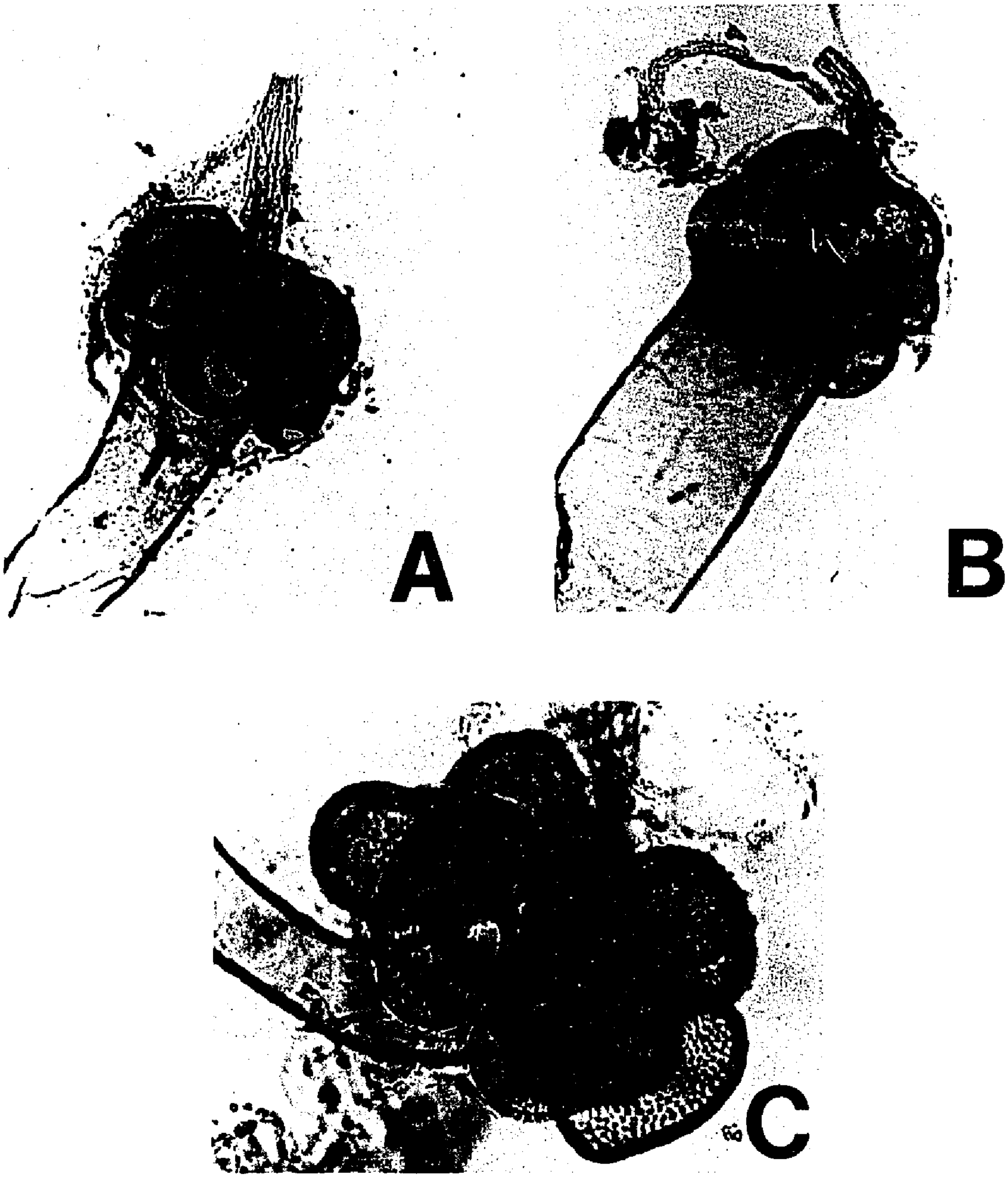
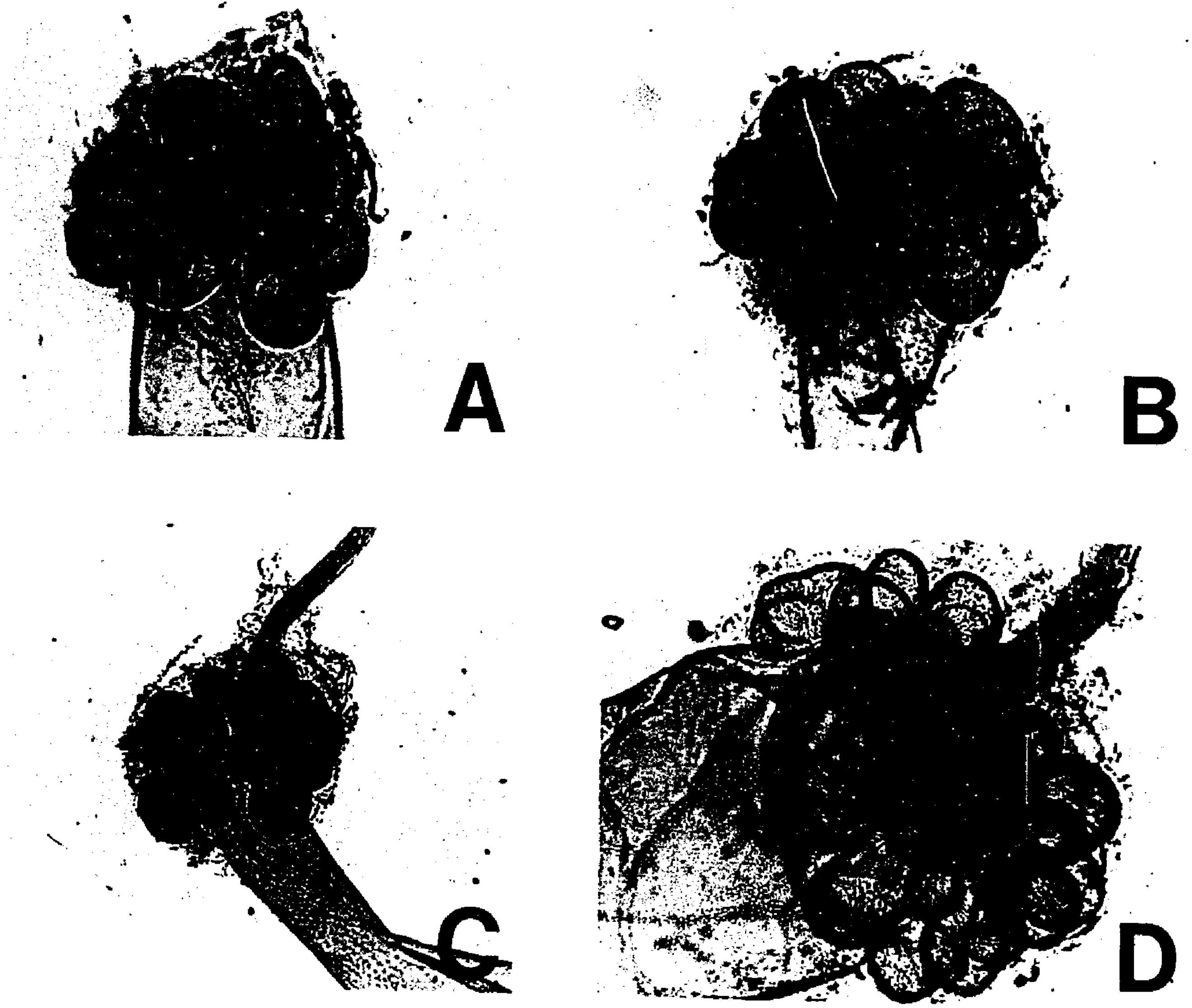

A
B
C

Figure 13. Isolated ampullae from the superficial ophthalmic capsule of the following species: A. *R*. *garmani* (Disc 180, female). B. *R*. *bigelowi* (Disc 196, male). C. *R*. *radiata* (Disc 199, male). D. *B*. *richardsoni* (Disc 538, female).


A
B
C
D

purpuriventralis) whereas three species (G. plutonia, R. alba and R. porosa) possess lower average counts than the 3.8 of R. laevis. Over 50% of the ancillary species have ampullae from capsules other than the hyoid exhibiting the largest average number of alveoli for that particular species, but it remains the mandibular which exhibits the least.

In contrast to the rajoids, the alveoli from the galeoid sharks are arranged in a single, concentric row encircling the terminal end of the ampulla (figure 14). By comparison, there are generally fewer alveoli (Table 16), with combined, averaged values for all of the innervation areas ranging from 23.6 (C. plumbeus) to 34.2 (O. taurus). Normally, those ampullae from the superficial ophthalmic (DIVISION I and III) or the outer buccal (O. taurus) regions exhibit the most numerous alveoli, ranging from 11.0 (G. cuvieri) to 7.4 (C. plumbeus); whereas those from the mandibular region exhibit the fewest alveoli of from 2.4 (C. plumbeus) to 5.2 (G. cuvieri and O. taurus). The variation within a specific innervation area is comparable to that found in the rajoids.

Considerable variation is also apparent in the length and width of ampullae within a single capsule as well as between capsules within the same specimen. Although not immediately apparent from individual capsules (Table 17), the combined, averaged measurements of ampullae from each capsule pair tend to exhibit an ontogenetic increase within each species (figures 15 and 16). While statistically suspect due to the low sample size, similar measurements from a more complete ontogenetic series of the superficial ophthalmic ampullae in R. eglanteria confirm this trend. Both the lengths and the widths of these ampullae are found to be proportional to the natural logarithm of the

Figure 14. Isolated ampullae from C. plumbeus (120 cm TL, female): A. Lateral view from the outer buccal area. B. Apical view from the superficial ophthalmic area.

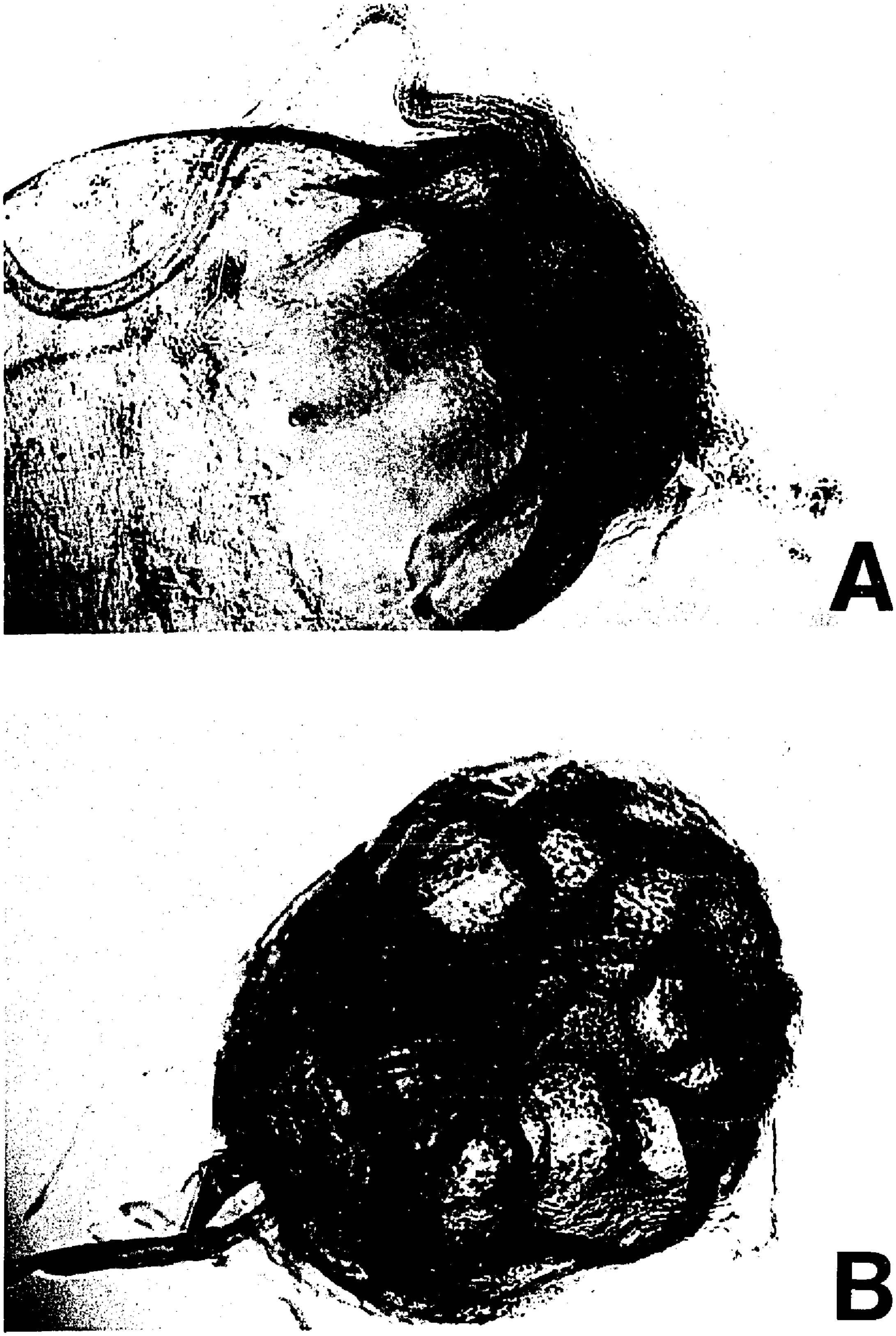

A
B

Figure 15. Relationship between width of ampullae and disc width for the seven principal species of skates. Data points represent the average width of five ampullae totalled for the four capsules (inner buccal capsule of *R. laevis* is omitted).

