HEXATRYGONIDAE, A NEW FAMILY OF STINGRAYS (MYLIOBATIFORMES: BATOIDEA) FROM SOUTH AFRICA, WITH COMMENTS ON THE CLASSIFICATION OF BATOID FISHES

By

P.C. Heemstra and M.M. Smith

Abstract

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A new species of stingray, *Hexatrygon bickelli* Heemstra and Smith, is described from a specimen washed up on a beach at Port Elizabeth on the south coast of South Africa. This new species differs from all other batoid fishes in having six gill arches and a peculiar hypertrophied snout that appears to be a well-developed electroreceptive organ, and in the configuration of its spiracles. Other characters that separate *H. bickelli* from previously known rays (myliobatiforms) are its small simple brain (other rays have a very large complex brain) and the absence of supraorbital crests on the cranium. In addition, all myliobatiforms are neritic (with none having been recorded below 200 m), and *H. bickelli* is.presumed to live in moderately deep water (400 to 1000 m).

The classification of batoid fishes is reviewed, and *Hexatrygon* is placed in a new family and suborder of the Myliobatiformes.

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On July 5th 1980, during an evening stroll along the Summerstrand Beach in Port Elizabeth, Mr Dave Bickell noticed a peculiar stingray lying dead on the tide line. An angling columnist for the *Eastern Province Herald*, Mr Bickell knows the local fish fauna well and realized that the ray was quite unusual. He telephoned Mr Malcolm Smale of the Port Elizabeth Museum, who put the specimen in 10% formalin and brought it to the J.L.B. Smith Institute of Ichthyology.

Considering the circumstances of its discovery, the specimen is in good condition. It had evidently been dead for only a short time, as neither the nasal lamellae nor the gills show any sign of having been nibbled by the isopods that quickly attack beached fishes. Much of the epidermis on the dorsal surface and on the periphery of the disc had been abraded, probably when the ray was being tossed about in the surf on this sandy beach. The right pelvic fin was damaged, presumably from the bite of some fish, as most of the radial cartilages and muscle tissue had been torn away.

There was no evidence of the specimen having been caught by an angler and discarded on the shore, and it appears to be an inhabitant of moderately deep water (*i.e.* 400 to 1 000 m): the skin on the dorsal surface is thin and black; the elongated snout is thin and flaccid, and provided with numerous well-developed ampullae of Lorenzini; the eyes are relatively small, compared to neritic stingrays; and the skeleton is not well calcified. An additional indication of a deep-water habitat for this ray is the chemistry of its liver oil. According to A.A. Spark[1] (personal communication) the composition of the liver oil is typical of fishes from deep water and quite different from the ordinary fish oil of *Dasyatis pastinaca* and other neritic species. Furthermore, if this new ray is normally a resident of South African waters, it seems unlikely that it occurs in depths shallower than 400 m, or it would have been discovered in trawler catches long ago.

Hexatrygonidae fam. nov.

DIAGNOSIS.—Six gill openings and six gill arches; gill filaments well developed on each arch. Snout elongate, thin (depressed), translucent, filled with a clear gelatinous substance and provided with numerous ampullae of Lorenzini. Nostrils wide apart, not connected to mouth by a nasoral groove; anterior nasal flaps short and fleshy, not joined medially to form a broad nasal curtain that reaches mouth. No supraorbital crests on chondrocranium. Spiracles large, well back from eyes, closed dorsally by a thin flap extending from anteromedial rim of spiracle to form an oblique slit at posterolateral edge of orifice. Cranium large; brain very small, occupying less than a tenth of the volume of the cranial cavity; cerebellum small, divided into two almost symmetric non-convoluted lobes; olfactory peduncles very long and slender; telencephalon small. Tail with two well-developed serrate spines (stingers) and prominent dorsal and ventral fins supported by cartilaginous radials and extending from tip of spine to tip of tail.

REMARKS.—This new family is based on the sole genus described below. Its relationships with other batoid families are discussed on page 12.

Hexatrygon gen. nov.

DIAGNOSIS (family characters not repeated). —Disc longer than broad; snout length (to front of mouth) greater than half disc width; longitudinal eye diameter contained 9 times in distance between eyes and 3 times in distance from eye to spiracle. Length of tail (from anterior end of cloaca) about two-thirds disc length. Mouth width 18% disc width and two-thirds distance between lateral edges of nares. No papillae on floor of mouth; oral valve of upper jaw rudimentary; medial (pharyngeal) surface of gill arches smooth (no "gill rakers" or papillae). Skin smooth; no dermal denticles (although much of the epidermis of the dorsal surface has been lost, the dermal layer of the skin is intact and shows no sign of denticles).