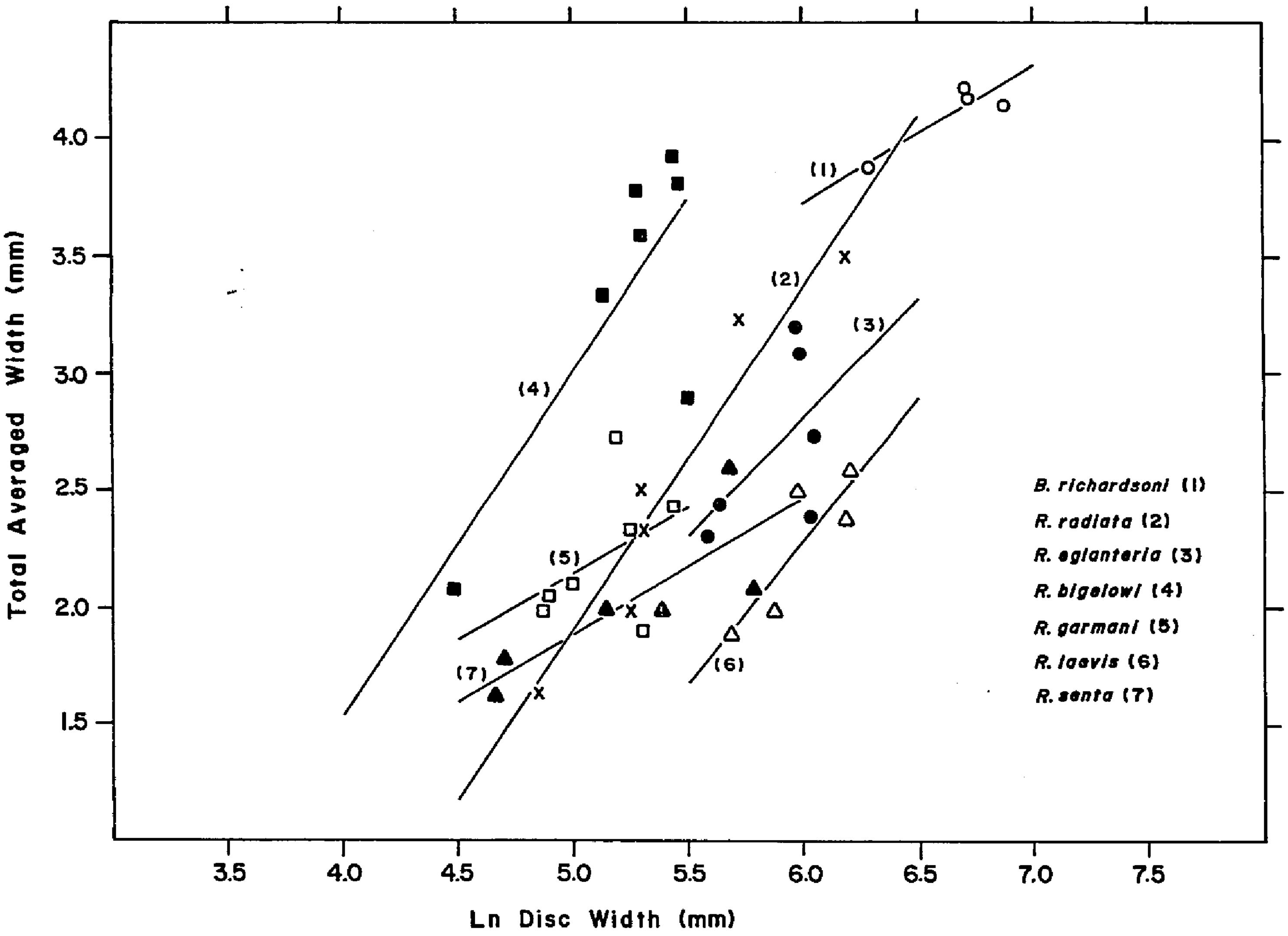
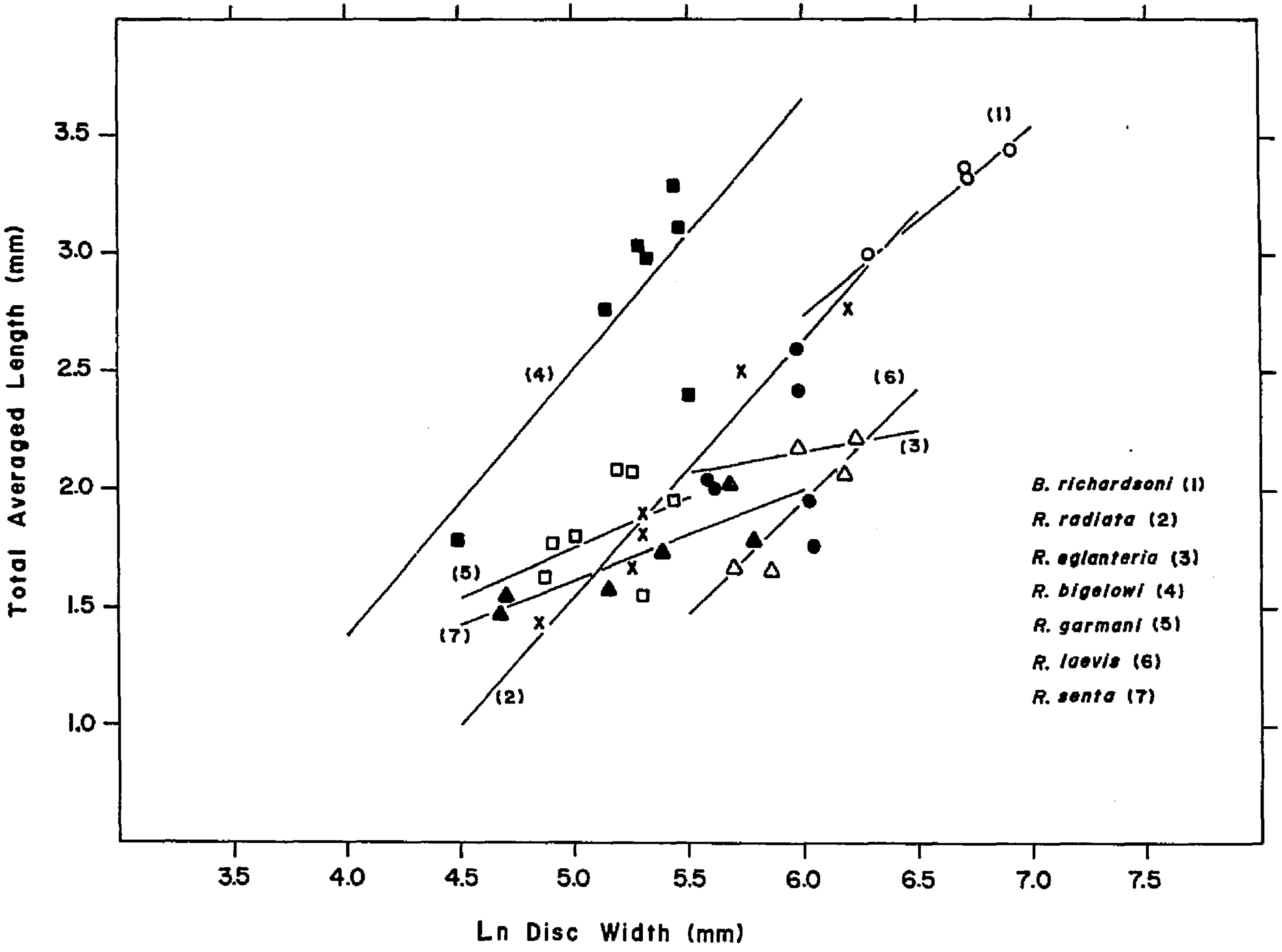
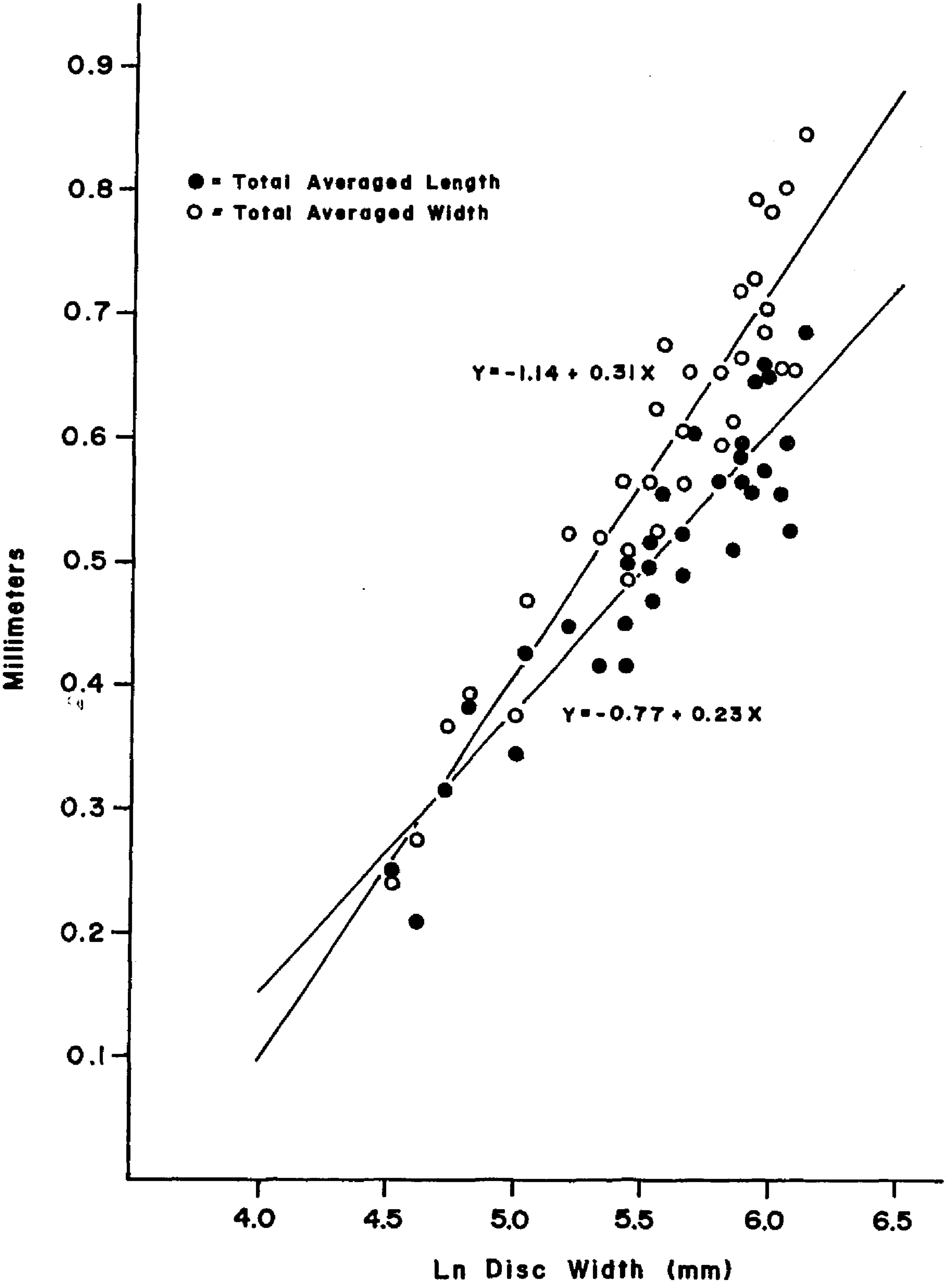

Total Averaged Width (mm)
4.0
3.5
3.0
2.5
2.0
1.5
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
Ln Disc Width (mm)
(1)
(2)
(3)
(4)
(5)
(6)
(7)
B. richardsoni (1)
R. radiata (2)
R. eglanteria (3)
R. bigelowi (4)
R. garmani (5)
R. laevis (6)
R. senta (7)

Figure 16. Relationship between length of ampullae and disc width for the seven principal species of skates. Data points represent the average length of five ampullae totalled for the four capsules (inner buccal capsule of *R. laevis* is omitted).



Total Averaged Length (mm)
3.5
3.0
2.5
2.0
1.5
1.0
Ln Disc Width (mm)
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
(1)
(2)
(3)
(4)
(5)
(6)
(7)
B. richardsoni (1)
R. radiata (2)
R. eglanteria (3)
R. bigelowi (4)
R. garmani (5)
R. laevis (6)
R. senta (7)

Figure 17. Relationship between the disc width (ln) and the overall dimensions of the superficial ophthalmic ampullae from R. eglanteria. Each data point represents either the averaged length or width of five ampullae from each specimen.



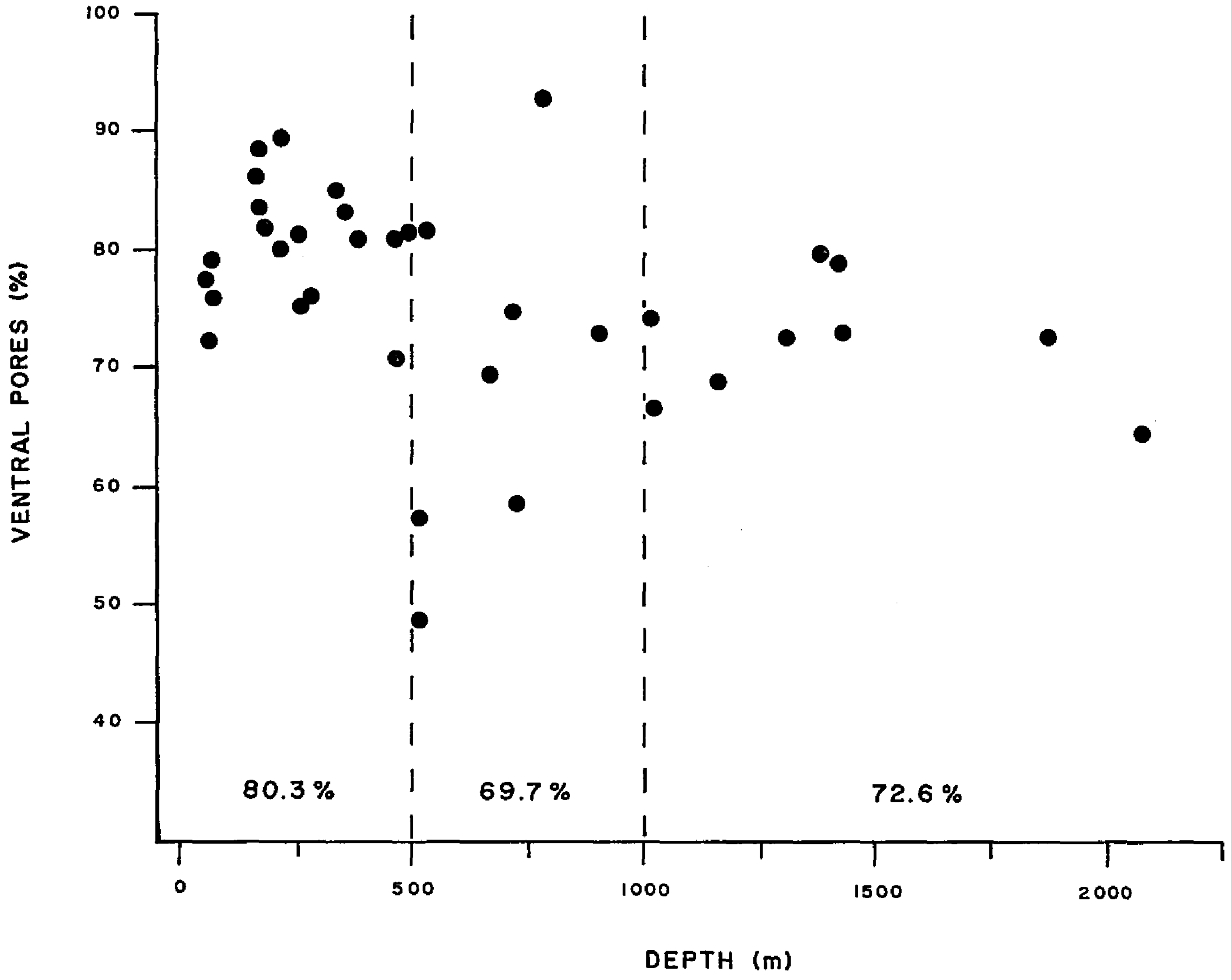
● = Total Averaged Length
○ = Total Averaged Width
Y = -1.14 + 0.31X
Y = -0.77 + 0.23X
Millimeters
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
4.0
4.5
5.0
5.5
6.0
6.5
Ln Disc Width (mm)

disc width (figure 17), as indicated by a deviation from regression analysis (Sokal and Rohlf, 1969). The logarithmic plot of ampullae length and disc width yields a nonsignificant deviation from the regression ($F = 1.36$; 31,132) but a correspondingly significant curvilinear regression ($F = 208.67^{**}$; 1,31), resulting in the following equation: $Y = -0.77 + 0.23 \ln X$, where Y is the ampullae length and X is the disc width ($t = 16.34^{**}$). A similar plot of the width of the ampullae produces a correspondingly significant curvilinear regression ($F = 215.25^{**}$; 1,31), expressed by $Y = -1.15 + 0.31 \ln X$, where Y is the ampullae width and X is disc width ($t = 23.36^{**}$). Both relationships allow for a further comparison of principle and ancillary species (Table 18).

DISCUSSION

The general arrangement of the ampullae of Lorenzini in the rajoids appears to compensate for reduced sensory stimuli during feeding. The predominance of ventrally located pores (Tables 8 and 12) on a dorsoventrally flattened body potentially provides the adequate cues necessary for the suction-grasping type of feeding mechanism (Moss, 1977) characteristic of this group. The rapid dissipation of a stationary dipole field requires the close approach of the skate to a prey item (Kalmijn, 1971 and 1972) which diminishes the function of the dorsally located eyes. A reduced importance of mechanoreceptive information during prey capture may further be inferred from the generally diminished lateralis system on the ventrum as compared to the dorsal surface. The increased pore density which is located around the mouth in all species (figures 1, 5, 6, 7) provides the greater resolution necessary to direct the feeding strike once the source is located. Furthermore, the relative proportion of the pores which are ventrally located generally decreases with depth of occurrence. Compared to the shallower dwelling species (those inhabiting depths less than 500 m), those skates from depths exceeding 1000 m exhibit a significant reduction (t = 3.697**) by nearly 10% in the number of ventral pores, from 80.3% to 72.6% (figure 18). This shift of ampullary pores to the dorsal surface may reflect the lack of adequate visual stimuli in deeper waters. Moreover, both the largest, 92.3% on _A_. _longirostris_, and the smallest, 48.4% on _R_. _clarkii_, proportion of

Figure 18. The relationship between the percentage of total ampullary pores associated with the ventral surface and the mean depth of occurrence for each species of skate. Each point represents the averaged value for a different species.


VENTRAL PORES (%)
100
90
80
70
60
50
40
80.3 %
69.7 %
72.6 %
0
500
1000
1500
2000
DEPTH (m)

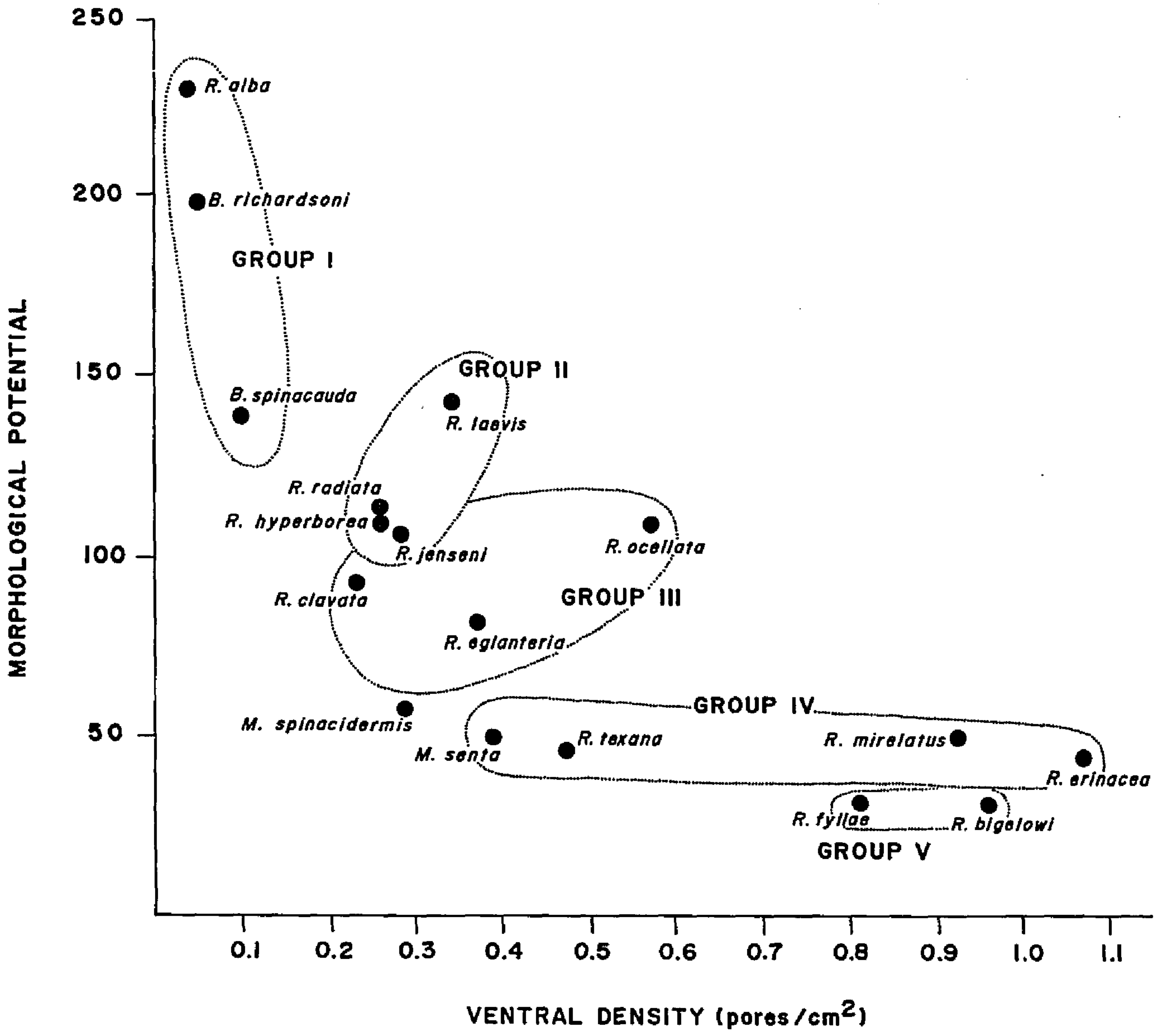
ventral pores are found on those species inhabiting intermediate depths (from 500m to 1000m). This region is characterized by near-threshold light intensities (Marshall, 1971) and variations in the dorsal-ventral pore distribution may represent experimentation in the electrosensory system to compensate for the lack of visual input.