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Figure 1. Dorsal view of *Hexatrygon bickelli*, disc length 640 mm.
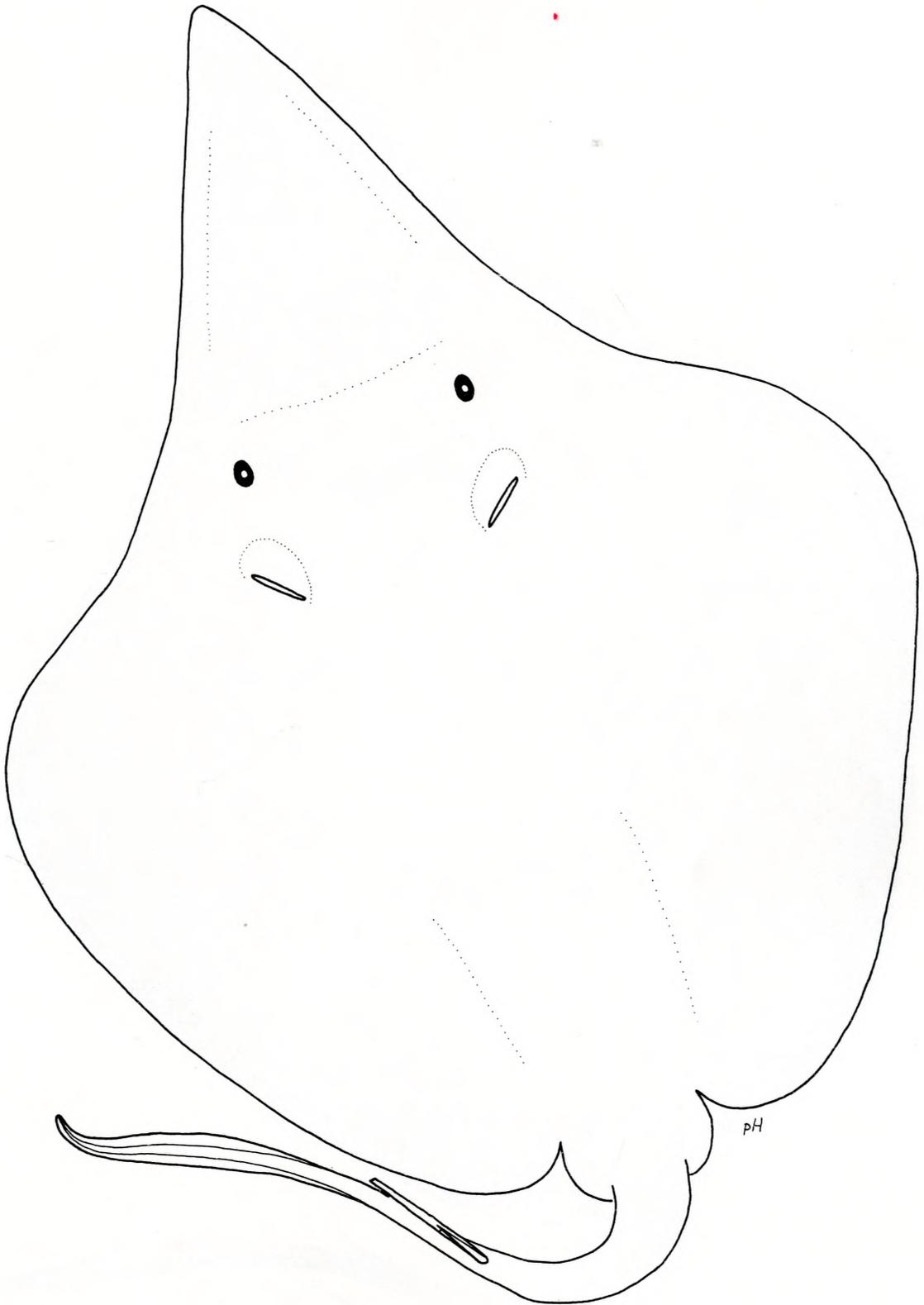
Figure 2. *Hexatrygon bickelli*, dorsal view with reconstructed (normal) fin margins. Disc width and length is slightly greater than shown in Figs. 1 & 3, because specimen was initially preserved in a tub that was a bit small, and the margins of the disc were slightly abraded and perhaps somewhat dessicated before being fixed.
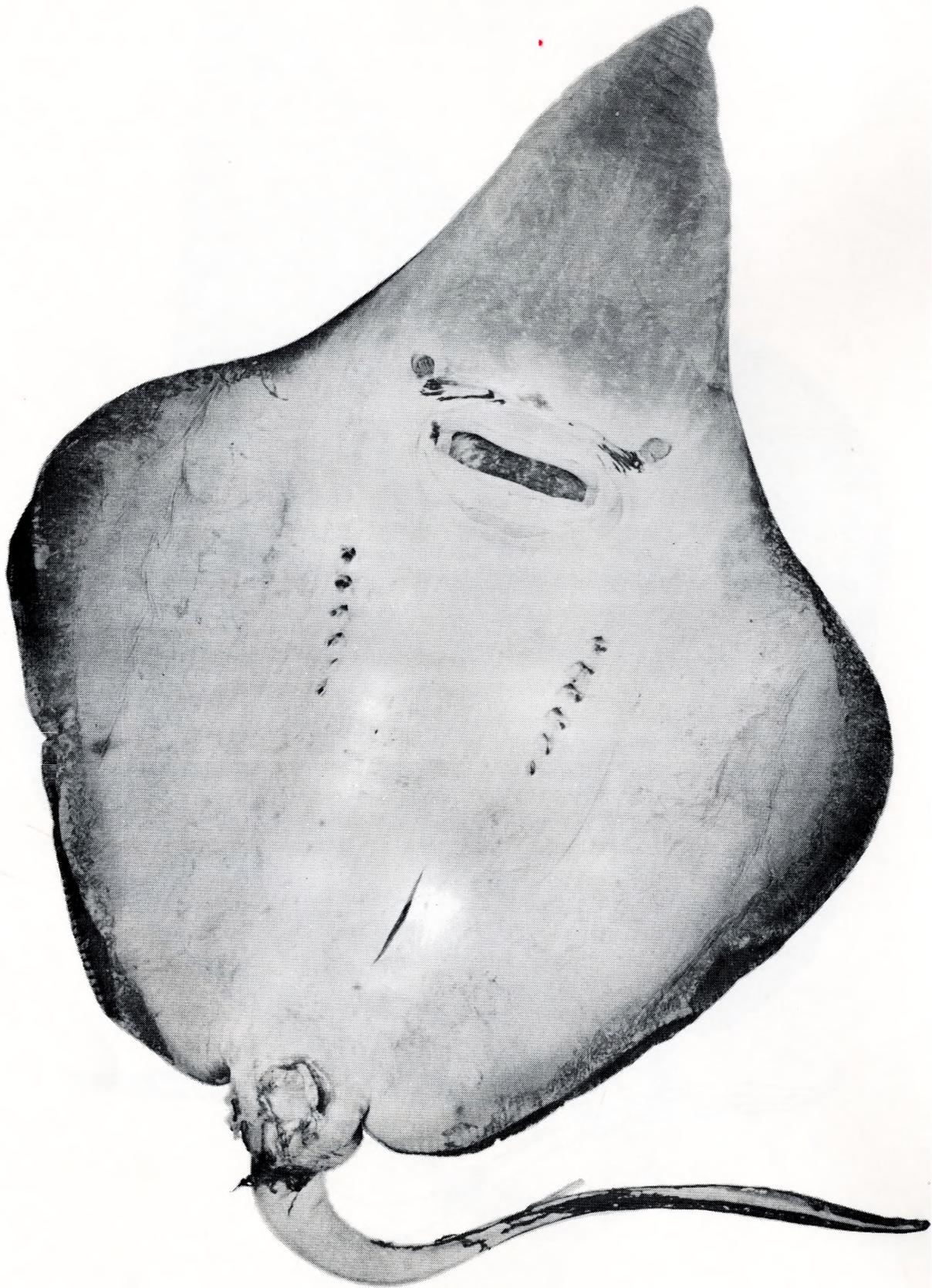
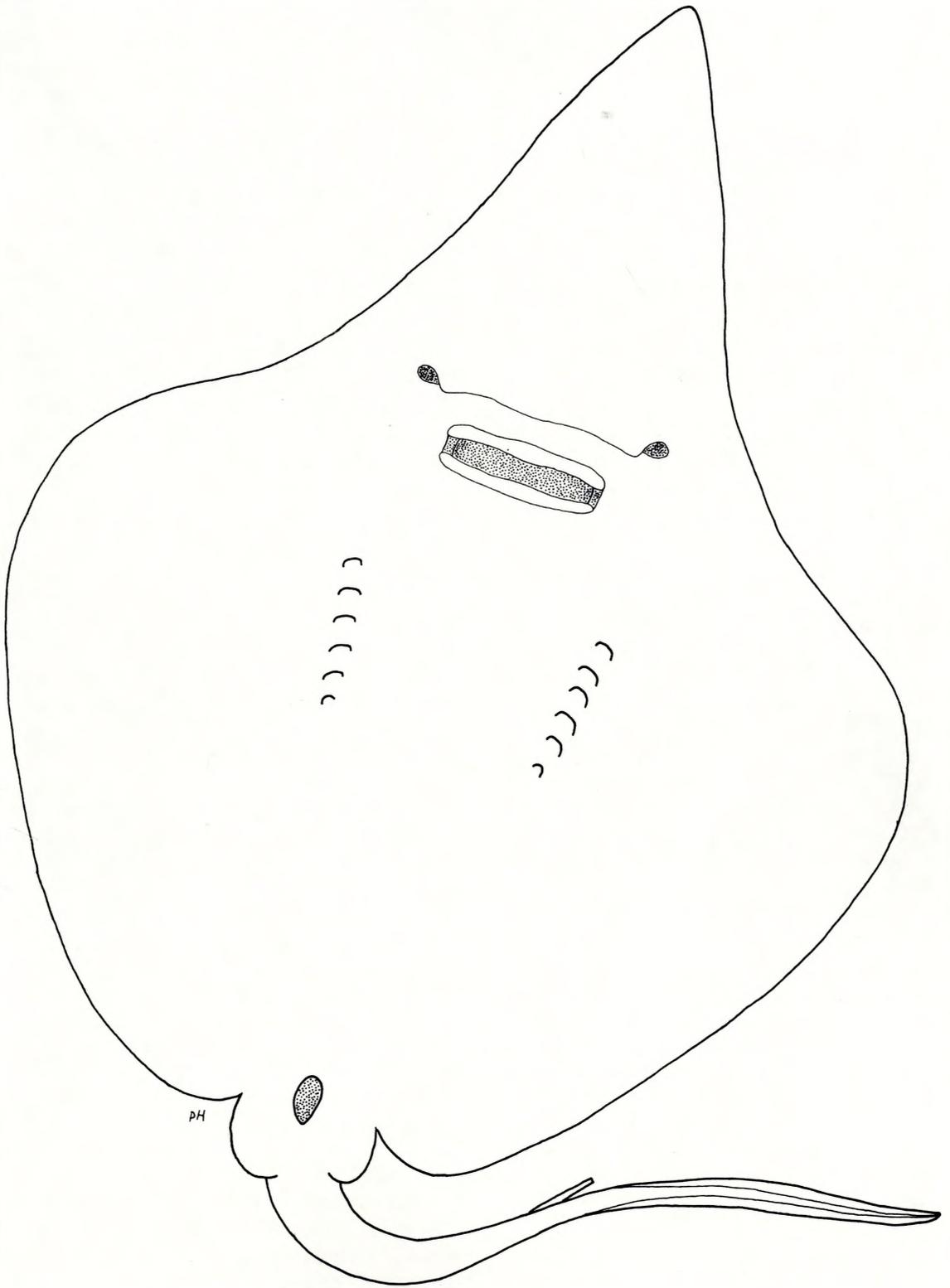**Figure 3**. Ventral view of *Hexatrygon bickelli*.

Figure 4. *Hexatrygon bickelli*, ventral view with reconstructed (normal) fin margins.

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ETYMOLOGY AND GENDER.—*Hexa-* from the Greek word *hex* meaning six, and *trygon*, the Greek word for a stingray. *Hexatrygon* is feminine in gender.

TYPE-SPECIES.—*Hexatrygon bickelli* Heemstra and Smith.

Hexatrygon bickelli sp. nov.
Sixgill stingray
(Figs 1—13 & 15)

HOLOTYPE.—Female, 103 cm total length; found on beach at Port Elizabeth, south coast of South Africa; collected by D. Bickell, 5 July 1980; J.L.B. Smith Institute of Ichthyology catalogue no. 997.

DESCRIPTION (measurements in mm).—Disc length (snout tip to rear end of pectoral fins 640; greatest disc width 500; body depth (greatest thickness) 77; snout tip to anterior end of cloaca 600, to end of pelvic fins 660, to base of tail spine 765, to front of mouth 265, to front of nostril 243, to front of eye 249. Mouth width 88. Distance between lateral edges of nostrils 138; between medial edges 76; nostril length (greatest diameter) 31; distance from nostril to mouth 27, to edge of disc 51. Diameter (width) of gill openings: 1st 13, 2nd 14, 3rd 15, 4th 13, 5th 10, and 6th 7.5; distance from 1st gill opening to mouth 65, to antero-lateral edge of disc 115; distance from last gill opening to anterior end of cloaca 203; distance between 1st gill openings 128, between 6th gill openings 112.

Distance from anterior end of cloaca to tip of tail 430; width of tail at end of pelvic fins 35, depth (thickness) 28, tail width at base of spines 13, depth 17; greatest height of dorsal tail fin 6.9, of ventral tail fin 6.0. Length of upper (replacement) tail spine 39, of lower (posterior) spine 74+ (tip broken); greatest width of upper spine 5.0, of lower spine 7.1.

Distance between eyes 117; longitudinal eye diameter 13.2, transverse eye diameter 8.0; pupil diameter 4.4; least distance from eye to spiracle 41; least distance between spiracles 101, distance between lateral ends of spiracles 152; spiracle length 31.

EXTERNAL MORPHOLOGY.—The snout (Figs. 1-4) is elongate, flaccid, and of nearly uniform thickness (16-18 mm) anterior to the initial steep declivity from the skull. It is filled with an acellular gelatinous substance, and its form and support are provided mainly by the rostral extensions of the left and right propterygial cartilages. Judging from radiographs, the rostral extensions of the propterygia are not well calcified; and, as there is no rostrum (median process from front of cranium), the entire snout is quite flexible. Unlike the opaque white skin of the ventral surface of the disc, the underside of the snout (Fig. 3) is flesh-coloured, translucent, and provided with numerous evenly-spaced pores of the well-developed ampullae of Lorenzini.

Although much of the epidermis is now missing, the dorsal surface of the disc and tail appears to have been uniformly dark greyish brown (almost black). The spiracular flaps and eyes are black; the dorsal surface of the snout is brownish and paler than the body colour. The ventral surface of the disc and pelvic fins is mostly white; the margin of the disc up to the level of the nostrils is dark greyish brown to black distally. There are irregular patches of dusky black pigment between the nostrils and mouth, at the corners of the mouth and rear edge of each gill opening. There is a dusky area around the cloaca and distal edge of the pelvic fins. Based on what little is left of the epidermis, the colour of the ventral surface of the tail was black.

The eyes (Figs. 1, 2 & 5) are small (greatest diameter 2.1% disc length) and far apart (distance between eyes 23% disc width). The pupil is circular and lacks an operculum pupillare. The lens is well developed. As in other batoids, there is no free upper eyelid, the cornea being completely adnate to the skin surrounding the eye.

The spiracles (Figs. 1, 2 & 5) are large and well back from the eyes. They are closed dorsally by a thin flap supported by a large spiracular cartilage and extending from the anteromedial edge of the spiracle to form an oblique slit at the posterolateral edge of the orifice. There are no spiracular gill filaments.

The nostrils (Fig. 6) are large, transverse, set wide apart and completely separate from the mouth. The anterior margin is provided with a short fleshy flap that becomes progressively shorter medially until, at the midline, it is represented by only a slight ridge. There is no lobe on the posterior margin of the nostril.

The mouth width is greater than the distance between the nostrils. The teeth are small, bluntly rounded, exposed when the mouth is closed, and arranged in a quincunx with 62 series in the upper jaw and 66 in the lower jaw. The buccal cavity is darkly pigmented dorsally and devoid of denticles.

The pelvic fins are small, broadly rounded and fleshy. The right fin was damaged, but the distance between the lateral edges of the intact pelvic fins is estimated at 138 mm.

Figure 5. Right eye and spiracle of *Hexatrygon bickelli*.

Figure 6. Nostrils and mouth of *Hexatrygon bickelli*.

The small upper (anterior) tail spine (Fig. 7) is obviously a replacement for the much larger lower (posterior) spine. The serrations on the lower spine are less distinct (worn?) than those on the upper one. The dorsal tail fin originates about level with the tip of the lower spine and extends to the tip of the tail; the ventral tail fin is longer, arising below the base of the tail spines and reaching to the tip of the tail.

INTERNAL ANATOMY.—The two lobes of the liver (Fig. 8) are about equal in size, pale brown in colour, and together occupy about a third of the abdominal cavity. The cardiac stomach is 60 mm long (from oesophagus to the bend). There are 13 turns in the spiral valve, and the intestine is 130 mm long (from anterior end of spiral valve to cloaca). The spleen is 25 mm long and located on the dorsal side of the pyloric stomach. The rectal gland is well developed. The left oviduct is not large, and the right one is rudimentary. The ovary and shell gland are not apparent.

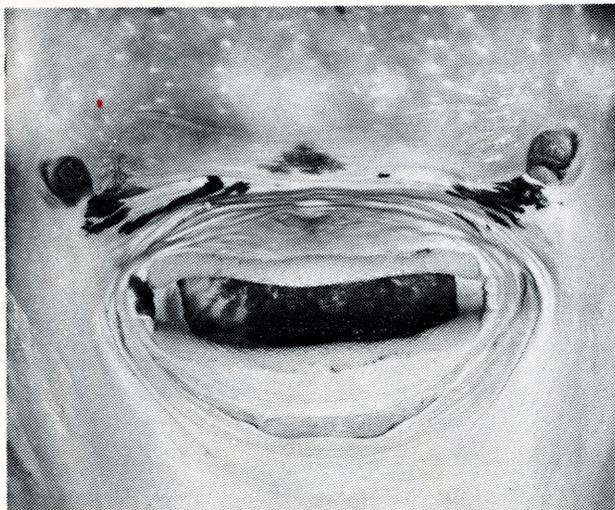The conus arteriosus has a single transverse row of three valves.

SKELETON.—The chondrocranium (Fig. 9) is broader (156 mm across the nasal capsules) than it is long (145 mm). In addition to lacking a rostrum and suborbital shelves, the cranium also has no supraorbital crests. The cartilage that composes the skull is only slightly (if at all) calcified, and even the thickest part of the skull roof can be cut easily with a sharp scalpel. The anterior fontanelle is continuous with the supracranial (frontoparietal) fontanelle, and both are closed by a sheet of connective tissue. The distal end of the preorbital process curves dorsally to form a shallow bifurcation. The canal for the superficial ophthalmic nerve through the anterior wall of the orbit is large (greatest diameter of preorbital foramen 19 mm). The "postorbital process" is a broad, thin (1 mm thick) flat shelf. The width of the rear end of the skull (65 mm) is distinctly greater than that of the anterior end of the synarcual (34 mm).

The anterior synarcual bears a dorsal median crest, but no lateral crests; there are 41 dorsal nerve root foramina. Between the first synarcual and the cloaca, there are 50 centra visible on a radiograph. There are 51 centra from the cloaca to the base of the tail spines. The centra of the posterior half of the tail are fused.
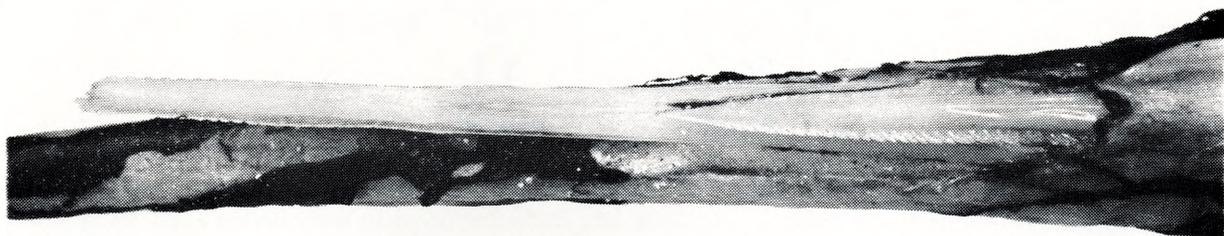