The significance in the general arrangement of the ampullary system in the galeoid sharks is less clear. The lateral, or nearly lateral, position of the eyes on a more conically-shaped head facilitates extensive use of vision during the initial stages of prey capture and appropriately, the number of pores associated with either the dorsal (A-E, I) or the ventral surface (F-H, C', D', J) are more nearly equal (Table 19). The lateralis system is also more evenly distributed. However, the ampullary system of certain elasmobranchs has been shown both theoretically (Kalmijn, 1973) and behaviorally (Kalmijn, 1978a & b) to play a major role in electroorientation and navigation of the more migratory species. As a shark moves through the earth's magnetic field, dorsally and ventrally located pores evaluate the ohmic voltage gradient induced by the horizontal component while the more laterally located pores evaluate the vertical component (Kalmijn, 1981). This favors a more even distribution of pores. This functional duality of the electroreceptive system in the more mobile species of sharks may mask any clear anatomical relationships to feeding. In further contrast to the rajoids, a greater proportion of the ampullary pores are concentrated in the snout region (figure 8 and 10). In all but G. cuvieri, the majority of the corresponding ampullae are located within the rostrum (Table 9, superficial ophthalmic I-III). Although Schaeffer (1967) has suggested that the evolution of the rostrum is associated with the elaboration of the ampullary system, with the rostral length directly reflecting electroreceptive acuity (Compagno, 1979), the total number of ampullae within this region does not confirm this hypothesis. While *P. glauca* exhibits the longest rostrum and *G. cuvieri* the shortest (Table 21), measured as either the relative length of the medial cartilage (Compagno, 1979) or externally between the tip of the snout and the level of the nares (Bigelow and Schroeder, 1948); it is *G. cuvieri* which possess the greater number of ampullae (Table 9). Similarly, *O. taurus* exhibits a significant reduction of from 2/3 to 1/2 of the number of ampullae as compared to *C. plumbeus* and *C. obscurus* and yet possesses a snout of nearly the same length.

In the rajoids, the general arrangement and relative density of ventral ampullary pores appears accurately to reflect specific food preferences for each species. Since each ampulla functions independently (Waltman, 1966) and supplies separate sensory information to the central nervous system, pore densities represent a measure of the electroreceptive resolution. Differences in this parameter determine both the accuracy and capabilities of this system. However, in order to compare the ampullary system with prey selectivity certain generalizations must be made. Several species inhabit geographically wide ranges, throughout which preferred prey items may change significantly as a result of either changes in the prey species' distribution or through interspecific competition. Such a situation has been well documented for *R. erinacea* in the Delaware Bay (McEachran, 1976). More significant however, is the wide diversity of prey species included in stomach contents of most rajids.

The majority of skates are extremely catholic in their prey selection and this necessitates the categorization of prey items into more general, often artificial, groups. The relative mobility of each prey species is of most interest from an electroreceptive standpoint. In this study, overall diets are classified according to general locomotory capabilities into one of the following five categories. The first (Group 1, figure 19) consists of larger, pelagic fish and cephalopods while the second (Group 2) includes an additional smaller fraction of the larger, more mobile crustaceans. The third group includes nearly equal amounts of both active and sedentary fish and crustacea. The final two diet classes (Group 4 and 5 in figure 19) include primarily benthic invertebrates, epifaunal species in the former and infaunal species in the latter. The six principal species for which stomach content information is available (Table 4) fit into these five groups. The first includes Bathyraja richardsoni which feeds primarily on larger, more active, teleosts such as macrourids (Templeman, 1973; Campbell et al., 1980). Both R. laevis and R. radiata are included in the second group; R. laevis feeding primarily upon active fish (including clupeids, stromateids and gadids) and larger crustacea (Homarus, Cancer, etc.) (Bigelow and Schroeder, 1953b; Liem and Scott, 1966) along with smaller quantities of molluscs (both bivalves and gastropods) and polychaetes (Bigelow and Schroeder, 1953a). Similarly, adult R. radiata feed primarily on fish (McEachran et al., 1976) as well as smaller quantities of invertebrates. Published accounts of the stomach contents from R. eglanteria include large amounts of both invertebrates and fish and therefore place it within the third group. For example, although Fritz and Daiber (1963) found invertebrates comprising 97% of the total number of items found in

Figure 19. The relationship between food preference and ventral pore densities among the skates (both principal and ancillary species). Morphological potential, as defined in the text, is the product of relative mouth width (% TL) and total length (mm).


250
200
150
100
50
MORPHOLOGICAL POTENTIAL
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
VENTRAL DENSITY (pores/cm^2)
R. alba
B. richardsoni
GROUP I
B. spinacauda
GROUP II
R. laevis
R. radiata
R. hyperborea
R. jenseni
R. ocellata
R. clavata
GROUP III
R. eglanteria
M. spinacidermis
GROUP IV
M. senta
R. texana
R. mirelatus
R. erinacea
R. fyllae
R. bigelowi
GROUP V

stomachs of *R. eglanteria*, additional studies by both Hildebrand and Schroeder (1927) and Bigelow and Schroeder (1953a) suggest that fish species, such as *Peprilus* and *Stenotomus*, are occasionally the principal component. Finally, while both *M. senta* and *R. bigelowi* feed on smaller benthic invertebrates; the first concentrates on epifaunal groups, such as smaller decapods, euphausids, amphipods and mysids (McEachran et al., 1976), while the second presumably on infaunal amphipods (Sedberry, pers. comm.).

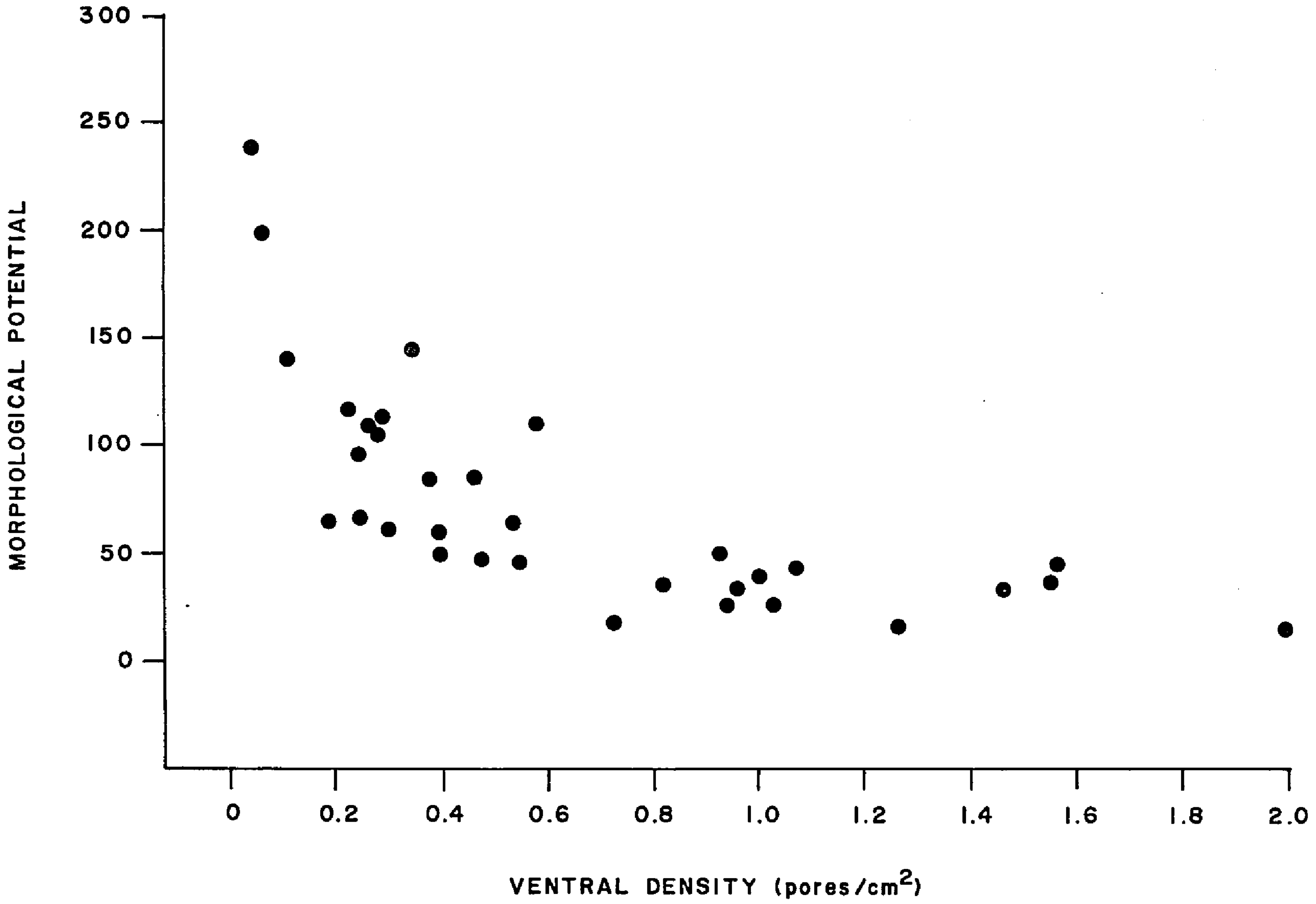
Ventral pore densities of the principal species (Table 8) are inversely related to general prey mobility. Those rajoids which feed primarily on the more active prey, such as *B. richardsoni* (Group 1) and *R. radiata* and *R. laevis* (Group 2), exhibit the lowest pore densities of 0.05 pores/cm^2, 0.26 pores/cm^2 and 0.34 pores/cm^2 respectively. On the other hand, those rajids which feed on more sedentary prey species, *R. eglanteria* (Group 3), *M. senta* (Group 4) and *R. bigelowi* (Group 5), exhibit much higher densities of 0.37 pores/cm^2, 0.39 pores/cm^2 and 0.96 pores/cm^2 respectively. The ventral pore densities (Table 12) of the twelve ancillary species for which food habit information is available (Table 20) follow a similar trend. *B. spinacauda* and *R. alba* are both primarily piscivorous (Group 1) and possess reduced ventral pore densities of 0.10 pores/cm^2 and 0.04 pores/cm^2 respectively. *R. binoculata*, *R. hyperborea* and *R. jenseni* belong in Group 2, feeding on larger teleosts and, to a lesser extent, active crustaceans. Pore densities for these species range from 0.06 pores/cm^2 to 0.26 pores/cm^2 and 0.27 pores/cm^2 and compare favorably with those principal species with similar food habits. Ample food habit data places *R. clavata* and *R. ocellata* into the third group. Ventral pore densities of

0.24 pores/cm^2 and 0.57 pores/cm^2 for these two species are intermediate between Groups 1 and 5. Lastly, R. texana, R. mirelatus, R. erinacea, M. spinacidermis and R. fyllae possess diets which consist primarily of smaller invertebrates. The first three feed predominantly on epifaunal species (Group 4) and possess ventral pore densities of 0.47 pores/cm^2, 0.92 pores/cm^2 and 1.07 pores/cm^2 respectively whereas R. fyllae typically consumes infaunal species (Group 5) and exhibits a pore density of 0.81 pores/cm^2. A ventral pore density of 0.29 pores/cm^2 on M. spinacidermis appears anomalous probably due to the very small sizes of the individuals examined by Templeman (1965). This relationship between prey selection and the ventral pore density is presented along the horizontal axis of figure 19.

The reduced pore densities on the more piscivorous rajoids do not necessarily reflect decreased pore numbers nor does it indicate merely increased surface areas. However, those species which do feed on the larger-sized prey items exhibit certain size-related modifications including generally larger body sizes as well as proportionally larger mouths. Increased mouth sizes have previously been used as a "morphological potential" to interpret prey selection in a number of other fish groups including mesopelagic and bathypelagic teleosts (Ebeling and Cailliet, 1974) and benthic macrourids (McLellan, 1977). A similar trend is found in these rajoids as shown along the vertical axis of figure 19. The substitution of this "morphological potential" for actual prey preferences in those species lacking stomach content information further demonstrates the relationship between ventral pore densities and prey selection (figure 20).

The reduced pore densities among those skate species which feed on

Figure 20. The relationship between morphological potential (as defined in Figure 19) and ventral pore densities.


MORPHOLOGICAL POTENTIAL
300
250
200
150
100
50
0
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
VENTRAL DENSITY (pores/cm2)

highly mobile prey may reflect the distance from which the feeding strike is initiated. Normally, those species which select infaunal, or more sedentary epifaunal prey, have the opportunity to remain relatively stationary above the prey location. The individual food item may be drawn closer to the jaws by creating a negative pressure beneath the body, as described for Torpedo (Belbenoit and Bauer, 1972), or by excavating the surrounding sediment (Howard, et al, 1977; Gregory et al, 1979). Electroreceptive information from the ampullae concentrated around the mouth may then help to quickly grasp the prey item between the jaws. However, Kalmijn and Weinger (1981) used computer simulated bioelectric fields in a recent study to observe the feeding strike of two elasmobranch species on actively moving prey. In this situation Raja erinacea initiated the attack at a distance of 15 to 25 cm away and uses no further course corrections. An evaluation of the prey-generated, bioelectric information from this distance should favor a different configuration of pores which more evenly cover a larger portion of the ventral surface. This may be of additional significance in light of recent evidence which suggests a somatotopic arrangement of the electroreceptor terminals in the dorsal octavolateral nucleus in R. erinacea (Bodznick and Schmidt, 1982).

Because of the difficulties involved in measuring the surface area of the individual galeoid heads, specific pore densities are unavailable. However, a comparison of the relative numbers of ampullary pores (Table 9) among the different shark species suggests modifications in electroreceptive acuity along similar directions. C. plumbeus normally inhabits shallower, often murky, coastal waters and yet selectivity feeds on many smaller, often cryptic prey species

(Table 22). This strongly indicates the extensive use of the ampullary system in prey capture as exemplified by its ability to feed predominantly on Callinectes (Medved and Marshall, 1981). A disproportionately large fraction of those crabs taken by young C plumbeus appear to be freshly molted (VIMS unpublished data), a condition which is characterized by increased osmotic activity and may therefore exhibit bioelectric fields of increased magnitude similar to that observed in other wounded crustaceans (Kalmijn, 1974). By comparison, C. obscurus is as selective in its food habits which consists primarily of active fish and cephalopods but is more pelagic in its distribution despite periodically entering estuarine waters. As a result of feeding higher in the clearer water column, vision may play a more significant role. Similarly, P. gluaca is selective in its food habits and is normally restricted to extremely clear pelagic waters (Table 22). Both species exhibit reduced pore densities with respect to C. plumbeus; C. obscurus due to slightly decreased numbers of pores on a much larger body (Table 21), P. glauca due only to extremely reduced pore numbers. G. cuvieri and O. taurus also exhibit possess similarly reduced pore numbers (Table 9). These two species normally inhabit shallow coastal waters but feed much less discriminantly and include not only a wide variety of prey species, but a large fraction of inanimate objects as well (Table 22). In these cases, reduced electroreceptive acuity is not compensated for by increased visual input but rather probably through reduced prey selectivity.

Each of the principal species of rajoids exhibits a characteristic number of alveoli on ampullae from each capsule pair (for example, figures 12 and 13). These values are generally greater in the the two deeper dwelling species, *B. richardsoni* and *R. bigelowi*. Since intraspecific variation within each capsule is relatively small (Table 14) and since there are very few ontogenetic differences (figure 11), the average number of alveoli within each capsule may be interspecifically compared. Figure 21 demonstrates a generally increased number of alveoli within each capsule of the deeper dwelling species. Furthermore, a total average number of alveoli for all of the major capsules (omitting the inner buccal) exhibits a similar depth related increase for the majority of both principal and ancillary species (figure 22). The alveoli counts (Tables 14 and 15) for those species found in waters shallower than 500 m average 38.8/species (range of 23.0, on *R. porosa*, to 71.4 on *R. binoculata*) whereas similar counts for those species inhabiting waters deeper than 1000 m average 70.0/species, or nearly twice that of the shallow, with a range from 59.4 (*R. hyperborea*) to 79.6 (*M. fuliginea*). Again of particular interest are those ampullae from the species inhabiting intermediate depths (500-1000 meters). The number of alveoli in this group ranges between from 17.7 (*G. plutonia*) and 46.6 (*G. atripinna*), overlapping the lower range of the shallow group and exhibit an average of 38.3/species which is slightly below that of the shallow group.

In addition, ampullae from deeper dwelling rajoids are generally larger in size. Comparisons of ampullary widths (figure 15) and lengths (figure 16) among the principal species strongly indicates that those inhabiting shallower waters, such as *R. eglanteria* and *R. laevis*, possess smaller ampullae for any given sized individual when compared to the deeper species, such as *R. bigelowi* and *B. richardsoni*. By

Figure 21. The averaged number of alveoli on ampullae from individual capsules of the seven principal species of skates. Capsules are abbreviated at the bottom of each histogram as follows: M, mandibular; O, outer buccal; I, inner buccal; S, superficial ophthalmic; and H, hyoid. Species are arranged in order of increasing total numbers of alveoli.