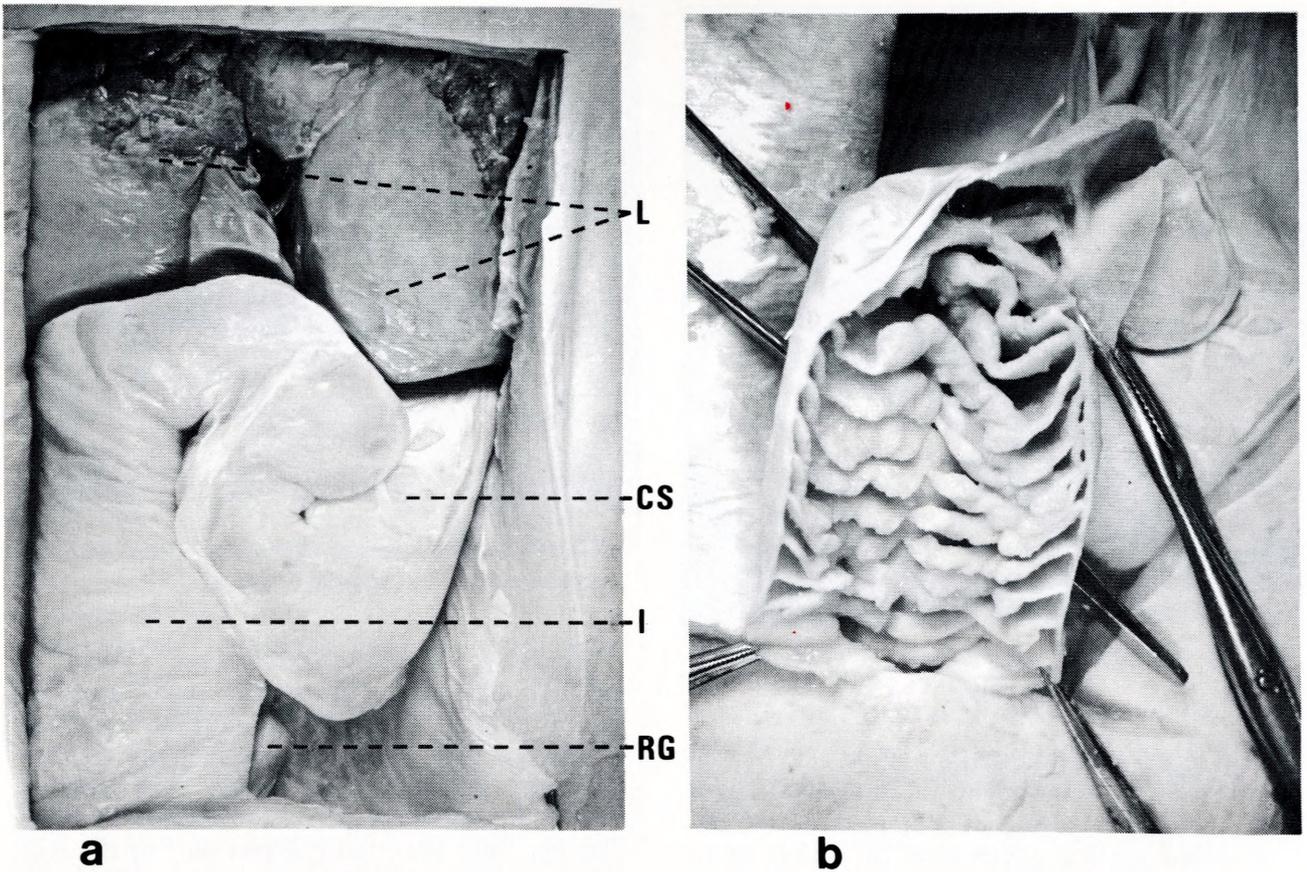Figure 7. Tail spines of *Hexatrygon bickelli*.

Figure 8. Viscera of *Hexatrygon bickelli.* **a.** Ventral view: L, liver; CS, cardiac stomach; I, intestine; RG, rectal gland. **b.** Intestine opened to show spiral valve.
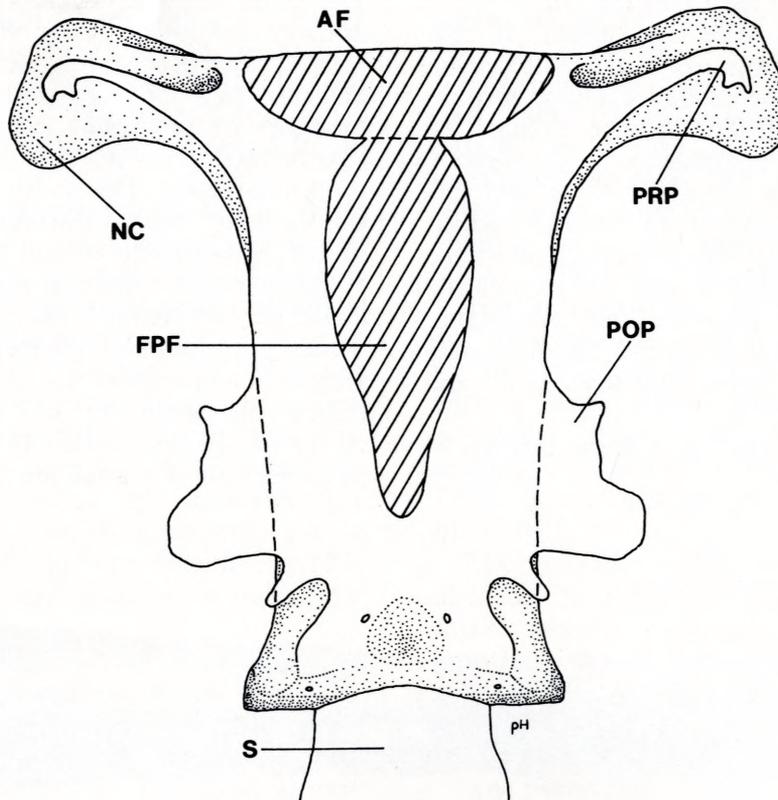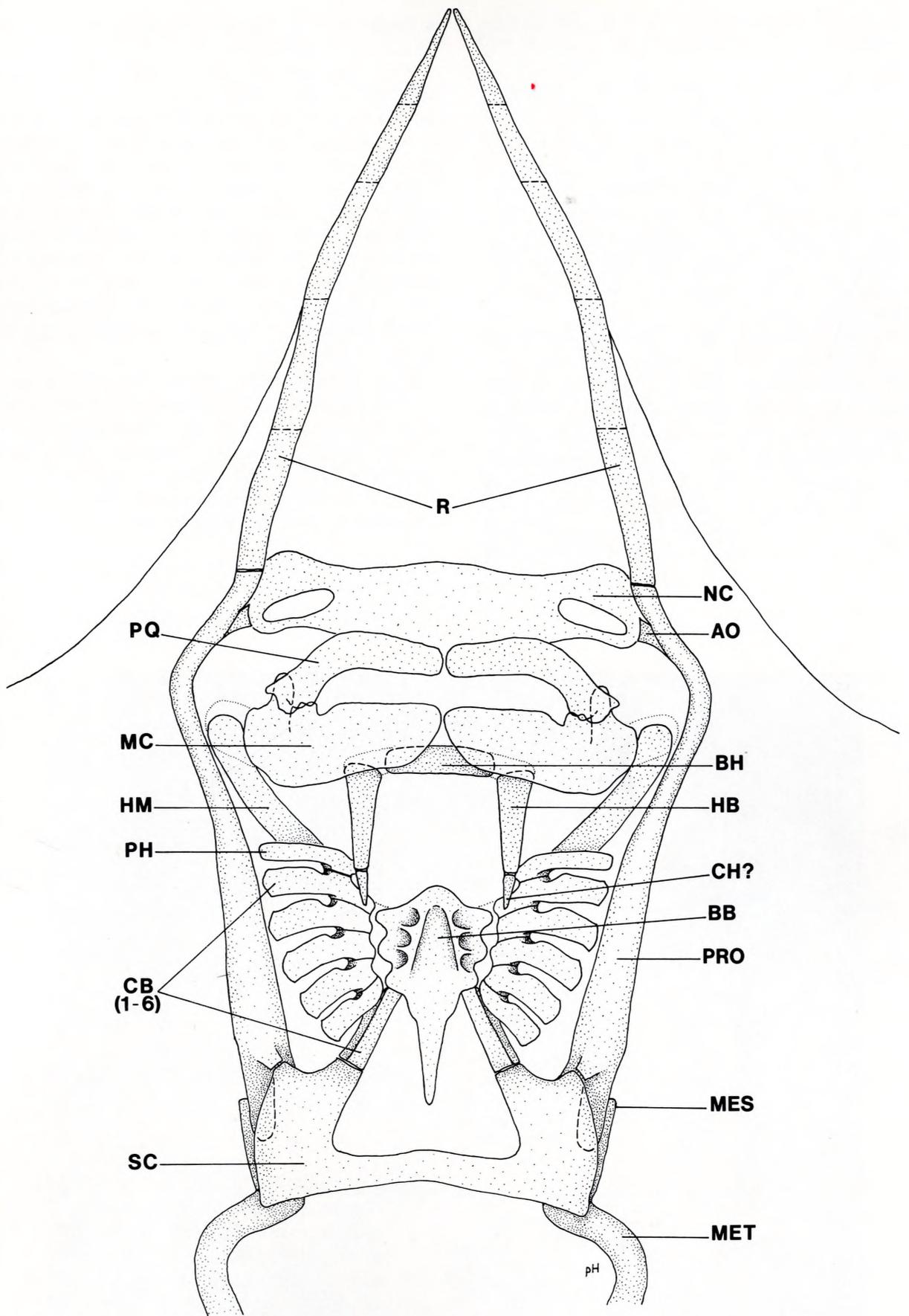