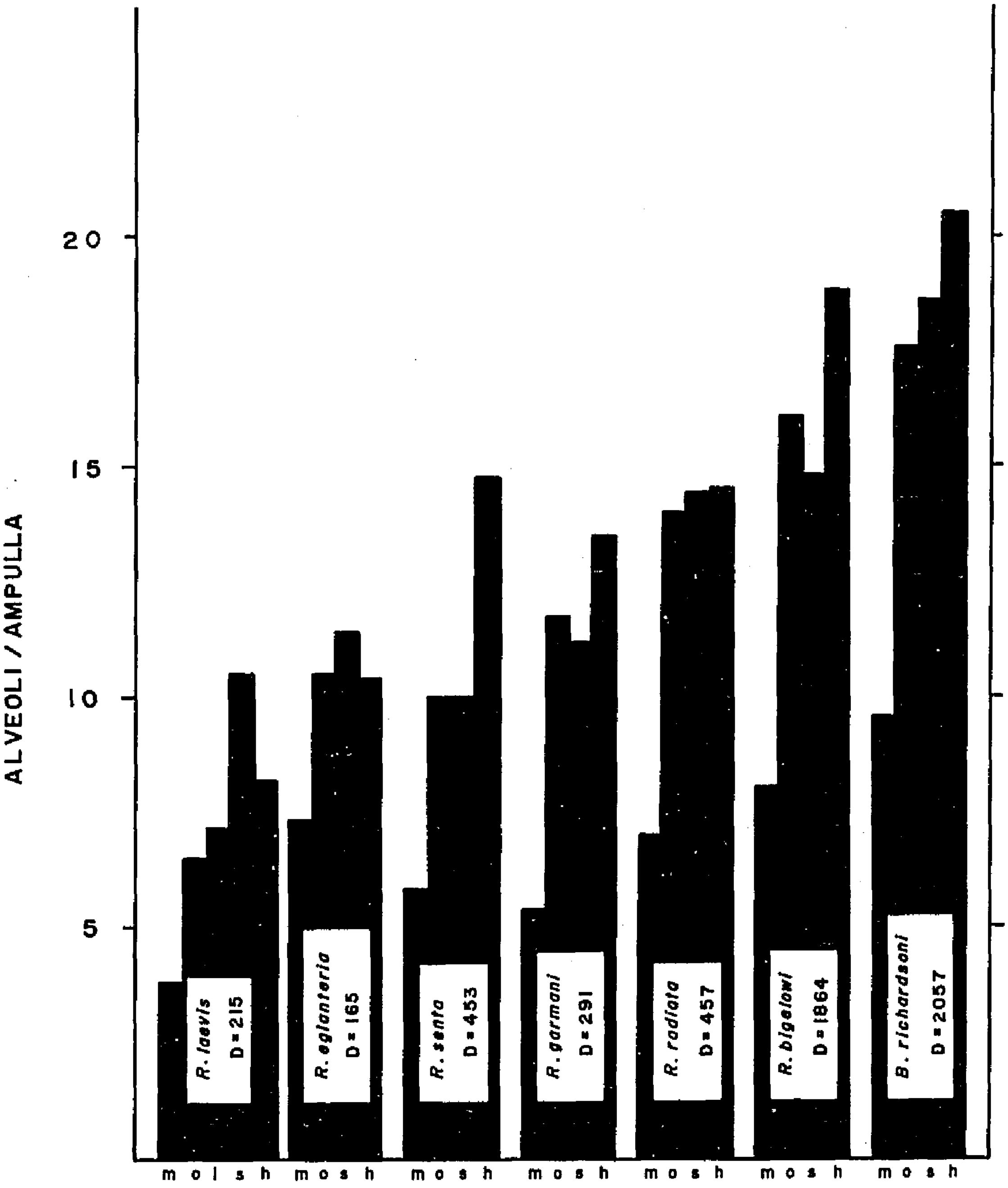

ALVEOLI / AMPULLA
20
15
10
5
R. laevis
D = 215
R. eglanteria
D = 165
R. senta
D = 453
R. garmani
D = 291
R. radiata
D = 457
R. bigelowi
D = 1864
B. richardsoni
D = 2057
m o l s h
m o s h
m o s h
m o s h
m o s h
m o s h
m o s h

Figure 22. Relationship between the average number of alveoli on each ampulla and depth of occurrence. Mean depths for each species of skate is represented by a single point within the published depth ranges. Alveoli values consist of total, averaged counts for four of the capsule pairs (inner buccal values are not included).

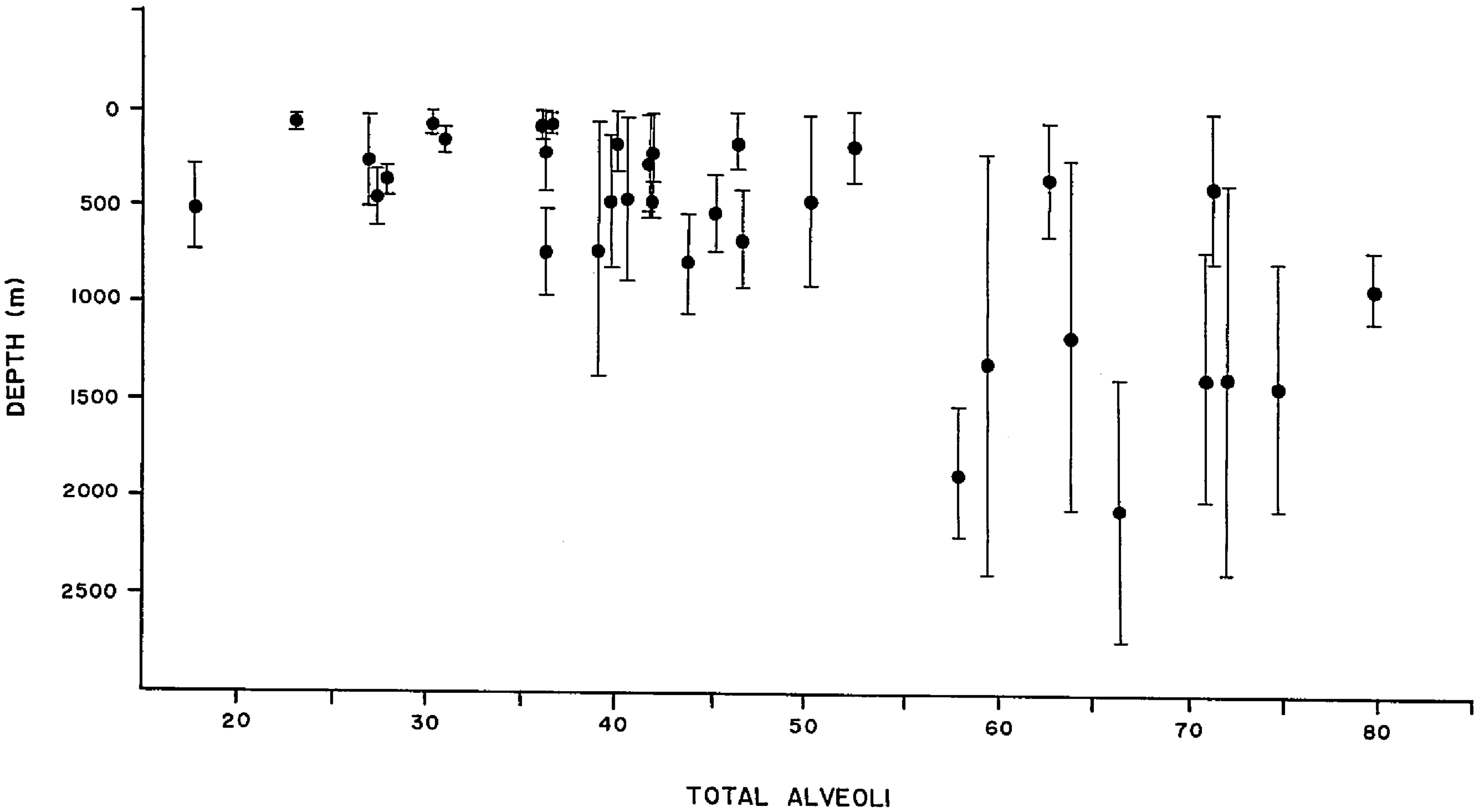

DEPTH (m)
0
500
1000
1500
2000
2500
20
30
40
50
60
70
80
TOTAL ALVEOLI

Figure 23. Comparison of ampullary width and size of specimen for both shallow and deep species of skate. Individual points represent all available specimens (both principal and ancillary species) and are the averaged widths for five ampullae for each specimen.

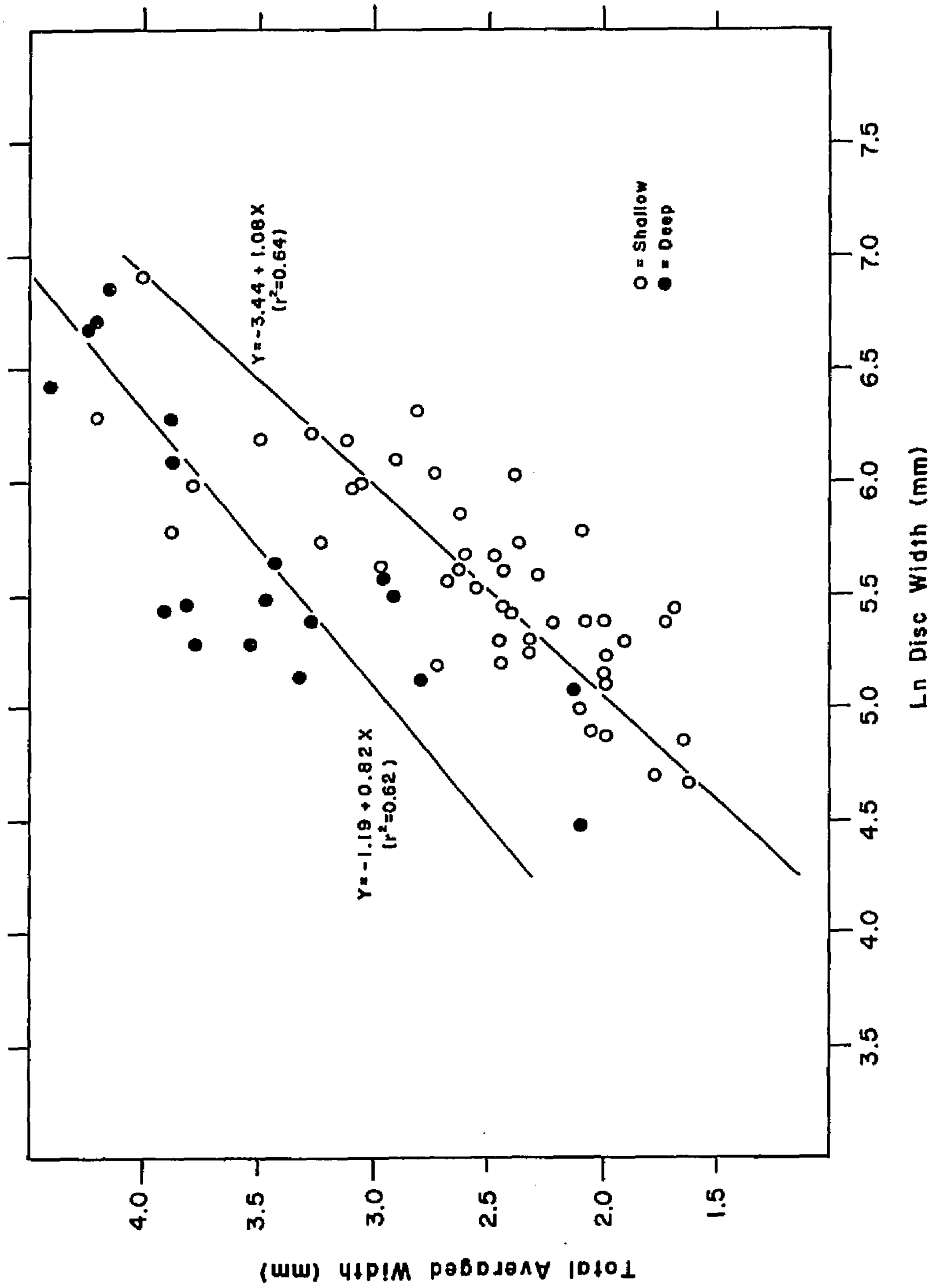
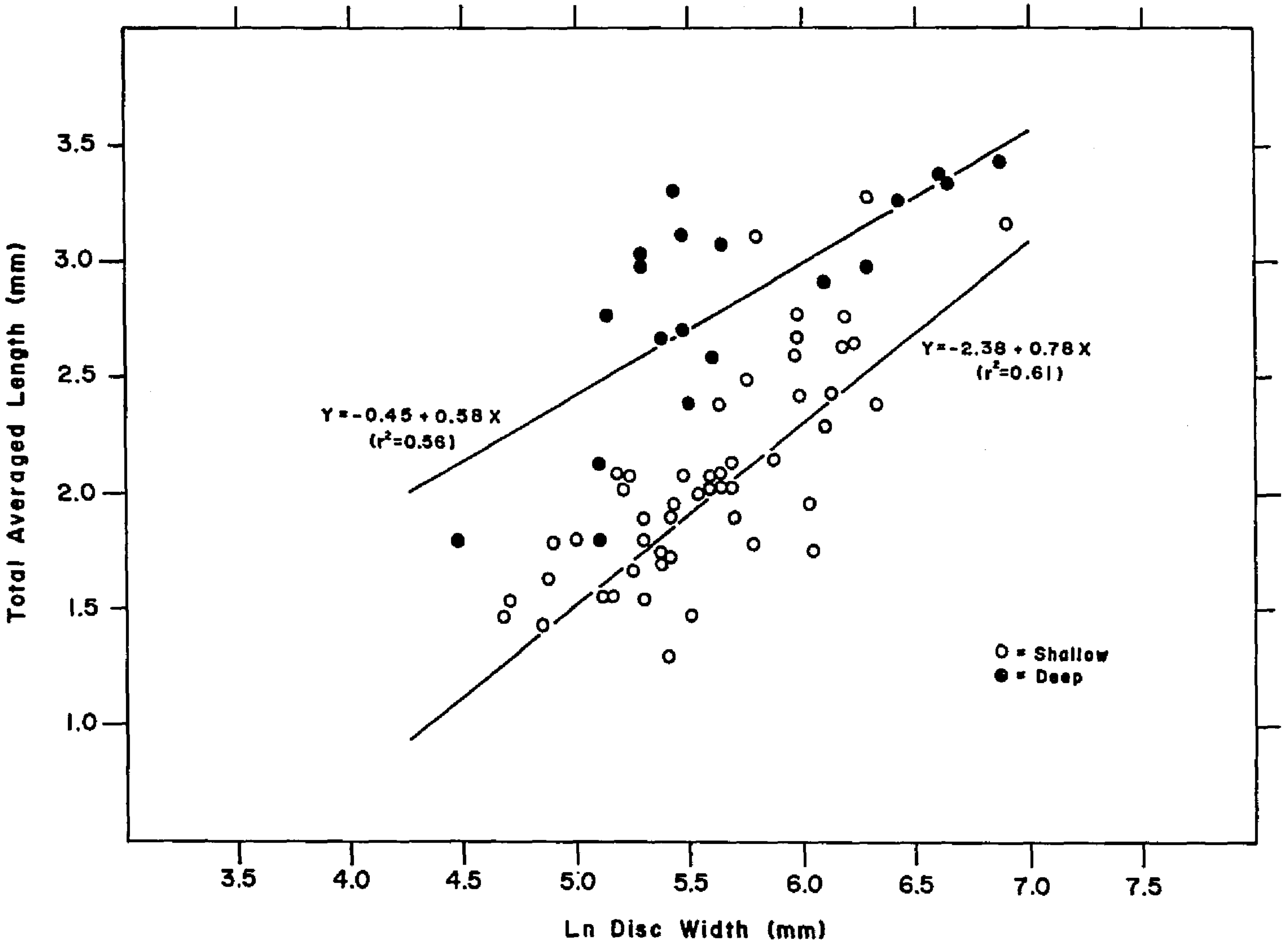

Y=-3.44+1.08X
(r²=0.64)
Y=-1.19+0.82X
(r²=0.62)
○ = Shallow
● = Deep
Total Averaged Width (mm)
4.0
3.5
3.0
2.5
2.0
1.5
Ln Disc Width (mm)
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5

Figure 24. Comparison of ampullary lengths and size of specimen for both shallow and deep species of skate. Individual points represent all available specimens (both principal and ancillary species) and are the averaged lengths for five ampullae for each specimen.


Total Averaged Length (mm)
3.5
3.0
2.5
2.0
1.5
1.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
Ln Disc Width (mm)
Y = -0.45 + 0.58 X
(r^2=0.56)
Y = -2.38 + 0.78 X
(r^2=0.61)
○ = Shallow
● = Deep

combining lengths or widths for all of the species in the shallow group or with those of the deep group (figures 23 and 24), it becomes apparent that the differences in their slopes are insignificant (width F= 1.91; d.f.= 1,64 and length F= 2.93; d.f.= 1,64) whereas their elevations are not (width F= 57.77**; d.f.1,65 and length F= 95.14**; d.f.= 1,65). Therefore, ampullae from deeper dwelling species are longer and wider than those from the shallower waters.

Since the sensory epithelium is restricted to the alveoli (Murray, 1974, Waltman, 1966), the increased lumenal surface area in deep-sea rajoids which results from the combined effect of increased overall size with greater numbers of alveoli indicates an increased population of receptor cells. This may have several major physiological implications. An increased number of receptor cells associated with each neuron is likely to reduce the stimulus threshold level. Since the release of neurotransmitter appears to based on a quanta-synapse relationship (Bennett and Clusin, 1978), with a certain number of quanta required for spike initiation; a lower stimulus strength should initiate the same impulse through the combined release of neurotransmitter from a larger number of receptor cells. Secondly, an increased number of neurons from each ampulla, may affect central nervous system processing through an increased number of fibers carrying a particular signal, and thereby the signal-to-noise ratio. Unfortunately, little information is available regarding the relationship between the number of neurons innervating each ampulla and the corresponding number of alveoli, nor is the material available from this study of sufficient histological quality to permit such a determination. Peabody (1897) lists an average value of 7-10 nerves innervating each ampulla in M. canis. The average number of nerve fibers (six) associated with each mandibular ampulla recorded for R. ocellata by Murray (1965) is substantially fewer (2 SD) than the average number of alveoli observed in this study (Table 15) for that capsule. Therefore increased receptor cells probably provide a combination of both effects.

Furthermore, an increased population of receptor cells may enhance the overall sensitivity of the ampulla. Spontaneous receptor cell activity increases the negativity of the ampullary lumen (Obara and Bennett, 1972) and thereby helps to excite surrounding receptor cells. Increased numbers of receptor cells may generally raise the lumenal negativity and as such increase the gain of the system in a manner similar to that proposed by Bennett and Clusin (1978) for more general tonic activity.