Figure 9. Dorsal view of chondrocranium of *Hexatrygon bickelli.* AF, anterior fontanelle; FPF, frontoparietal fontanelle; NC, nasal capsule; POP, postorbital process; PRP, preorbital process; S, synarcual.

Figure 10. Ventral view of hypobranchial and pectroal fin skeleton of *Hexatrygon bickelli*;
branchial rays not shown. AO, antorbital; BB, basibranchial; BH, basihyal; CB, ceratobranchials;
CH?, ceratohyal rudiment? HB, hypobranchial; HM, hyomandibula; MC, Meckel's cartilage (lower jaw);
MES, mesopterygium; MET, metapterygium, NC, nasal capsule; PH, pseudohyoid;
PQ, palatoquadrate (upper jaw); PRO, propterygium, R, rostral extensions of propterygia.

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The hypobranchial skeleton (Fig. 10) and six branchial arches appear perfectly normal. The copula comprises three pieces: a transverse medial cartilage (basihyal) that is joined at each end by thick connective tissue to the hypobranchial cartilages. The hypobranchials articulate posteriorly with the pseudohyoid cartilages of the first gill arch and a small conical cartilage (perhaps a remnant of the ceratohyal) that projects posteriorly from the end of the hypobranchials. The first gill arch bears a complete hemibranch on its posterior surface. The median basibranchial cartilage is flat except for the paired low archways that bridge the anterior three major branchial arteries on each side.

The suprascapulae (Fig. 11) are almost completely fused to the sides of the first synarcual, but still recognizable as a large knob that articulates with the dorsal tip of the scapulocoracoid. The lateral face of the scapulocoracoid is penetrated by two large fenestrae: one dorsal and one ventral to the junction of the pterygial cartilages. Anteriorly, the scapulocoracoid articulates with the sixth cerato- and epibranchials and the propterygia.

The propterygia are laterally compressed anteriorly, where they curve sharply round the lateral ends of the jaws and hyomandibulae. The antorbital cartilages are partially fused with the propterygia. The propterygia articulate with their rostral extensions at the nasal capsules and just in front of the antorbitals. Judging from radiographs, the rostral extensions appear to be divided into five segments. The metapterygia comprise six segments and extend to the rear end of the disc. The lengths of these segments (from anterior to posterior) are 89, 52, 31, 20, 13 and 9 mm.

The pectoral and pelvic fins are plesodic with no trace of ceratotrichia. The pelvic girdle (Fig. 12) is of the ordinary dasyatid type, with a very slight median process. The radial cartilages of the left pelvic fin are tortuously curved (perhaps an artifact of preservation or an abnormality of this particular specimen).
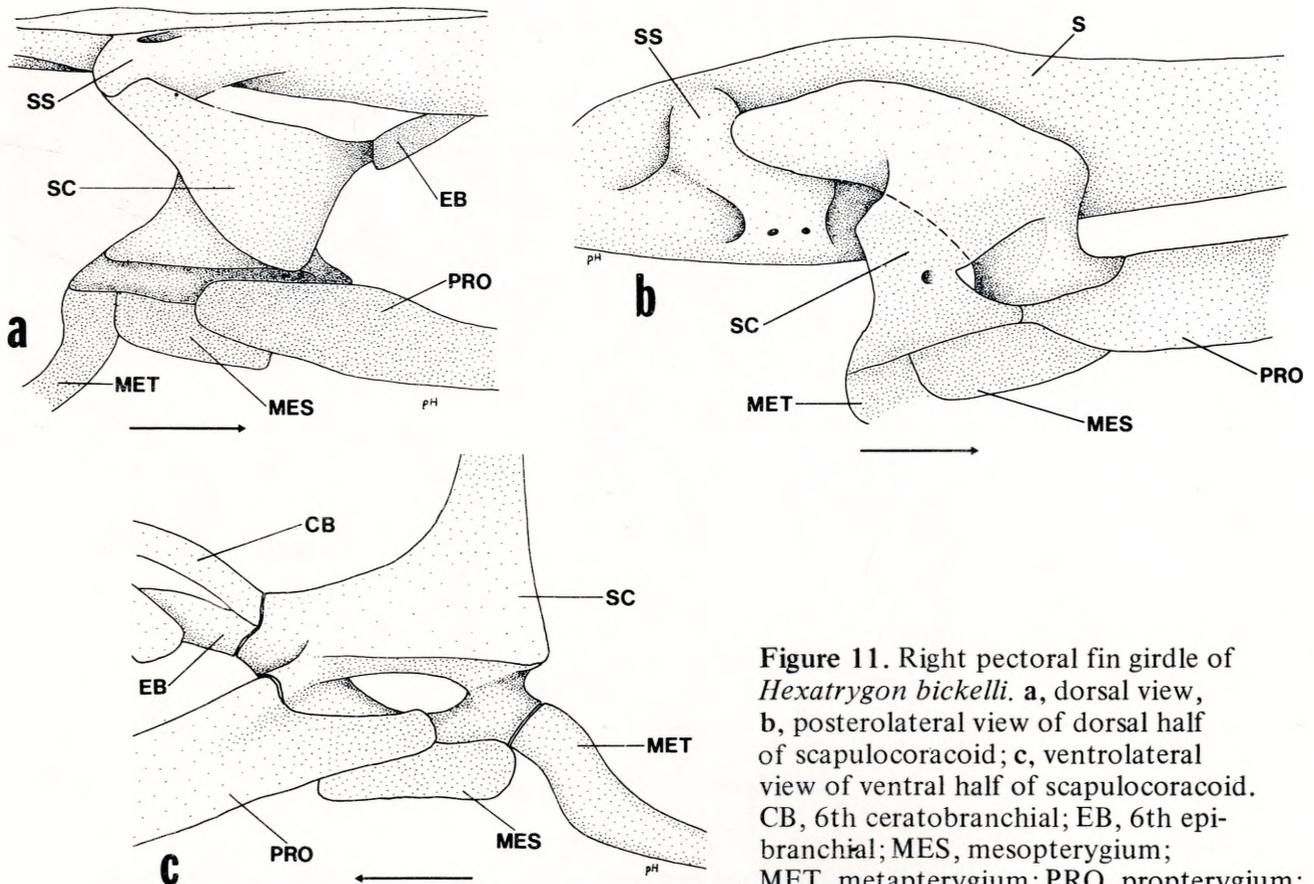
Figure 11. Right pectoral fin girdle of *Hexatrygon bickelli*. a, dorsal view, b, posterolateral view of dorsal half of scapulocoracoid; c, ventrolateral view of ventral half of scapulocoracoid. CB, 6th ceratobranchial; EB, 6th epibranchial; MES, mesopterygium; MET, metapterygium; PRO, propterygium; S, Synarcual, SC, scapulocoracoid; SS, suprascapula. Radial cartilages of pectoral fin not shown; arrow indicates anterior.
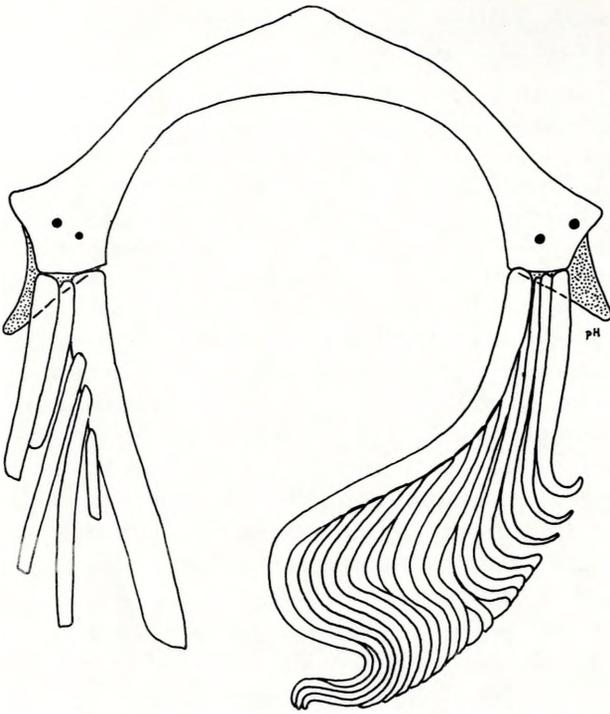
Figure 12. Ventral view of pelvic girdle and pelvic fin skeleton of *Hexatrygon bickelli*. Right pelvic fin skeleton damaged. Stippled cartilage projects dorsally.