These proposed modifications in the receptor mechanism reflects differences in prey capture. The density of benthic organisms, as a potential prey source generally decreases with depth. Studies of the western North Atlantic infauna show this decrease to be an order of magnitude from the shallow inshore waters to the bottom of the continental slope and of a second order of magnitude onto the abyssal plain (Sanders and Hessler, 1979). Similar decreases are observed in several individual faunal components including the epibenthic macrofauna, such as fish and arthropods (Haedrich, et al., 1975), and macro-infauna (Carey, 1981). Moreover, general biomass significantly decreases from the shallow to the deep-sea (Marshall, 1979). The existence in an energy impoverished environment, such as the deep-sea, imposes energetic constraints on predators which may necessitate changes in feeding strategies. By searching the bottom from a position higher in the water column, a rajoid is presumably able to search a larger area of the bottom in the same amount of time when compared with its shallow water counterpart, but at the expense of weaker fields. Since impulse frequency is directly related to the relative field strength (Murray 1965, 1967), the increased sensitivity may help to compensate for this a situation. Similar types of modifications in other sensory systems from several taxa of deep-sea fish have been documented and are reviewed by Marshall (1979).

The alveoli structure of the shark ampullae is much simpler than that of the rajoids. However, differences between these two groups in the location and arrangement of individual alveoli prevent a comparison of the relative amount of sensory epithelium at this time. Within the galeoids, those two species which inhabit the shallow murky waters, *G. cuvieri* and *O. taurus*, appear to possess slightly increased numbers of alveoli on each ampulla whereas the only strictly pelagic species, *P. glauca*, exhibits somewhat fewer. Unfortunately, the range of species is not diverse enough at present to provide any clear trend. In addition, the impact of electro-orientation on the overall structure of the alveoli is uncertain. Clearly, these observations may only provide the beginnings for similar investigations into this group.

SUMMARY

A comparison of several aspects of the ampullary system in a wide variety of skates as well as within a subsequent group of galeoid sharks emphasizes the importance of electroreception in prey capture. The majority of pores (normally between 70% and 80%) are located on the ventral surface of the dorsoventrally flattened skates whereas they are more evenly distributed (between 50% and 62% ventral) on the more conically shaped head of the sharks. This appears to partially compensate for reduced visual input available from the dosally located eyes during the prey-oriented strike of the skates in contrast to the more laterally located eyes of the galeoids. Additional compensation for the loss of visual input is also apparent through the increased proportion of dorsally located pores (from 80.9% in the shallow to 73.2% in the deep-sea) on those skates which inhabit deeper aphotic waters.

Prey preferences are further reflected in the general pore distribution and overall resolution, as indicated by ventral pore densities. Piscivorous species of skates have previously been observed to initiate their feeding strike from relatively great distances (ca. 25 cm). Ventral pores cover the majority of the body surface but at a significantly reduced density, reflecting the more diffuse fields as well as possibly increased visual input. On the other hand, those skate species feeding predominantly on more sedentary prey, such as infaunal invertebrates, exhibit more reduced ventral pore distributions but

heavily concentrated around the mouth region. This may in turn reflect the more stationary feeding strategy employed by this group. Interspecific comparisons within the skates yield a inverse relationship between overall prey mobility and ventral pore densities. A similar trend is observed in the galeoid sharks. Those species which inhabit environments which potentially yield greater visual input, such as the clearer pelagic waters, or those species which are much less selective in their food habits possess greatly reduced ampullary systems.

Lastly, both the size and structure of the individual ampulla varies with respect to the bathymetric range of each skate species. Whereas the number of alveoli remains ontogenetically constant for each ampullary capsule, significantly greater numbers are found on ampullae from deeper dwelling species. Moreover, the overall size of the ampullae, as indicated by both individual lengths and widths, increase significantly in those species inhabiting the deep-sea. These differences yield correspondingly greater amounts of sensory epithelium and thereby further increase the signal - to - noise ratio. Such an increase may be one mechanism to allow these skates to search for prey items from a slightly higher position in the water column in order to cover larger amounts of the bottom.

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Table 1. Collection data for the seven principal species of skates (Rajidae) examined during this study.

Species	Subgenus (where known)	TL (mm)	Disc Width (mm)	Sex	Coll. #[1]	Locality	Depth (M)
Bathyraja richardsoni	-	752	538	F	VIMS 03342	36°38'N;74°28'W	1700
	-	1238	829	M	St J S0273	41°45'N;65°06'W	2100-2190
	-	1297	830	M	" S0276	43°03'N;65°06'W	1810-2010
	-	1410	963	F	" S0254	41°11'N;65°53'W	2160-2230
	-	1491	1000	F	" S0255	54°52'N;51°59'W	2190-2220
Raja bigelowi	Rajella	171	89	F	VIMS 03346	37°09'N;73°55'W	2100
	"	340	171	F	" 03347	36°13'N;74°30'W	1600
	"	380	196	M	" 03347	36°13'N;74°30'W	1600
	"	389	199	M	" 05562	36°40'N;74°25'W	1645
	"	440	245	M	" uncat	37°02'N;73°59'W	2257
	"	444	230	M	" 05562	36°40'N;74°25'W	1645
	"	445	235	M	" 00756	39°09'N;72°12'W	1280
Raja eglanteria	Raja	427	276	M	VIMS uncat	36°47'N;75°55'W	8-13
	"	437	268	M	" uncat	36°47'N;75°55'W	8-13
	"	550	395	F	" uncat	36°47'N;75°55'W	8-13
	"	584	393	M	" uncat	36°47'N;75°55'W	8-13
	"	605	414	F	" uncat	37°06'N;76°45'W	4-7
	"	653	424	F	" 03041	36°56'N;76°15'W	7
Raja garmani	-	265	134	F	VIMS 01369	34°37'N;75°41'W	280
	-	269	130	F	" 01369	34°37'N;75°41'W	280
	-	280	149	M	" 01369	34°37'N;75°41'W	280
	-	359	190	M	" 01370	37°08'N;74°34'W	175
	-	364	201	M	" 01369	34°37'N;75°41'W	280
	-	385	180	F	" uncat	36°45'N;74°39'W	186
	-	412	230	F	" 01400	40°12'N;70°54'W	137-143

Species	Subgenus (where known)	TL (mm)	Disc Width (mm)	Sex	Coll. #[1]	Locality	Depth (M)
Raja laevis	Dipturus	430	295	F	VIMS 00185	38°08'N;74°35'W	35
	"	532	397	M	MCZ uncat	-	-
	"	537	355[4]	M	USNM 25837	-	-
	"	675	501	F	MCZ 36302	Off Nantucket	-
	"	700	490	F	VIMS 02345	43°55'N;68°38'W	80
Raja radiata	Amblyraja	192	128	F	VIMS 00796	41°03'N;66°49'W	73
	"	310	202	F	" 00796	41°03'N;66°49'W	73
	"	322	189	M	" uncat	36°43'N;74°37'W	642
	"	322	199	M	" 00796	41°03'N;66°49'W	73
	"	431	307	M	" 02284	37°04'N;74°32'W	550-800
	"	705	491	M	" uncat	37°08'N;74°32'W	534
Malacoraja[5] senta	-	177	110	M	VIMS 02283	46°56'N;60°01'W	157
	-	192	107	M	" 02283	46°56'N;60°01'W	157
	-	300	173	F	" 02110	46°21'N;60°35'W	110-113
	-	375	375	M	MCZ uncat	Off New England	-
	-	469	469	F	VIMS uncat	38°45'N;73°01'W	375
	-	513	513	F	" 01538	43°19'N;61°09'W	128-137

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[1] Abbreviations are as follows: VIMS, Virginia Institute of Marine Science; St J, Newfoundland Biological Station; MCZ, Museum of Comparative Zoology; and USNM, National Museum of Natural History.

[2] Total length of this specimen had to be estimated due to a damaged tail.

[3] Jaws were absent from this specimen and therefore pore counts from the "J" subarea and the examination of any ampullae from the mandibular capsules were not possible.

[4] Disc width had to be estimated due to the poor condition of the pectoral fin margin.

[5] This species was recently placed in this newly erected genus.

Table 2. Collection data for the ancillary species of skates (Rajidae) examined during this study.

Species	Subgenus (where known)	TL (mm)	Disc Width (mm)	Sex	Coll. #[1]	Locality	Depth (M)
Anacanthobatis longirostris	-	429	250	M	VIMS uncat	29°00'N;79°47'W	624
Bathyraja kincaidi	-	464	298	F	MML-DB-60 (0406)	35°27'N;121°60'W	120-220
Bathyraja spinacauda	-	1479	996	F	St J S0257	47°01'N;44°13'W	540-562
Gurgesiella atripinna	Fenestraja[2]	221	144	F	VIMS 02240	34°09'N;75°45'W	480-990
Gurgesiella ishiyamai	Fenestraja[2]	220	104	M	UMML 13832	24°24'N;80°22'W	805
	"	317	162	F	UMML 13832	24°24'N;80°22'W	805
Gurgesiella plutonia	Fenestraja[2]	233	112	M	VIMS uncat	29°10'N;79°59'W	428
	"	246	111	F	VIMS 06682	33°34'N;76°34'W	427
Raja agassizi	Atlantoraja	373	218	M	VIMS uncat	29°52'S;49°37'W	-
Raja alba	Rostroraja	302	221	M	RUSI 8065	East Province, S. Afr.	-
Raja bathyphila	Rajella	280	161	M	ISH 177d/73	65°03'N;33°04'W	1503-1535
Raja binoculata	Dipturus	228	181	F	-	-	-
Raja bullisi	Dipturus	173	126	F	UMML 1110	24°29'N;83°27'W	388
Raja clarkii	Leucoraja	438	272	M	USNM uncat	7°26'N;53°16'W	604-631
	"	760	450	M	USNM 205389	"off Mexico"	430
	"	845	558	M	USNM 205391	"off Florida"	907
Raja clavata	Raja	320	249	F	RUSI 7850	"Algoa Bay"	-
	"	342	263	F	ISF 6/62	50°31'N;01°20'E	32
Raja doutrei	Dipturus	372	265	M	UMML 15151	4°20'N;09°26'W	732
Raja erinacea	Leucoraja	-	-	M	VIMS uncat	42°19'N;65°21'W	120
Raja flavirostris	Dipturus	287	224	F	VIMS uncat	41°57'S;59°45'W	80
Raja floridana	Dipturus	280	310	F	UMML 11018	29°33'N;80°11'W	300-304

Species	Subgenus (where known)	TL (mm)	Disc Width (mm)	Sex	Coll. #[1]	Locality	Depth (M)
Raja fyllae	Rajella	437	239	F	MCZ 38363	42°17'N;65°01'W	494-622
	"	484	270	M	MCZ 38364	-	-
Raja hyperborea	Amblyraja	771	617	F	MCZ 36551	-	-
Raja jenseni	-	610	448	F	MCZ 37899	-	-
Raja mirelatus	Raja	356	219	M	UMML-SOSC 535	30°32'N;34°47'E	59
	"	444	275	F	UMML 21309	4°32'N; 5°07'E	64-119
Raja ocellata	Leucoraja	258	167	M	VIMS 01657	41°14'N;68°28'W	53
	"	448	274	F	VIMS 00479	38°27'N;74°39'W	33
Raja olseni	Dipturus	350	240	M	USNM uncat	27°47'N;95°21'W	183
	"	400	397	F	USNM uncat	19°28'N;92°55'W	613
Raja oxyrhynchus	Dipturus	301	200	F	USNM 28468	"Italy"	-
Raja platana	Atlantoraja	602	447	F	USNM 55578	"Argentina"	-
Raja porosa	Okamejei	481	326	F	USNM 86923	"China"	-
Raja rhina	Dipturus	742	535	F	USNM 116319	"Shelikof Strait"	46-110
Raja sadowskii	Rajella	334	165	F	ISF 1973/68	22°30'S;40°07'W	800
Raja teevani	Dipturus	203	152	F	UMML 13677	24°28'N;83°26'W	384
		565	460	F	MCZ 41902	16°38'N;79°53'W	914
Raja texana	Raja	381	234	M	USNM 155731	28°28'N;91°14'W	58
	"	390	252	M	TAM 2481.1	"off Freeport"	46
Malacoraja fuliginea	-	380	170	F	MCZ 47835	10°56'N;67°38'W	1079
Malacoraja purpuriventralis	-	385	218	F	USNM uncat	7°31'N;53°19'W	604-713
	"	482	281	M	USNM uncat	7°21'N;53°19'W	604-713
Malacoraja spinacidermis	Malacoraja	298	186	M	MCZ 38276	42°40'N;63°52'W	759-768

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[1] Abbreviations are as follows: MML, Moss Landing Marine Laboratories; UMML, Rosenstiel School of Marine and Atmospheric Science; RUSI, J. L. B. Smith Institute of Ichthyology; ISH, Institut für Seefischerei; TAM, Texas Cooperative Wildlife Collection. Remaining abbreviations as in Table 1.

[2] See footnote #5 of Table #1.

Table 3. Morphometric characteristics for the seven principal species of skates (Rajidae) examined in this study.

Species	Maximum TL (mm)	Ref.	Surface Area (cm^2)	Drawing Ref.	Mouth Width[1] (as % TL)	Ref.
Bathyraja richardsoni	1740	Templeman, 1973	7067.5	Garrick, 1961	11.4[2] 13.8-11.4[3]	Garrick, 1961 Templeman, 1973
Raja bigelowi	467-500[4]	Stehmann, 1978	389.9	Bigelow & Schroeder, 1953a	4.9-6.5	Stehmann, 1978
Raja eglanteria	762-940[5]	Bigelow & Schroeder, 1953b	1169.0-1773.2	Hildebrand & Schroeder, 1927	7.5-8.7	Bigelow & Schroeder, 1953a
Raja garmani	432	Bigelow & Schroeder, 1953a	301.5[6]	Bigelow & Schroeder, 1953a	5.7-5.9	Bigelow & Schroeder, 1953a
Raja laevis	1473	Bigelow & Schroeder, 1953a	4388.6	Leim & Scott, 1966	9.2-9.8	Bigelow & Schroeder, 1953a
Raja radiata	1020	Bigelow & Schroeder, 1953a	2410.2	Bigelow & Schroeder, 1953	10.1-10.7	Bigelow & Schroeder, 1953a
Malacoraja senta	610	Bigelow & Schroeder, 1953a	751.1	Leim & Scott, 1966	7.3-8.1	Bigelow & Schroeder, 1953a

[1] Mouth width is defined as the distance between the lateral skin folds on each side of the mouth opening.

[2] Garrick's (1961) measurement is based on an estimated total length due to the holotype's damaged tail.

[3] Measurements are expressed as percentages of length from the snout to the anterior origin of the first dorsal fin.

[4] The largest actual specimen listed by Stehmann (1978) is 467 mm TL, but estimates the maximum size as up to 500 mm TL.

[5] The surface area reported here is for size at sexual maturity (400 mm TL).

Table 4. Synopsis of natural history information for the seven principal species of skates (Rajidae) examined during this study.

Species	Mean Depth (M)[1,2] (range)	Ref.	Food Habits	Ref.
Bathyraja richardsoni	2057.5 (1370-2745)	Templeman, 1973 Musick, 1975	Holotype taken on "mackerel baits"[3]	Garrick, 1961
			"bait used was mainly squid (*Loligo* spp.), although mackerel, herring and rarely other fish were tried."[3]	Forster, 1968
			"by far the greatest portion of the food appears to be fish with, as is usual for skates, some shrimp and bottom invertebrates."	Templeman, 1973
			"(*Coryphaenoides armatus*)....from *B. richardsoni*..."	Campbell et al, 1980
Raja bigelowi	1864.0[4,5] (1528-2200)	Stehmann, 1978	benthic amphipods[6]	-
Raja eglanteria	164.5 (0-329) 111$^+$	Bigelow & Shroeder, 1953a Edwards et al, 1962 McEachran & Musick, 1975	"crabs, shrimp, and fish; ---(*Callinectes*) ...(*Synodus*)"	Hildebrand & Schroeder, 1927
			squid, "Butterfish (*Poronotus*) and scup (*Stenotomus*) are a dominant food during September and October..."	Bigelow & Schroeder, 1953a
			"invertebrates made up over 97% of the total number of items"	Fritz & Daiber, 1963
			"*Crangon septemspinosa* accounted for more than 70%..."	
Raja garmani	291.0) (33-549)	McEachran et al,1975 Bigelow & Schroeder, 1953b	None	-
Raja laevis	215.0 (0-430)	Bigelow & Schroeder, 1953a	"...bivalve molluscs, squid, rock crabs, lobsters, shrimp, worms and...spiny dogfish, alewifes, herring, butterfish, sand lance, cunner, hake, and flatfish."	Leim & Scott, 1966
			"...worms, various crustaceans...large crabs, lobsters, shrimp, squid, and on fish." (see fish list)	Bigelow & Schroeder, 1953b
			Adds isopods, bivalves (*Yoldia* & *Ensella*) and large gastropods (*Buccinum* & *Lunatia*).	Bigelow &
Raja radiata	457.0 (18-896) 238-239[7]	Bigelow & Schroeder, 1953a McEachran et al, 1975	"shrimp, spider crabs, see anemones, and small fishes."	Leim & Scott, 1966
			Adds hydroids, worms, gammarids and *Ammodytes* (from various areas).	Bigelow & Schroeder, 1953a
			400 mm TL fed on amphipods, 400 mm TL fed on polychaetes and decapods. "Fishes were a major component of the skates above 70 cm TL." (see text comparison with *R. senta*)	McEachran et al, 1976

Species	Mean Depth (M)[1,2] (range)	Ref.	Food habits	Ref.
Malacoraja senta	452.5 (31-874)	McEachran et al, 1975	Decapods, Euphausids, amphipods and mysids. "Fishes and polychaetes contributed little ..." "...consumed mostly epifaunal crustaceans and rarely infaunal organisms such as polychaetes."	McEachran et al, 1976

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[1] Mean depth is defined here as the average of the deepest and shallowest recorded depths.

[2] Depth range was determined from the shallowest end of the shallow range and the deepest end of the deep range.

[3] Caution should be used here because while the bait indicates that certain items may be ingested, it does not necessarily mean that they are normally included as natural prey items.

[4] Stehamnn (1978) notes that only a few specimens (4 juveniles) were found between 672-897 M and feels this species migrates there only to reproduce (this accounts for this descrepency with Table 1).

[5] Bigelow and Schroeder's (1953a) range is omitted due to a possible confusion in identification.

[6] Identified by G. Sedberry.

[7] McEachran's (1975) records are just for the shelf depths between Nova Scotia and Cape Hatteras; the range listed here is for both the average total depth range and the depth range at which it is most abundant.

Table 5. Collection data for the five principal species of galeoid sharks examined during this study.