BRAIN AND CRANIAL NERVES.—(Figs. 13 & 15). The brain is small (41 mm from rear end of tenth cranial nerve base to front of telencephalon) and occupies only a very small portion (less than 10%) of the cranial cavity: length of cranial cavity 115 mm, width at level of telencephalon 43 mm (width of telencephalon 12 mm), distance from dorsal surface of telencephalon to roof of cranium 30 mm. The brain is located in the rear half of the cranium (distance from front of telencephalon to membrane across anterior fontanelle is 72 mm), and the olfactory peduncles are consequently quite long and slender. As expected from the well-developed network of ampullae of Lorenzini in the snout, the superficial ophthalmic ramus of the anterior lateral-line nerve is much larger than the olfactory tract. The telencephalon is approximately spherical. The cerebellum corpus is divided into two lobes: the anterior lobe is virtually smooth, the posterior lobe is slightly corrugated and not quite symmetrical. The optic nerve runs under the lateral edge of the telencephalon and crosses under the olfactory tract.

Figure 13. Dorsal view of brain of *Hexatrygon bickelli.*

GUT CONTENTS.—The stomach and intestine were empty except for a considerable amount of coarse beach sand that was undoubtedly washed into the gut while the specimen was being tossed about in the surf. The gill cavities were also packed with the same kind of sand.

PARASITES.—The only "parasites" found were five juvenile *Gnathia africana* Barnard, 1914 that were collected from the gill filaments (identification by M.A.A. Baker). The juveniles of this isopod are found on a wide range of fishes. The free-living adults are known only between Lambert's Bay on the west coast and Port Elizabeth in depths of 34 to 200 m (Kensley, 1978).

LIVER OIL.—The composition of the liver oil was determined by Dr A.A. Spark and we quote from his letter of 12 September: "...even before you mentioned it I would have guessed that this is a deep sea animal. The liver oil contained 4% hydrocarbon (squalene), 24% wax ester, 7% alkyldiglyceride, 34% triglyceride, and the rest (alcohols, sterols, free fatty acids) rather high for a fish oil (total 23%). .... Alkyldiglycerides are common in deep sea shark livers. The fatty acid pattern ... is totally different from *Dasyatis pastinaca*."

Discussion of Relationships

Hexatrygon bickelli is unquestionably a member of the taxon Batoidea (or Batoidei) as defined by Bigelow and Schroeder (1953) and Compagno (1973, 1977). It is a moot point whether to recognize the batoids as an order (as done by Bigelow & Schroeder, and others) or as a superorder (as done by Compagno). The classification of batoids proposed by Compagno (1973) is an improvement over that of Bigelow and Schroeder (1953) in that it is based on a more thorough analysis of anatomical characters and better expresses the interrelationships of the component taxa. (We do, however, take exception to Compagno's use of the common name "ray" for all batoid fishes. We believe that the name "ray" should be restricted to the Myliobatiformes. This usage is in accord with Bigelow and Schroeder (1953) and the majority of other recent works on elasmobranchs; and it does not preclude the name "electric ray" for the torpediniforms.)
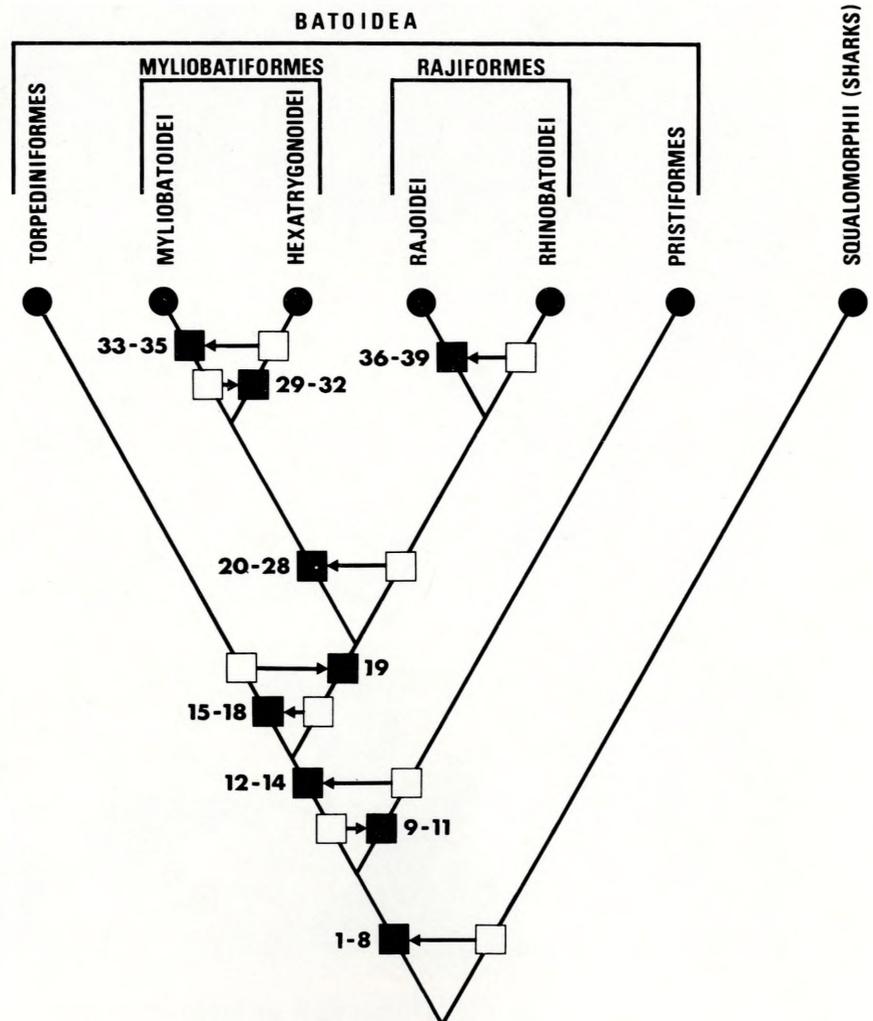

Figure 14. Hypothesis of phyletic relationships of Recent batoid fishes. Shared derived (synapomorphic) characters that distinguish each taxon or monophyletic group are indicated by black boxes and numbered; open boxes represent the alternate primitive (ancestral or plesiomorphic) condition. See text for list and discussion of characters.

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Compagno (1973) recognizes four orders of batoids: 1. Rajiformes; with suborders Rhinobatoidei (guitarfishes) and Rajoidei (skates), 2. Pristiformes (sawfishes), 3. Torpediniformes (electric rays), and 4. Myliobatiformes (rays). The placement of *Hexatrygon* in this classification is complicated by its confusing array of supposedly primitive and derived characters. We can rule out any close relationship of *Hexatrygon* with either Pristiformes or Torpediniformes, as it lacks the unique specializations (synapomorphies of Hennig, 1966) that distinguish these two orders.

We believe that *Hexatrygon* is more closely related to the Myliobatiformes than to the Rajiformes (Fig. 14). How one chooses to express this relationship in a classification is another problematic question of ranking. There are two possible solutions: 1) include *Hexatrygon* in a redefined (expanded) Myliobatiformes; or 2) recognize *Hexatrygon* in a new order, which together with the Myliobatiformes, constitutes a new superorder. We choose the first alternative, but feel compelled (based on the evidence and argument below) to place *Hexatrygon* in a monotypic suborder, Hexatrygonoidei, with the remaining rays falling in the sub-order Myliobatoidei.