Species	TL (cm)	SL (cm)	Sex	Locality
<u>Carcharhinus obscurus</u>	98	73	F	36°56'N; 76°01'W
	98	76	F	36°56'N; 76°01'W
	105	75	F	36°55'N; 75°42'W
	109	77	M	36°55'N; 75°42'W
	160	-	M	37°12'N; 76°00'W
	170	-	F	37°12'N; 76°00'W
	182	-	F	37°12'N; 76°00'W
	197	-	M	37°03'W; 74°37'W
	217	-	F	36°55'N; 75°42'W
<u>Carcharhinus plumbeus</u>	117	-	F	37°12'N; 76°00'W
	88	66	M	37°12'N; 76°00'W
	120	86	F	36°55'N; 75°42'W
	136	-	M	37°12'N; 76°00'W
	131	-	F	37°03'N; 74°37'W
	-	127	F	37°12'N; 76°00'W
	-	116	F	37°00'N; 75°21'W
	208	153	F	36°55'N; 75°42'W
	211	-	F	37°03'N; 74°37'W
<u>Galeocerdo cuvieri</u>	173	123	F	37°07'N; 75°41'W
	204	149	F	37°00'N; 75°21'W
	213	152	M	37°00'N; 75°21'W
	271	-	F	37°00'N; 75°21'W
	Fork = 198		F	37°17'N; 75°46'W
<u>Odontaspis taurus</u>	247	186	M	37°00'N; 75°21'W
	248	-	M	37°00'N; 75°21'W
	235	-	M	37°00'N; 75°21'W
	ca. 180	-	M	37°00'N; 75°21'W
<u>Prionace glauca</u>	281	-	M	37°03'N; 74°37'W
	165	-	M	37°03'N; 74°37'W
	181	-	M	37°03'N; 74°37'W
	202	-	F	37°03'N; 74°37'W
		- Not Available -		Off Bermuda

Table 6. Morphometric characteristics of the ancillary species of skates (Rajidae) examined in this study.

Species	Maximum TL (mm)	Ref.	Surface Area (cm^2)	Drawing Ref.	Mouth Width[1] (as % TL)	Ref.
Anacanthobatis longirostris	745	Bigelow & Schroeder, 1968	1246.7	Bigelow & Schroeder, 1962	4.9-5.3	Bigelow & Schroeder, 1962 Bigelow & Schroeder, 1968
Bathyraja kincaidii	840	Hart, 1973	1326.4	Hart, 1973	5.0-6.9	Garman, 1908 Schultz, 1937
Bathyraja spinacauda	1720	Bigelow & Schroeder, 1953a	7292.0	Bigelow & Schroeder, 1953a	8.1	Bigelow & Schroeder, 1953a
Gurgesiella atripinna	291	Bigelow & Schroeder, 1962	103.4	Bigelow & Schroeder, 1953a	5.0-5.3	Bigelow & Schroeder, 1953a
Gurgesiella ishiyamai	362	Bigelow & Schroeder, 1962	213.1	Bigelow & Schroeder, 1962	5.3	Bigelow & Schroeder, 1962
Gurgesiella plutonia	275	Bigelow & Schroeder, 1968	87.1	Bigelow & Schroeder, 1953a	5.1-5.6	Bigelow & Schroeder, 1953a
Raja agassizi	490	Figureiredo, 1977	515.5	Figureiredo, 1977	5.2	None[1]
Raja alba	2286[2]	Wallace, 1967	9059.4	Wheeler, 1969	8.1-10.1	Hulley, 1970
Raja bathyphila	900	Stehmann, 1978	1487.4	Stehmann, 1978	6.2-9.1	Stehmann, 1978
Raja binoculata	2438	Miller & Lea, 1972	14990.2	Hart, 1973	None	-
Raja clarkii	747[3]	Bigelow & Schroeder, 1958	1713.1	Bigelow & Schroeder, 1958	8.7	Bigelow & Schroeder, 1958
Raja clavata	1100	Soljan, 1963	2879.6	Wallace, 1967	8.5 (SE=0.5)	Wallace, 1967
Raja doutrei	931	Hulley, 1970	2317.1	Blache et al., 1970	8.1-9.9	Cadenat, 1960 Hulley, 1970
Raja erinacea	530	Bigelow & Schroeder, 1953a	-[4]	-	8.0-8.2	Bigelow & Schroeder, 1953a
Raja flavirostris	720	Norman, 1937	1663.0	Bigelow & Schroeder, 1958	None	-

Species	Maximum TL (mm)	Ref.	Surface Area (cm^2)	Drawing Ref.	Mouth Width[1] (as % TL)	Ref.
Raja floridana	772[5]	Bigelow & Schroeder, 1962	1413.2	Bigelow & Schroeder, 1962	8.3	Bigelow & Schroeder, 1962
Raja fyllae	555[6]	Bigelow & Schroeder, 1954b	433.0[6]	Bigelow & Schroeder, 1953a	5.8	Bigelow & Schroeder, 1953a
Raja hyperborea	870	Templeman, 1965	1600.8	Bigelow & Schroeder, 1953a	12.3-12.5	Bigelow & Schroeder, 1953a
Raja jenseni	850	Bigelow & Schroeder, 1953a	1609.6	Bigelow & Schroeder, 1953a	12.5	Bigelow & Schroeder, 1953a
Raja mirelatus	600	Lythgoe & Lythgoe, 1975	608.5	Wallace, 1967	8.3 (SE=0.75)	Wallace, 1967
Raja ocellata	1090	Bigelow & Schroeder, 1953a	-[7]	-	9.9-10.1	Bigelow & Schroeder, 1953a
Raja olseni	568	Bigelow & Schroeder, 1962	757.6	Bigelow & Schroeder, 1953a	7.0-8.2	Bigelow & Schroeder, 1951 Bigelow & Schroeder, 1953a
Raja porosa	495	Ishiyama, 1958	601.4	Lindberg & Legeza, 1967	None	-
Raja rhina	1372	Miller & Lea, 1972	4153.6	Hart, 1973	7.9-8.2	-[8]
Raja sadowskii	630	Krefft & Stehmann, 1974	749.9	Krefft & Stehmann, 1974	5.9-6.9	Krefft & Stehmann, 1974
Raja teevani	840	Bigelow & Schroeder, 1968	1608.3	Bigelow & Schroeder, 1953a	7.0-7.7	Bigelow & Schroeder, 1953a
Raja texana	610	Hoese & Moore, 1977	772.6	Bigelow & Schroeder, 1953a	7.5	Bigelow & Schroeder, 1953a
Malacoraja fuliginea	445	Bigelow & Schroeder, 1968	295.7	Bigelow & Schroeder, 1954a	5.3-7.8	Bigelow & Schroeder, 1968
Malacoraja purpuriventralis	510	Bigelow & Schroeder, 1962	460.8	Bigelow & Schroeder, 1962	7.3	Bigelow & Schroeder, 1962

Species	Maximum TL (mm)	Ref.	Surface Area (cm^2)	Drawing Ref.	Mouth Width[1] (as % TL)	Ref.
Malacoraja spinacidermis	639	Hulley, 1970	826.8	Bigelow & Schroeder, 1953a[9]	8.0-9.2	Bigelow & Schroeder, 1953a[9] Templeman, 1965

[1] Measurement from the specimen examined during this study.

[2] Wallace's (1967) records indicate that this species may attain a still larger size than is recorded here.

[3] This species attains a larger size than listed here (USNM specimen 205391 examined during this study was 845 mm TL).

[4] Surface areas were not calculated for this species, rather the ventral pore densities were taken from Raschi (1978).

[5] The maximum TL listed here is from an immature male specimen, and therefore, both the maximum TL and surface area can be expected to be somewhat greater.

[6] Bigelow and Schroeder (1953a) feel that this species may attain a greater size than is presently recorded.

[7] See footnote #1.

[8] Listed under the junior synonym, *Raja mollis* (see Hulley and Stehmann, 1970).

[9] See footnote #4.

Table 7. Unilateral counts of ampullae from the seven principal species of skates (Rajidae) examined in this study.

	Superficial Ophthalmic		Outer Buccal		Inner Buccal		Hyoid		Mandibular		Total	
Species	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Bathyraja richardsoni	80.6	12.4	39.0	2.6			136.6	17.8	10.8	4.2	267.0	27.2
Raja bigelowi	74.7	4.6	43.7	6.6			144.0	14.0	21.9	7.3	284.3	18.8
Raja eglanteria	116.8	11.2	110.7	18.4			151.7	15.9	24.8	3.7	404.0	34.7
Raja garmani	63.0	10.8	42.0	7.3			93.4	13.6	14.3	4.0	212.7	31.6
Raja laevis	65.6	14.5	179.0	10.7	101.8	11.8	344.2	32.7	49.2	4.8	739.8	35.4
Raja radiata	116.8	15.9	82.2	12.4			188.5	19.8	28.0	2.4	415.5	32.2
Malacoraja senta	53.0	5.2	32.2	3.4			80.0	8.8	18.2	2.5	183.3	9.3

Table 8. Distribution of somatic pores on the principal species of skates (surface areas from Table 3).

Species	Ventral Subtotal	Ventral %	Ventral Density (pores/cm)	Dorsal Subtotal	Dorsal %	Dorsal Density (pores/cm)	Total pores
Bathyraja richardsoni	365.8 ± 41.4	64.2	0.05	204.4 ± 46.4	35.8	0.03	570.2 ± 45.2
Raja bigelowi	375.7 ± 46.1	73.3	0.96	136.9 ± 16.2	26.7	0.35	512.6 ± 57.2
Raja eglanteria	657.0 ± 35.7	83.7	0.37	127.7 ± 9.7	16.3	0.07	784.7 ± 42.2
Raja garmani	284.4 ± 61.8	74.9	0.94	95.1 ± 13.3	25.1	0.32	379.6 ± 72.7
Raja laevis	1501.0 ± 66.3	88.8	0.34	189.6 ± 23.6	11.2	0.04	1690.6 ± 87.5
Raja radiata	630.5 ± 46.4	80.5	0.26	153.2 + 6.5	19.5	0.06	783.7 ± 49.3
Malacoraja senta	289.5 ± 22.2	70.7	0.39	120.2 ± 12.4	29.3	0.16	409.7 ± 25.0

Table 9. Unilateral counts of ampullae from each of the separate innervation areas as described for the five galeoid sharks. Numbers are based only on one dissection specimen from each species.

	Superficial Ophthalmic I	Superficial Ophthalmic II	Superficial Ophthalmic III	Outer Buccal	Mandibular	Total Ampullae	Total Pores
C. obscurus							
Dorsal	102	132	97	108	--	439	431.0
Ventral	5	219	54	155	19	452	517.4
Total	107	351	151	263	19	891	948.4
C. plumbeus							
Dorsal	135	184	179	140	--	638	591.8
Ventral	18	260	89	139	21	527	599.4
Total	153	444	268	279	21	1164	1191.2
G. cuvieri							
Dorsal	41	43	28	67	--	179	196.3
Ventral	--	50	25	104	22	201	296.5
Total	41	93	53	171	22	380	492.8
P. glauca							
Dorsal	17	57	38	26	--	138	179.7
Ventral	--	106	28	68	13	215	290.9
Total	17	163	66	94	13	353	470.6
O. taurus							
Dorsal	29	84	35	84	--	232	243.4
Ventral	--	113	19	73	18	223	324.1
Total	29	197	54	157	18	455	567.5

Table 10. Somatic pore counts (range, mean and standard deviation) for the principal species of skates. Subareas are from Raschi (1978), single values are presented for bilaterally arranged subareas.

Species	A	B	C	D	E	K	F	G	H	I	J
Rathyraja richardsoni	35-64.5	14-22	5-15	9.5-20	13-20.5	8-12	22-33.5	121-164	38.5-56.5	24.5-36.5	18-34
	45.5	16.4	7.8	12.1	16.1	10.0	27.4	139.6	44.9	30.5	23.3
	11.2	3.3	4.1	4.4	3.3	1.9	4.7	19.9	7.7	5.4	9.2
Malacoraja senta	26-34	6.5-8	2-4.5	3-6.5	10.5-15.5	3-7	11.5-15	92-120	42.5-54.5	12-14.5	28-42
	29.6	7.6	3.2	4.9	12.7	4.3	12.6	105.5	48.5	12.8	36.3
	3.5	0.8	0.9	1.2	2.1	1.4	1.4	13.8	5.2	0.9	5.0
Raja bigelowi	25-41.5	8-10	2-5	6-8.5	8-12	4-8	29-46	83-134	40-61	19-35.5	26-48
	35.8	8.7	4.1	6.4	10.5	6.0	37.8	107.3	49.3	27.6	39.0
	5.7	1.0	1.0	1.0	1.6	1.5	6.2	16.5	7.8	5.0	8.1
Raja eglanteria	26.5-32	7-11	5-9	7.5-10	6-9	7-12	25-54	223-262	105.5-133.5	35-46	30-51
	27.9	8.2	6.9	8.6	7.2	10.2	37.6	233.8	116.8	38.3	38.0
	1.6	1.7	1.7	9.0	1.1	1.8	10.9	14.5	9.5	4.1	7.3
Raja garmani	20.5-31.5	4.5-5	3.5-6	3-6	5.5-12.5	3-4	17-37.5	61-123	27-58.5	15-25.5	14-38
	23.7	4.7	5.0	4.1	8.1	3.7	24.9	86.9	38.2	21.4	27.2
	4.0	0.4	0.9	0.9	2.4	0.5	6.4	22.4	11.0	4.6	7.9
Raja laevis	32-49	8-10	14.5-22	8-12	7-15.5	9-21	92-107	327-390	393.5-460.5	-	79-112
	41.3	9.3	17.4	9.7	12.1	14.8	100.7	367.2	419.0		94.4
	7.3	0.8	3.4	1.6	3.1	6.1	6.4	24.2	29.1		13.2
Raja radiata	32.5-43	6-8.5	7-9.5	7-9.5	11-14	5-11	38.5-71	170-275	83-104	25-42.5	50-64
	37.6	7.2	8.3	7.7	12.3	7.3	54.8	209.0	90.8	37.1	56.0
	3.4	1.0	1.1	1.1	1.1	2.1	11.4	35.6	7.9	6.3	4.9

Table 11. Somatic pore counts (range, mean and standard deviation) for the ancillary species of skates. Subareas are from Raschi (1978), single values are presented for bilaterally arranged subareas.

Species	A	B	C	D	E	K	F	G	H	I	J
Anacanthobatis longirostris	30.5	5.5	4.0	-	9.0	6.0	9.0	411.0	380.5	-	47.0
Bathyraja kincaidii	50.5	11.0	9.5	7.0	11.5	-	51.5	174.0	69.5	30.5	35.0
Bathyraja spinacauda	45.0	10.0	14.5	8.5	11.0	4.0	46.5	229.0	139.5	55.0	30.0
Gurgesiella atripinna	36.5	7.5	3.0	5.5	8.0	3.0	13.0	99.0	37.5	24.0	34.0
Gurgesiella ishiyamai	28.5	8.5	1.5	4.5	5.5	3.0	9.0	42.0	16.5	21.0	16.0
Gurgesiella plutonia	26.5	6.0	1.0	2.5	5.0	-	6.0	33.5	10.0	14.0	17.0
Raja agassizi	54.0	11.5	-	5.5	8.5	7.0	38.5	126.0	116.0	25.5	42.0
Raja alba	26.0	10.5	6.5	5.5	7.5	9.0	20.5	114.0	69.0	19.0	42.0
Raja bathyphila	41.0	11.0	6.0	12.5	12.0	7.0	47.0	233.0	90.0	53.5	48.0
Raja binoculata	44.5	13.0	16.0	12.0	14.5	13.0	57.5	286.0	227.5	-	64.0
Raja clarkii	130.3	4.3	4.3	5.7	11.2	5.0	24.2	85.0	47.3	25.7	16.7
Raja clavata	36.0	9.8	12.8	8.5	12.0	7.0	47.5	198.5	120.8	46.3	64.5
Raja doutrei	39.5	11.0	17.5	5.0	11.5	8.0			- No Count Available -		
Raja flavirostris	39.0	12.0	11.5	8.0	12.5	9.0	58.5	264.0	292.5	-	102.0
Raja floridana	32.0	10.5	12.0	5.5	10.5	8.0	42.0	193.0	199.5	-	66.0
Raja fyllae	42.5	7.5	7.8	7.5	10.8	4.0	30.8	103.0	40.3	30.8	43.0

Species	A	B	C	D	E	K	F	G	H	I	J
Raja hyperborea	33.5	11.0	8.0	9.5	10.5	6.0	28.5	164.0	49.0	30.0	32.0
Raja jenseni	35.0	12.5	10.0	11.5	11.0	3.0	27.5	159.0	55.0	39.0	40.0
Raja mirelatus	34.5	10.0	8.0	5.8	10.8	6.0	34.8	174.0	84.5	49.3	47.0
Raja olseni	30.0	13.0	12.0	7.5	11.0	6.0	62.0	300.0	328.5	25.0	52.0
Raja oxyrhynchus	82.0	15.5	45.5	12.0	13.5	44.0		- No Count Available -			
Raja platana	53.5	17.0	7.0	8.5	11.0	6.0		- No Count Available -			
Raja porosa	48.5	17.5	7.5	9.0	15.0	8.0	21.0	183.0	103.0	25.0	43.0
Raja rhina	41.0	11.0	15.0	19.0	8.5	13.0	71.0	309.0	345.0	-	73.0
Raja sadowskii	37.0	8.0	4.0	8.0	10.0	4.0	39.0	120.0	53.5	31.0	38.0
Raja teevani	11.0	5.5	12.0	5.0	7.0	6.0	9.5	149.0	95.0	-	28.0
Raja texana	23.9	9.0	4.8	6.5	6.3	5.0	12.8	136.5	64.3	13.0	47.0
Malacoraja fuliginea	41.0	10.0	10.5	7.0	15.0	-	37.0	145.0	51.5	34.0	42.0
Malacoraja purpuriventralis	41.3	10.8	8.3	11.0	14.0	6.5	58.8	245.0	91.8	50.3	67.5
Malacoraja spinacidermis	32.5	6.5	2.0	5.5	10.5	5.0	9.5	77.0	39.0	13.5	34.0

Table 12. Distribution of somatic pores on the ancillary species of skates (pore totals from Table 11, surface areas from Table 6).