In the following list of characters, the derived condition is given first, followed by the primitive condition; the numbers correspond to those of the black boxes on Figure 14. Characters 1-7, 10-12, 18 and 22-28 are compiled from Compagno (1973, 1977), and his work should be consulted for a more complete discussion and illustrations of these features.

BATOIDEA: 1. Pectoral fins enlarged, with expanded anterior lobes fused to sides of head over gill openings; pectorals not fused to sides of head over gill openings. 2. Propterygia of pectoral fins elongated anteriorly and larger than mesopterygia; propterygia not elongated anteriorly and not larger than mesopterygia. 3. Anterior vertebrae fused to form a well-developed synarcual; anterior vertebrae not fused (except in *Squatina*, in which the first two vertebrae are fused). 4. Suprascapulae joined over vertebral column, articulating with column or synarcual, or fused with synarcual; suprascapulae, if present, not connected to each other or to vertebral column. 5. Cornea attached directly to skin about the eyes, *i.e.* no free upper eyelid; free upper eyelid present. 6. Antorbital cartilages present; antorbitals absent. 7. Palatoquadrates not articulating with cranium; palatoquadrates articulating with cranium. 8. Scapulocoracoid articulating with distal ends of posteriormost ceratobranchials; scapulocoracoid not joined to ceratobranchials.

PRISTIFORMES: 9. Rostrum greatly elongated, flattened and provided with large teeth laterally; rostrum not modified into a huge "saw". 10. Anterior end of synarcual with a collar that fits into foramen magnum of cranium; no collar on front end of synarcual. 11. Hypobranchials fused into a single median plate; hypobranchials not fused into a plate (independently fused in some myliobatiforms). 12. Basal angle on ventral surface of cranium absent; basal angle present in pristids. 13. Propterygia elongate, extending to nasal capsules; propterygia not reaching head in pristids. 14. Pectoral and pelvic fins plesodic, without ceratotrichia; pectoral and pelvic fins aplesodic, with well-developed ceratotrichia in pristids.

TORPEDINIFORMES: 15. Electrogenic organs developed between propterygia and head; no pectoral electrogenic organs. 16. No supraorbital crests on cranium; supraorbital crests present (independently lost in *Hexatrygon*). 17. Antorbital cartilages enlarged, expanded distally, branched, and not articulating directly with propterygia; antorbitals simple, joined directly to propterygia. 18. Unique pectoral girdle, with a strut-supported posterior tubular extension bearing a rhinobatoid-like articular surface for the pterygial cartilages; pectoral girdle (scapulocoracoid) not as stated.

19. Suprascapulae fused or articulating with synarcual or vertebral column; suprascapulae not directly connected to synarcual or vertebral column in torpediniforms.

MYLIOBATIFORMES: 20. No rostrum on front of cranium; cranium with rostrum (independently lost in a few species). 21. Prominent serrate spine on tail (secondarily lost in a few species); no serrate spine on tail. 22. Anterior fontanelle delimited in front by a transverse ridge; anterior fontanelle not delimited by a transverse ridge. 23. Frontoparietal fontanelle present and more or less continuous with anterior fontanelle; frontoparietal fontanelle, if present, not connected with anterior fontanelle. 24. Postorbital "processes" very wide and flat; postorbital processes small. 25. Preorbital processes well developed, but secondarily reduced in some families; preorbital processes poorly developed. 26. Thoracolumbar synarcual present; thoracolumbar synarcual absent. 27. Suprascapulae fused to sides of synarcual and forming a complex socket and posterior condyle on each side of synarcual for articulation with dorsal tips of scapulocoracoid; suprascapulae fused or articulating with dorsal edge of synarcual or vertebral column, but not forming sockets or condyles. 28. Lateral prepelvic

processes absent; lateral prepelvic processes present (independently reduced in Pseudorajidae).

HEXATRYGONOIDEI: 29. Six gill arches and six gill openings; five gill arches and five gill openings. 30. Snout elongate, thin (depressed), translucent, filled with a clear gelatinous substance and provided with numerous prominent ampullae of Lorenzini; snout and ampullae of Lorenzini not hypertrophied. 31. No supraorbital crests on cranium, supraorbital crests present. 32. Spiracles well back from eyes, closed *dorsally* by a thin flap extending from anteromedial rim of spiracle to form an oblique slit at posterolateral edge of orifice; spiracles near eyes, closed internally by a valve.

MYLIOBATOIDEI: 33. Brain large, with a highly convoluted cerebellum divided into three or more asymmetric lobes (Fig. 15); brain very small, with a small cerebellum divided into two lobes and not convoluted. 34. Nostrils close together, with anterior nasal flaps connected to form a broad nasal curtain overlapping upper jaw; nares wide apart, with anterior nasal flaps short and fleshy, not forming a broad nasal curtain overlapping upper jaw. 35. Nasoral grooves present, usually well developed; nasoral grooves absent.

RAJOIDEI: 36. Dorsal and caudal fins small to rudimentary or absent, and not supported by ceratotrichia; dorsal and caudal fins well developed, supported distally by ceratotrichia. 37. Propterygia extending beyond
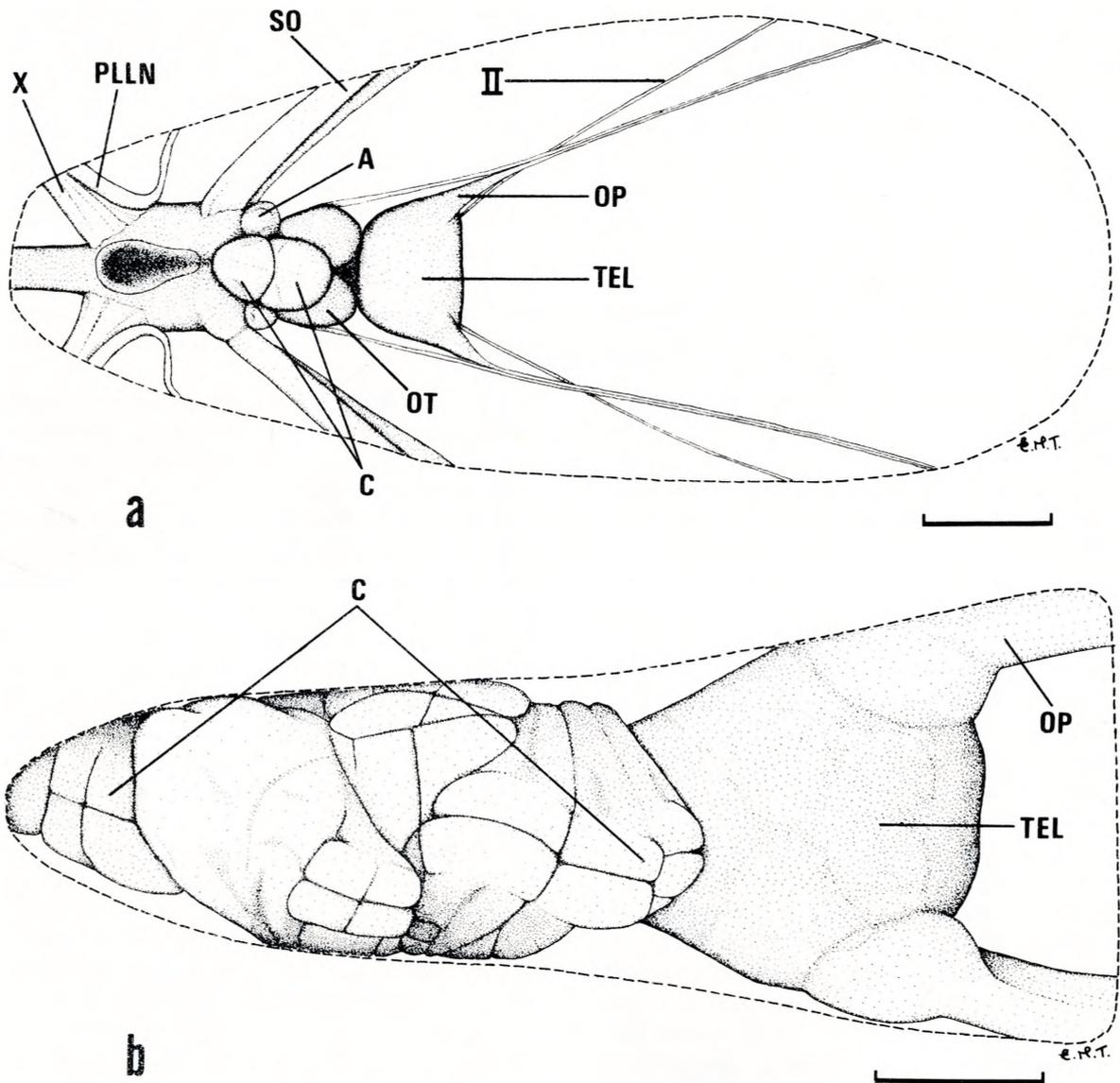

Figure 15. Dorsal view of brains of **a**, *Hexatrygon bickelli* and **b**, *Dasyatis pastinaca* total length 763 mm. Scale lines are 10 mm A, auricle; C. cerebellum OP, olfactory peduncle; OT, optic tectum, PLLN, posterior lateral-line nerve; SO, superficial ophthalmic ramus of anterior lateral-line nerve; TEL, telencephalon; II, optic nerve; X, tenth cranial nerve. Broken line indicates extent of cranial cavity.

nasal capsules; propterygia not extending in front of nasal capsules. 38. Tail slender to whip-like, well marked off from body; tail stout, not much differentiated from body. 39. Pelvic fins with prominent, more or less separate anterior lobe; pelvic fins without anterior lobe.