Species	Ventral Subtotal	Ventral %	Ventral Density (pores/cm)	Dorsal Subtotal	Dorsal %	Dorsal Density (pores/cm)	Total Pores
Anacanthobatis longirostris	1238	92.3	0.99	104	7.7	0.08	1342
Bathyraja kincaidii	512	74.1	0.39	179	25.9	0.13	691
Bathyraja spinacauda	741	80.4	0.10	181	19.6	0.02	922
Gurgesiella atripinna	282	69.5	2.73	124	30.5	1.20	406
Gurgesiella ishiyamai	152.5	60.6	0.72	99	39.4	0.46	251.5
Gurgesiella plutonia	110	57.6	1.26	81	42.4	0.93	191
Raja agassizi	526	76.0	1.02	166	24.0	0.32	692
Raja alba	373	75.5	0.04	121	24.5	0.01	494
Raja bathyphila	662	79.4	0.45	172	20.6	0.12	834
Raja binoculata	920	81.2	0.06	213	18.8	0.01	1133
Raja clarkii	296	48.4	0.17	315	51.6	0.18	611
Raja clavata	692	80.7	0.24	165	19.3	0.06	857
Raja flavirostris	1068	85.9	0.64	175	14.1	0.11	1243
Raja floridana	742	83.3	0.53	149	16.7	0.11	891
Raja fyllae	349.5	69.4	0.81	154	30.6	0.36	503.5

Species	Ventral Subtotal	Ventral %	Ventral Density (pores/cm)	Dorsal Subtotal	Dorsal %	Dorsal Density (pores/cm)	Total Pores
Raja hyperborea	411	73.1	0.26	151	26.9	0.09	562
Raja jenseni	442	73.1	0.27	163	26.9	0.10	605
Raja mirelatus	558	79.8	0.92	141	20.2	0.23	699
Raja olseni	1183	88.5	1.56	153	11.5	0.20	1336
Raja porosa	524	72.1	0.87	203	27.9	0.34	727
Raja rhina	1214	85.7	0.29	202	14.3	0.05	1416
Raja sadowskii	405	74.6	0.54	138	25.4	0.18	543
Raja teevani	386	81.6	0.24	87	18.4	0.05	473
Raja texana	363.5	77.6	0.47	105.5	22.4	0.14	469
Malacoraja fuliginea	432	73.3	1.46	157	26.7	0.53	589
Malacoraja purpuriventralis	714	80.1	1.55	177	19.9	0.38	891
Malacoraja spinacidermis	235	66.4	0.29	119	33.6	0.14	354

Table 13. Unilateral counts of ampullae from the ancillary species of skates (Rajidae) in this study[1]

Species	S.O.	O.B.	I.B.	H.	M.	Total
Anacanthobatis longirostris	47	147	90	77	22	383
Bathyraja kincaidi	91	84		153	17	345
Bathyraja spinacauda	115	124		197	15	451
Gurgesiella atripinna	57	25		96	17	195
Gurgesiella ishiyamai	32	7		87.5	9	135.5
Gurgesiella plutonia	21	11		63	8.5	103.5
Malacoraja fulginea	91	61		155	21	328
Malacoraja purpuriventralis	144.5	100		196	30	470.5
Malacoraja spinacidermis	48	23		85	17	173
Raja agassizi	65	81		179	21	346
Raja alba	70	49		99	21	239
Raja bathyphila	127	88		202	24	441
Raja binoculata	57	134	88	231	26	536
Raja clarkii	55.7	32.3		215	10	313
Raja clavata	116	122		172	41	451
Raja doutrei	62	105	52	189	49[2]	457
Raja erinacea[3]	109.2	91.2		139.4	21.3	361.1
Raja flavirostris	53	129	85	261	44	572
Raja floridana	46	86	46	205	28	411
Raja fyllae	72	46.5		135	21	274.5
Raja hyperborea	87	43		133	16	279
Raja jenseni	86	44		139	20	289
Raja mirelatus	103.5	98		154	23.5	379
Raja ocelatta	153	136.5		210.5	31.5	531.5
Raja olseni	66	118.5	81.5	218	27.5	511.5
Raja porosa	34	83	53	125	19	314
Raja rhina	92	185		292	37	683
Raja sadowski	71	59	77	133	19	282
Raja teevani[4]	78	68		88	14	248
Raja texana[5]	74.5 (42)	56	(40)	71.5	20	222

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[1] Where more than one specimen of a species was examined, counts given are averages.

[2] The mandibular capsule was lost from this specimen and therefore the number of somatic pores from 1/2 of subarea "J" is substituted.

[3] Counts are averaged values from both right and left sides in Raschi (1978)

[4] Morphometric differences, along with variations in the general anatomy of the ampullary system, suggest these two specimens to be different species. Ampullae counts are therefore presented only for the one specimen identified by the authors of the original species description.

[5] In only one of the specimens from this species were the superficial ophthalmic and inner buccal capsules sufficiently distinct to allow for separate counts (in parentheses).

Table 14. Counts of alveoli from the ampullae of the seven principal species of skates.

Species	Capsule	Range	Mean	S.D.
B. richardsoni	Hyoid	12-28	20.5	4.5
	S.O.	13-27	18.6	3.7
	Mand.	5-13	9.6	2.5
	O.B.	12-24	17.6	3.3
R. bigelowi	Hyoid	11-31	18.8	4.8
	S.O.	10-19	14.8	2.1
	Mand.	6-12	8.1	1.4
	O.B.	10-25	16.1	3.6
R. eglanteria	Hyoid	7-25	10.2	4.1
	S.O.	7-21	11.4	3.2
	Mand.	4-11	7.3	2.0
	O.B.	7-18	10.5	2.8
R. garmani	Hyoid	6-26	13.5	4.8
	S.O.	6-16	11.0	2.5
	Mand.	3- 8	5.5	1.2
	O.B.	6-16	11.2	2.7
R. laevis	Hyoid	3-20	8.3	5.3
	S.O.	5-21	10.6	4.6
	Mand.	2- 7	3.8	1.5
	O.B.	4-11	6.5	1.8
	I.B.	5-10	7.1	1.6
R. radiata	Hyoid	7-25	14.5	4.3
	S.O.	8-18	14.4	2.3
	Mand.	4-12	7.0	2.0
	O.B.	11-18	14.1	2.0
M. senta	Hyoid	9-28	14.8	4.4
	S.O.	5-18	9.9	2.9
	Mand.	4- 8	5.8	1.1
	O.B.	5-19	10.0	3.0

Table 15. Counts of alveoli (range, mean and standard deviation) from ampullae taken from the ancillary species of skates (Rajidae).

Species	Hyoid	S.O.	Mand.	O.B.	I.B.	Total
Anacanthobatis	8-12	11-17	3-5	13-17	11-15	
longirostris	11.0	13.4	4.0	15.2	13.2	43.6 (56.8)
	1.7	2.5	0.7	1.4	1.6	
Bathyraja	10-25	7-10	5-7	8-10		
kincaidi	15.4	8.4	5.8	9.4		39.0
	5.7	1.5	0.8	0.9		
Bathyraja	11-16	8-12	5-6	9-13		
spinacauda	13.0	10.6	5.2	10.8		39.6
	1.9	1.7	0.4	1.6		
Gurgesiella	11-26	9-18	4-7	7-12		
atripinna	18.8	12.2	5.8	9.8		46.6
	6.5	3.5	1.3	2.2		
Gurgesiella	8-16	6-15	4-6	4-10		
ishiyamai	12.9	11.4	4.8	7.2		36.3
	2.6	2.8	0.7	1.6		
Gurgesiella	5-8	2-5	2-4	3-5		
plutonia	6.7	3.4	3.4	4.2		17.7
	1.5	1.1	0.7	0.6		
Malacoraja	19-36	18-29	8-10	15-24		
fuliginea	28.4	22.4	9.0	19.8		79.6
	6.3	4.6	0.7	3.5		
Malacoraja	3-10	7-9	3-4	5-6	6-9	
purpuriventralis	6.8	7.4	3.2	5.6	0.5	23.0 (29.8)
	2.6	0.9	0.4	0.5	1.3	

Species	Hyoid	S.O.	Mand.	O.B.	I.B.	Total
Malacoraja spinacidermis	18-22	11-27	6	9-13		
	20.2	16.6	6.0	10.8		53.6
	1.6	7.1	0.0	1.8		
Raja agassizi	6-15	8-13	4-6	6-8		
	8.6	9.8	5.0	6.8		30.2
	3.8	2.4	0.7	0.8		
Raja alba	5-11	8-10	3-4	6-7		
	7.4	9.2	3.5	6.8		26.9
	2.3	0.8	0.6	0.5		
Raja bathyphila	21-31	18-22	10-12	17-22		
	25.4	19.6	10.6	19.0		74.6
	4.4	1.5	0.9	2.1		
Raja binoculata	18-25	18-23	6-10	20-27	13-19	
	20.8	20.6	7.6	22.4	16.0	71.4 (87.4)
	3.0	1.8	1.5	2.8	2.4	
Raja clarkii	12-18	8-16	4-8	6-12		
	15.1	10.6	5.9	10.2		41.8
	1.8	2.4	10.2	1.6		
Raja clavata	9-25	8-15	5-9	8-14		
	16.4	12.2	6.4	10.8		48.5
	6.0	2.6	1.5	2.2		
Raja doutrei	3-6	8-13	-	7-11	8-10	
	4.6	10.0	_1	8.8	9.4	27.2 (36.6)
	1.1	2.2	-	2.0	0.9	
Raja erinacea	7-14	8-9	4-7	10-13		
	10.6	8.4	5.8	11.2		36.0
	3.0	0.5	1.3	1.3		

Species	Hyoid	S.O.	Mand.	O.B.	I.B.	Total
Raja flavirostris	7-20	12-19	3-6	10-16	5-11	
	14.4	15.8	4.2	12.0	7.4	46.4 (53.8)
	5.3	3.1	1.3	2.3	2.6	
Raja floridana	4-10	7-10	3-4	7-13	9-17	
	6.6	8.0	3.8	9.4	11.0	27.8 (38.8)
	2.7	1.4	0.4	2.6	3.4	
Raja fyllae	14-28	11-19	7-10	16-21		
	22.7	14.4	8.8	17.8		63.7
	4.1	2.4	1.2	1.4		
Raja hyperborea	11-20	12-23	5-9	18-24		
	15.0	17.6	6.8	20.0		59.4
	4.1	3.9	1.5	2.5		
Raja jenseni	17-28	17-24	8-12	14-24		
	23.2	20.6	10.2	18.0		72.0
	4.5	3.3	1.6	3.7		
Raja mirelatus	9-15	6-18	3-7	9-17		
	11.8	12.0	5.3	12.5		41.6
	2.6	3.9	1.4	2.8		
Raja ocellata	11-18	10-17	8-14	12-18		
	13.9	13.1	10.6	14.8		52.4
	2.4	2.6	2.0	2.1		
Raja olseni	4-15	8-19	3-5	4-10	6-10	
	9.4	10.2	4.3	7.0	7.5	30.9 (38.4)
	4.1	3.6	0.7	2.3	1.3	
Raja porosa	3-10	7-9	3-4	5-6	6-9	
	6.8	7.4	3.2	5.6	6.8	23.0 (29.8)
	2.6	0.9	0.4	0.5	1.3	

Species	Hyoid	S.O.	Mand.	O.B.	I.B.	Total
Raja rhina	5-19	11-26	5-9	8-15	11-13	
	14.4	18.2	6.8	11.2	12.0	50.6 (62.6)
	5.7	6.2	1.5	3.3	1.0	
Raja sadowskii	13-29	12-19	4-14	14-23		
	23.0	15.2	8.6	18.6		65.4
	6.0	2.6	3.7	3.9		
Raja teevani[2]	7-20	10-20	3-7	10-15		
	11.6	15.2	5.3	13.0		45.1
	5.0	4.0	2.1	1.9		
Raja texana[3]	9-17	8-16	3-6	7-12	8-10	
	11.5	12.0	4.8	8.6	8.4	36.9 (45.3)
	2.5	2.3	1.0	1.6	1.5	

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[1] Ampullae from this capsule were lost and number of alveoli approximated from average counts from *R. laevis*.

[2] Due to the large differences in morphometrics and meristics of the ampullae, only one specimen was used in this analysis.

[3] An inner buccal capsule was noted in only the second specimen of this species, and therefore this is reflected in this table.

Table 16. Average counts (range, mean, standard deviation) of alveoli from the ampullae of the five galeoid species of sharks. Total values represent the sum of superficial ophthalmia Divisions I and II, outer buccal and mandibular.

Species	Superficial Ophthalmic				Outer	Mandibular	Total
	Div. I	Div. II	Div. III	Average	Buccal		
C. plumbeus	6-8	6-8	7-8	6-8	6-8	1-3	
	7.0	7.2	7.4	7.2	7.0	2.4	23.6
	1.00	0.94	0.55	0.87	1.00	0.89	
C. obscurus	7-8	7-11	7-11	7-11	7-9	3-6	
	7.6	8.3	9.0	8.3	7.8	4.6	28.3
	0.55	0.96	1.41	1.06	0.84	1.14	
G. cuvieri	8-10	8-12	8-13	8-13	9-11	3-7	
	8.8	9.5	11.0	9.6	9.6	5.2	33.1
	0.84	1.25	1.87	1.47	0.89	1.47	
O. taurus	8-11	8-10	----	8-11	9-12	3-7	
	9.6	9.0	----	9.3	10.4	5.2	34.2
	1.52	0.71	----	1.16	1.14	1.48	
P. glauca	7-9	6-10	7-8	6-10	6-9	4-5	
	8.0	7.8	7.4	7.8	7.6	4.5	27.9
	0.71	1.01	0.55	0.88	1.14	0.58	

Table 17. Dimensions of ampullae (length/width) from each of the major capsules from the principal species examined in this study. Individual measurements (mm) represent the average from five ampullae. Total counts in parentheses include I.B.

Species	Disc Width (mm)	Hyoid	S.O.	Mand.	O.B.	I.B.	Total
Bathyraja richardsoni	538	0.816/1.050	0.862/1.221	0.500/0.622	0.811/0.980		2.989/3.873
	829	0.928/1.170	0.958/1.203	0.779/0.933	0.684/0.893		3.349/4.199
	830	0.892/1.250	0.883/1.011	0.724/0.922	0.872/1.040		3.371/4.223
	963	0.995/1.356	1.020/1.100	0.597/0.694	0.832/1.000		3.444/4.150
	1000	0.955/1.350	0.944/1.070	- / -	0.852/1.030		- / -
Raja bigelowi	245	0.597/0.755	0.612/0.781	0.468/0.536	0.719/0.842		2.396/2.914
	235	0.928/1.080	0.821/0.990	0.475/0.623	0.888/1.120		3.112/3.813
	196	0.878/1.168	0.765/0.950	0.469/0.587	0.913/1.087		3.025/3.792
	171	0.755/0.995	0.714/0.831	0.444/0.556	0.846/0.948		2.759/3.330
	89	0.551/0.638	0.449/0.525	0.286/0.342	0.505/0.561		1.791/2.066
	230	0.893/1.090	0.894/1.040	0.556/0.648	0.959/1.132		3.302/3.910
	199	0.933/1.207	0.831/0.900	0.449/0.556	0.811/0.923		3.024/3.586
Raja eglanteria	414	0.536/0.617	0.556/0.639	0.362/0.525	0.495/0.607		1.949/2.388
	393	0.714/0.898	0.571/0.704	0.576/0.638	0.739/0.959		2.600/3.199
	395	0.561/0.699	0.653/0.787	0.388/0.541	0.821/1.060		2.423/3.087
	268	0.444/0.571	0.526/0.622	0.398/0.459	0.536/0.643		2.025/2.295
	276	0.648/0.719	0.556/0.678	0.311/0.439	0.510/0.602		2.025/2.438
	424	0.485/0.678	0.597/0.769	0.362/0.500	0.309/0.791		1.753/2.738
Raja garmani	201	0.459/0.556	0.393/0.525	0.276/0.296	0.418/0.521		1.546/1.898
	190	0.669/0.806	0.627/0.643	0.260/0.270	0.510/0.602		2.066/2.321
	180	0.561/0.735	0.582/0.755	0.327/0.434	0.612/0.806		2.082/2.730
	134	0.556/0.638	0.536/0.574	0.214/0.250	0.459/0.592		1.765/2.054
	149	0.541/0.643	0.520/0.536	0.255/0.327	0.480/0.597		1.796/2.103
	130	0.490/0.602	0.480/0.582	0.225/0.255	0.424/0.546		1.619/1.985
	230	0.561/0.719	0.495/0.612	0.316/0.388	0.577/0.699		1.949/2.418
Raja laevis	295	0.526/0.597	0.388/0.444	0.347/0.383	0.408/0.454	0.464/0.592	2.133/2.470 (1.669/1.878)
	490	0.449/0.541	0.627/0.730	0.577/0.525	0.408/0.582	0.576/0.735	2.637/3.113 (2.061/2.378)
	355	0.373/0.475	0.582/0.643	0.255/0.327	0.449/0.551	0.495/0.612	2.154/2.608 (1.659/1.996)
	501	0.592/0.648	0.627/0.853	0.413/0.429	0.526/0.663	0.490/0.678	2.648/3.271 (2.158/2.593)
	397	0.628/0.617	0.648/0.846	0.413/0.424	0.480/0.622	0.500/0.566	2.669/3.075 (2.169/2.509)

Species	Disc Width (mm)	Hyoid	S.O.	Mand.	O.B.	I.B.	Total
Raja radiata	189	0.444/0.500	0.480/0.572	0.286/0.372	0.449/0.521		1.659/1.965
	491	0.674/0.970	0.826/0.985	0.485/0.546	0.785/1.000		2.770/3.501
	307	0.699/0.909	0.750/0.903	0.408/0.531	0.648/0.883		2.505/3.226
	199	0.480/0.663	0.536/0.628	0.291/0.347	0.510/0.679		1.817/2.317
	128	0.444/0.515	0.413/0.454	0.209/0.230	0.368/0.444		1.434/1.643
	202	0.566/0.760	0.525/0.679	0.301/0.347	0.510/0.663		1.902/2.449
Malacoraja senta	325	0.561/0.684	0.490/0.515	0.291/0.362	0.434/0.531		1.776/2.092
	289	0.582/0.755	0.541/0.704	0.306/0.388	0.587/0.750		2.016/2.597
	173	0.541/0.704	0.367/0.449	0.271/0.327	0.388/0.500		1.567/1.980
	110	0.551/0.612	0.316/0.398	0.260/0.291	0.418/0.464		1.545/1.765
	107	0.561/0.617	0.347/0.383	0.215/0.255	0.337/0.367		1.460/1.622
	220	0.566/0.658	0.454/0.485	0.255/0.317	0.459/0.531		1.734/1.991

Table 18. Dimensions of ampullae (length/width) from each of the major capsules from the ancillary species examined in this study. Individual measurements (mm) represent the average from five ampullae.

Species	Disc Width (cm)	Hyoid	S.O.	Mand.	O.B.	I.B.	Total
Anacanthobatis longirostris	250	0.627/0.888	0.735/0.847	0.255/0.265	0.592/0.801	0.607/0.709	2.816/3.510 (2.209/2.801)
Bathyraja kincaidi	298	0.551/0.689	0.459/0.541	0.276/0.306	0.474/0.587		1.760/2.123
Bathyraja spinacauda	996	0.750/1.090	0.883/1.120	0.653/0.735	0.888/1.110		3.174/4.055
Gurgesiella atripinna	144	0.582/0.740	0.464/0.536	0.322/0.403	0.505/0.571		1.873/2.250
Gurgesiella ishiyamai	162	0.638/0.770	0.678/0.745	0.337/0.459	0.556/0.638		2.209/2.612
	104	0.556/0.669	0.490/0.582	0.276/0.327	0.459/0.515		1.781/2.093
Gurgesiella plutonia	111	0.372/0.551	0.291/0.352	0.230/0.378	0.311/0.418		1.204/1.699
	112	0.490/0.602	0.276/0.332	0.250/0.362	0.332/0.393		1.348/1.689
Malacoraja fuliginea	170	0.633/0.996	0.582/0.684	0.367/0.398	0.546/0.689		2.128/2.767
Malacoraja purpuriventralis	281	0.958/1.148	0.883/0.923	0.408/0.449	0.786/0.923		3.035/3.443
	218	0.832/1.125	0.725/0.801	0.352/0.434	0.755/0.908		2.664/3.268
Malacoraja spinacidermis	186	0.775/0.835	0.650/0.775	0.330/0.370	0.485/0.600		2.240/2.580
Raja agassizi	218	0.464/0.653	0.580/0.701	0.291/0.322	0.408/0.545		1.743/2.221
Raja alba	221	0.367/0.556	0.393/0.480	0.198/0.249	0.351/0.427		1.309/1.712
Raja bathyphila	161	0.549/0.648	0.469/0.520	0.296/0.339	0.474/0.592		1.788/2.099
Raja binoculata	181	0.475/0.617	0.449/0.520	0.245/0.255	0.469/0.571	0.398/0.490	2.036/2.453 (1.638/1.963)
Raja clarkii	450	0.797/0.919	0.566/0.821	0.332/0.403	0.602/0.760		2.297/2.903
	558	0.801/0.996	0.648/0.709	0.362/0.398	0.571/0.704		2.382/2.807
	272	0.704/0.945	0.541/0.679	0.306/0.378	0.536/0.658		2.087/2.660
Raja clavata	363	0.540/0.635	0.440/0.515	0.260/0.365	0.420/0.510		1.660/2.025
Raja doutrei	265	0.169/0.204	0.332/0.296	- / -	0.245/0.276	0.245/0.276	- / -

Species	Disc Width (cm)	Hyoid	S.O.	Mand.	O.B.	I.B.	Total
Raja flavirostris	224	0.429/0.597	0.449/0.556	0.204/0.266	0.454/0.576	0.367/0.408	1.903/2.403 (1.536/1.995)
Raja floridana	310	0.291/0.378	0.389/0.485	0.219/0.398	0.480/0.646	0.531/0.587	1.910/2.362 (1.379/1.775)
Raja fyllae	270	0.826/1.030	0.658/0.699	0.413/0.449	0.673/0.770		2.570/2.948
	239	0.791/1.106	0.694/0.877	0.403/0.464	0.821/1.025		2.709/3.472
Raja hyperborea	617	0.765/1.220	1.010/1.231	0.541/0.694	0.949/1.282		3.265/4.427
Raja jenseni	448	0.775/1.128	0.837/1.097	0.521/0.587	0.750/1.056		2.883/3.868
Raja mirelatus	275	0.704/0.975	0.673/0.816	0.332/0.408	0.673/0.781		2.382/2.980
	219	0.474/0.602	0.495/0.541	0.260/0.347	0.500/0.566		1.729/2.056
Raja ocellata	274	0.521/0.679	0.561/0.755	0.388/0.470	0.622/0.724		2.092/2.628
	167	0.408/0.567	0.398/0.546	0.291/0.342	0.408/0.520		1.505/1.975
Raja olseni	397	0.658/0.749	0.623/0.837	0.337/0.474	0.382/0.796	0.571/0.750	2.771/3.806 (2.200/3.056)
	240	0.474/0.633	0.505/0.571	0.271/0.296	0.383/0.490	0.454/0.521	2.087/2.511 (1.633/1.990)
Raja porosa	326	0.546/0.735	0.694/0.867	0.398/0.449	0.638/0.857	0.826/0.986	3.102/3.894 (2.276/2.908)
Raja rhina	535	0.719/0.959	0.888/1.132	0.363/0.434	0.714/0.879	0.643/0.801	3.327/4.205 (2.684/3.404)
Raja sadowskii	165	0.590/0.775	0.515/0.570	0.330/0.335	0.590/0.665		2.025/2.345
Raja teevani	460	0.505/0.673	0.888/0.908	0.468/0.493	0.561/0.689		2.442/2.763
Raja texana	252	0.510/0.668	0.469/0.551	0.243/0.376	0.362/0.495	0.419/0.459	2.003/2.549 (1.584/2.090)
	234	0.454/0.505	0.459/0.475	0.214/0.301	0.347/0.398		1.474/1.679

Table 19. Somatic pore counts (range, mean and standard deviation) for the shark species examined in this study. Subareas are illustrated in figure 9. Blanks are presented for those subareas found to be too indistinct to separate. Single, average values are listed for bilaterally arranged subareas.

Species	A	B	C	D	E	I	F	G	H	C'	D'	J
C. obscurus	103.0-132.0	9.0-12.5	28.0-42.0	132.5-177.0	82.0-109.0	10.0-15.0	215.5-240.5	76.5-89.0	14.5-19.0	32.0-37.5	43.0-46.0	103.0-120.0
	116.6	10.2	36.1	161.6	93.0	13.6	225.6	82.9	16.9	35.1	44.9	112.0
	8.6	1.7	5.6	15.8	10.4	1.6	8.6	4.2	1.7	2.4	1.0	6.5
C. plumbeus	116.0-198.0	17.0-23.5	20.0-46.0	192.0-247.0	115.0-179.0	18.5-23.0	237.5-291.0	69.0-98.5	18.0-23.5	39.5-49.0	36.0-47.5	133.0-178.0
	145.6	20.6	33.9	220.7	149.2	21.8	255.2	82.9	20.7	44.1	39.3	157.2
	24.8	2.0	7.4	17.4	18.1	1.5	16.4	8.1	1.8	3.1	3.6	15.5
G. cuvieri	48.5-70.0	6.0-8.0	17.0-32.0	55.0-79.0	28.0-61.0	-	40.0-62.0	60.0-103.0	16.5-22.0	15.0-43.0	13.0-57.5	62.0-124.0
	58.7	6.8	24.3	67.0	39.5		49.0	74.4	20.0	27.7	27.7	97.7
	9.2	0.8	6.7	9.2	13.7		7.8	15.9	2.5	10.5	15.5	27.6
O. taurus	35.5-44.5	-	17.5-34.5	137.5-208.5	-	3.0-6.0	125.0-127.0	114.0-127.0	17.0-17.5	20.0-28.0	-	
	40.0		26.0	173.0		4.4	126.0	120.8	17.3	24.0		36.0
	6.4		12.0	50.2		1.3	1.4	9.5	0.4	5.7		
P. glauca	30.0-44.5	1.0-2.5	14.5-21.5	57.5-80.5	37.0-65.0	-	96.0-157.0	30.0-42.0	6.0-14.5	12.0-21.5	20.5-39.5	60.0-89.0
	38.3	1.7	17.6	69.2	52.9		124.6	33.4	11.9	15.3	30.9	74.8
	5.3	0.6	3.4	8.2	11.2		22.3	4.9	3.4	4.0	7.9	11.6

Table 20. Synopsis of natural history information for the ancillary species of skates (Rajidae) examined during this study.

Species	Mean Depth (M) (range)	Ref.	Food Habits	Ref.
Anacanthobatis longirostris	791 (530-1052)	Bigelow & Schroeder 1968	None	-
Bathyraja kincaidii	714 (55-1372)	Miller & Lea, 1972	None	-
Bathyraja spinacauda	463 (121-805)	Bigelow & Schroeder, 1953a	"...fed on capelin (*Mallotus*) and on the starry skate (*Raja radiata*)."	Bigelow & Schroeder, 1953a
Gurgesiella atripinna	666 (413-918)	Bigelow & Schroeder, 1953a Bigelow & Schroeder, 1962	None	-
Gurgesiella ishiyamai	727.5 (503-952)	Bigelow & Schroeder, 1962	None	-
Gurgesiella plutonia	514 (294-734)	Bigelow & Schroeder, 1962	None	-
Raja agassizi	65 (0-130)	Figureiredo, 1977	None	-
Raja alba	265.5 (31-500)	Wallace, 1967 Wheeler, 1969	(fish)-*Argentina sphyraena*, *Trachinus vipera*, *Pagellus erhenbergi*, *Dentex dentex*, *Scyliorhinus canicula* (crustaceans)-*Squilla mantis*, *Goneplax rhomboides*, *Neptunus hastatus* (cephalopods)-*Sepia officinalis*, *Loligo* sp., *Sepiola* sp.	Azouz & Capape, 1971
Raja bathyphila	1410 (770-2050)	Stehmann, 1978	None	-
Raja binoculata	390 (3-777)	Grinols, 1965 Miller & Lea, 1972	"...food includes crustaceans and fishes such as great sculpins."	Hart, 1973
Raja clarkii	457.5 (366-549)[1]	Bigelow & Schroeder, 1965 Bigelow & Schroeder, 1962	None	-

Species	Mean Depth (M) (range)	Ref.	Food Habits	Ref.
Raja clavata	251 (2-500)	Wheeler, 1969 Lythgoe & Lythgoe, 1975	Adults-crustaceans (*Upogebia*, *Portunus*, *Corystes*) and sometimes fish (sand eels, herring, sprat) Young-amphipods & young brown shrimp	Wheeler,
			Teleosts (I.F.-0.12)-*Trachurus trachurus*, *Paracentropristis hepatus*, *Argentina sphyraena* Crustaceans (I.F.-0.91)-amphipods, *Pagurus arroser*, *Alpheus ruber*, *Dorippe lanata*, *Macropipus depurator*, *Geryon tridens* Cephalopods (I.F.-0.03)-*Loligo vulgaris*, Sepiola sp. Sipunculids (I.F.-0.017)-*Sipunculus nudus*	Azouz & Capape, 1971[2]
			Fish (I.F.-0.51) and crustaceans (I.F.-0.46)	Capape, 1975[2]
Raja doutrei	450 (300-600)	Blache et al., 1970	shrimp and galatheids	Cadenat, 1960
Raja erinacea	73 (0-146)	Bigelow & Schroeder,	epifaunal prey, particularly decapods	McEachran et al., 1976
			Active crustaceans-*Leptocheirus pinguis*, *Crangon septemspinosa*, *Cancer irroratus*	Richard et al., 1963
Raja flavirostris	157 (14-300)	Norman, 1937	None	-
Raja floridana	352.5 (293-412)	Bigelow & Schroeder, 1968 Bigelow & Schroeder, 1962	None	-
Raja fyllae	1163 (271-2055) 2055	Bigelow & Schroeder, 1953a Koefoed, 1927	copepods, amphipods, mysids	Bigelow & Schroeder, 1953a
Raja hyperborea	1306.5	Bigelow & Schroeder, 1953a	"...teeth suggest active prey." "...50 large pelagic amphipods (*Euthemisto libellula*), fragments of an Arctic prawn (*Hymenodora glacialis*), and three fishes, one of them a third as long (185 mm) as its captor (518 mm)." "Cephalopod fragments also..."	Bigelow & Schroeder, 1953a
Raja jenseni	1371.5[3] (366-2377)	Bigelow & Schroeder, 1953a	"...teeth suggests that it feeds chiefly on active prey such as small fishes and free swimming crustacea,..."	Bigelow & Schroeder, 1953a
			"...one well-digested redfish (135 cc)."	Templeman, 1965

Species	Mean Depth (M) (range)	Ref.	Food Habits	Ref.
Raja mirelatus	226 (12-440)	Wallace, 1967 Hulley, 1970	crustaceans (I.F.-0.91), teleosts (I.F.-0.11) crustaceans (I.F.-1.00), teleosts (I.F.-0.04), molluscs (I.F.-0.01) and other groups (I.F.-0.009)	Azouz & Capape, 1971^2 Capape & Azouz, 1975$^{2\ \&\ 4}$
Raja ocellata	185.5 (0-371)	Bigelow & Schroeder, 1953a McEachran et al., 1975	Infaunal invertebrates Small fish (see footnote 86 in reference)	McEachran et al., 1976 Bigelow & Schroeder, 1953a
Raja olseni	165 (92-238)	Bigelow & Schroeder, 1968 Bigelow & Schroeder, 1962	None	-
Raja porosa	65 (30-100)	Ishiyama, 1967	None	-
Raja rhina	347.5	Miller & Lea, 1972 Grinols, 1965	None	-
Raja spinacidermis	1010 (450-1569)	Templeman, 1965 Bigelow & Schroeder, 1953	Shrimp (Sabinea) euphausids, mysids, hyperiid amphipods (Parathemisto), isopod and calanoid copepods	Templeman, 1965
Raja teevani	526 (320-732)	Bigelow & Schroeder, 1968 Bigelow & Schroeder, 1965	None	-
Raja texana	62.5 (15-110)	Bigelow & Schroeder, 1965	"...feeds mostly on molluscs and benthic polychaetes."	Hoese & Moore, 1977
Malacoraja fuliginea	915 (732-1098)	Bigelow & Schroeder, 1954a Bigelow & Schroeder, 1968	None	-
Malacoraja purpuriventralis	1971 (732-2010)	Bigelow & Schroeder, 1965 Bigelow & Schroeder, 1962	None	-

Species	Mean Depth (M) (range)	Ref.	Food Habits	Ref.
Malacoraja sadowskii	1000 (800-1000)	Krefft and Stehmann, 1974	None	-

[1] One specimen (USNM 205391) was collected from a depth of 907 M and if included, would increase the average depth to 636.5 M.

[2] L'indice de frequence (I.F.) is enclosed in parentheses and is defined as the number of stomachs containing a particular prey item compared with the total number of full stomachs.

[3] *Raja jenseni* probably occurs down to depths greater than previously recorded (Templeman, 1965).

[4] The species list of prey items included in this reference (Tableau 6) indicate that the majority of teleosts are benthic (gobies, blennies and flatfish).

Table 21. Morphometric characteristics for the galeoid sharks examined in this study.

Species	Maximum TL (cm)	Ref.	Length of Snout[1]	
C. plumbeus	249	Garrick, 1982	1.7-3.6	(3.3-4.1)
C. obscurus	363	Garrick, 1982		(3.5-4.0)
G. cuvieri	740	Basset, et al., 1975	5.6-6.0	(1.9)
O. taurus	318	Bigelow and Schroeder, 1948	-	(3.3-3.4)
P. glauca	383	Bigelow and Schroeder, 1948	1.4-1.7	(3.8)

[1] Snout length is expressed here as both length of medial rostral cartilage in the nasobasal plate length after Campagno (1979) and as a percent of the total length after Bigelow and Schroeder (1948) (in parentheses).

Table 22. Synopsis of natural history information for the galeoid sharks examined in this study.

Species	General Distribution	Ref.	Food Habits	Ref.
C. plumbeus	"shoreline to 135 fathoms... enters bay mouths" "shallower part of the continental shelf"	Springer, 1960	"a discriminating feeder... a bottom feeder... prefers fresh fish to stale or decomposed fish" a wide variety of smaller teleosts, elasmobranchs and a number of mollusks	Springer, 1960
C. obscurus	shallow estuarine waters	Huish & Benedict, 1977	variety of teleosts, elasmobranchs, cephalopods and only a minor fraction of invertebrates	Clarke & von Schmidt, 1965
	"much more pelagic in habit than either milberti (p. 372) or leucas (341)"	Bigelow & Schroeder, 1948	"fish-eater"	Bigelow & Schroeder, 1948
G. cuvieri	"both deep oceanic and shallow coastal regions."	Castro, 1983	"most polyphagous of all sharks"	Castro, 1983
	shallow waters along the east coast of the U.S.	Gudger, 1948	dead and moribund birds	Dodrill and Gilmore, 1978
	year round off shore	Schwartz & Burgess, 1975	a variety of teleosts, elasmobranchs and "parts of sharks, birds, turtles, tunicates, octopuses, crabs, horseshoe crabs, mollusks, jelly fish, and assorted trash."	Clarke & von Schmidt, 1965
			a very large assortment of fish, mammal remains and turtles	Gudger, 1948
			"non-discriminating... filled with all sorts of small and large foreign bodies"	Gudger, 1949
O. taurus	as shallow as 6 meters	Clarke & von Schmidt, 1965	wide range of both fish and invertebrates	Castro, 1983
	offshore in deeper waters	Schwartz & Burgess, 1975		
	"most of those caught being taken in depths of not more than two to five fathoms;"	Bigelow & Schroeder, 1948		
P. glauca	pelagic	Strasburg, 1958; Stevens, 1976	cephalopods	Clark & Stevens, 1974
	only occasionally migrate inshore	Clark & Stevens, 1974	fraction of additional invertebrates	Strasburg, 1958, LeBrasseur, 1964
	"clear, deep, blue waters..."	Castro, 1983		

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