The diagram of phyletic relationships presented above is essentially the same as that of Compagno (1973: Fig. 5), with the addition of the Hexatrygonoidei. Compagno (1977: Fig. 15B) later decided that the torpediniforms might be the sister group of all other batoids and shows them branching off the batoid stem before the pristiforms are split off. However this hypothesis is based on only one dubious character: the supposedly primitive arrangement of ceratohyals in one family (Narkidae) of electric rays. As indicated in the diagram above, there are six characters (9-11 and 12-14) that indicate that the pristiforms are the earliest derived branch (*i.e.* sister group) of the batoid stem.

Some other innovative details of the phylogenetic analysis presented here require further comment. Character 8 (scapulocoracoid articulating with distal ends of posteriormost ceratobranchials) appears to be a good synapomorphy of the batoids that has been overlooked by previous workers. It is well illustrated in the figures of batoid skeletons published by Garman (1913).

The polarity of the morphoclines represented by characters 12-14 is based on out-group comparison with the Squalomorphii. Characters 13 and 14 are expressions of the increased "batoid specialization" toward fusion of the pectoral fins with the head and their increased use in propulsion.

The characters of *Hexatrygon* are a mosaic of specialized (derived) and primitive states. Based on out-group comparison, we regard characters 29-32 as derived (autapomorphic) states. The presence of six gill arches is therefore derived from the five gill arches of all other batoids. Schaeffer (1967:22) has argued that the "extra" gill arches of hexanchoid sharks and the pristiophorid shark *Pliotrema* are similarly derived states. De Beer (1937) is contradictory on the question of phylogenetic reduction of gill arches in elasmobranchs. At one point (p. 407) he claims that the "tendency is to reduction" and cites as evidence the observations that in young stages of "primitive" sharks (*e.g. Heptanchus*, in which the adult has 7 arches) as many as nine branchial arches may be present; and in *Chlamydoselache* (in which the adult has 6 arches) there may be rudiments of a 7th branchial arch. But later (p. 448) de Beer states that "The difference between Selachii with seven, six, or five branchial arches

is due not to excalation [the reduction of segments in phylogeny by deletion of pre-existing segments], but to transposition [*i.e.* "a redistribution at some very early stage in the unsegmented embryo of the formative substance" (Goodrich, 1913: 239)]. Versluys (1922) has, moreover, given reasons to suppose that the change is due to the persistence in the adult of an embryonic variation which resulted in the laying down *ab initio* of either X, or $X-1$, or $X+1$ branchial arches." The six gill arches of *Hexatrygon, Pliotrema*, and the hexanchoids are thus examples of convergent evolution and reflect a basic embryonic variability rather than a primitive (ancestral) condition.

If we are correct in our polarity of character 31, the absence of supraorbital crests is derived from a myliobatiform ancestor with supraorbital crests, and is an example of convergence with the torpediniforms.

Characters 30 and 32 represent unique derived conditions for *Hexatrygon*. The peculiar snout is unlike that of any other elasmobranch, and appears to be a highly specialized electroreceptive organ (see section on form and function below). The configuration of the spiracle (character 32) is also different from that of all other elasmobranchs.

Based on the examination of 8 species in three different families, all of the myliobatoids appear to have very large brains with a large, complexly convoluted cerebellum (Northcutt, 1978). It seems obvious that the hypertrophy and increased complexity of the brain of myliobatoids (Fig. 15) is derived from the smaller, more simple brain of a rhinobatoid-like ancestor. Consequently, the tiny, simple brain of *Hexatrygon* probably represents a primitive (ancestral) character state.

The nostril configuration of *Hexatrygon* also seems primitive compared with that of myliobatoids. The nostril configuration of myliobatoids can be derived from the *Hexatrygon* (ancestral) state by moving the nostrils closer together, lengthening the anterior nasal lobes, and developing a nasoral groove between each naris and the mouth. (We should point out that the nasoral grooves are variously developed in myliobatoids. In some species, the nasoral groove is a deep groove, but in others it is only a shallow trough.) That the morphologically antecedent condition is also phylogenetically primitive is corroborated by out-group comparison with the rhinobatoids and pristiforms. The movement of the nostrils closer together and fusion of the enlarged anterior nostril lobes to form a broad nasal curtain reaching the upper jaw appears to have been accomplished independently three times in batoid fishes (*viz.* torpediniforms, myliobatoids, and rajoids).

Classification

Using the sequencing convention adopted by Wiley (1979), we translate our hypothesis of phyletic relationships of batoids (Fig. 14) into the following classification:

Superorder Batoidea
　Order Pristiformes
　Order Torpediniformes
　Order Rajiformes
　　Suborder Rhinobatoidei
　　Suborder Rajoidei
　Order Myliobatiformes
　　Suborder Myliobatoidei
　　Suborder Hexatrygonoidei

The sequence of the orders in this classification denotes that the Pristiformes are the sister group of the other three orders combined and that the Torpediniformes are the sister group of the Rajiformes + Myliobatiformes. (See Compagno, 1973 for details of the lower level classification of these groups.)

Speculations on Form and Function

The following discussion is offered with the hope that it might prove heuristic in understanding the unusual features of *H. bickelli*.

This new ray differs notably from all other myliobatiforms in several anatomical features: six gill arches, configuration of the spiracle, morphology of the snout, and other modifications of the head. An additional difference, if we are correct in our supposition of a deep-water habitat (see p. 1) for *Hexatrygon*, is its adoption of a new biotope — all other marine rays are neritic, with none (as far as we know) having been reported below a depth of 200 m, and most are found in the upper 100 m.

The presence of an extra gill arch not only increases the respiratory surface, but also creates a larger pharynx. A larger pharynx would provide a greater volume of water that could be sucked in during feeding. Unlike other rays, which have a spiracle with an internal valve, *Hexatrygon* has a spiracle that is closed dorsally (externally) by a flap-like valve. The dorsally-closed spiracle would also contribute to a larger buccopharyngeal cavity that would be advantageous in feeding.

The peculiar enlarged snout of *Hexatrygon* appears to be a well-developed electroreceptive organ. That the ampullae of Lorenzini are primarily electroreceptors is now well established (Bennett & Clusin, 1978), and their role in the location of prey buried in the substrate has been demonstrated in the field as well as in controlled laboratory experiments (Kalmijn, 1978). The ability to detect the weak bioelectric fields produced by benthic prey organisms would be especially useful in a deep-water habitat, since vision is restricted by the absence of sunlight, and the prey may be well below the surface of the soft (poorly consolidated) sediments. David Eccles (personal communication) has proposed that elongation of the snout in *Hexatrygon* is analogous to the function of the magnetometer boom of a geophysical survey or anti-submarine aircraft, *i.e.* to physically remove the sensors as far as possible from endogenous sources of interference. And the clear gelatinous substance that fills the snout, Eccles suggests, "if not an insulator, being non-cellular, is likely to be inert and not to be a source of 'electrical noise'. This may be a more significant function than insulation. The posterior position of the brain in the cranial cavity may also serve to isolate it from the rostral ampullae."

Compared with a like-sized specimen of *Dasyatis pastinaca* (Linnaeus) (Fig. 15), the brain of *Hexatrygon* is remarkably small: about one-sixth the size of the *Dasyatis* brain. But the cranial cavity of *Hexatrygon* is much larger than that of the *Dasyatis* specimen. The brain volume of *Hexatrygon* is only about 3% of its cranial volume; whereas the *Dasyatis* brain volume is about 80% of its cranial volume. Why *Hexatrygon* has such a small brain in a very large cranium is not clear. Nor do we understand why the adult coelacanth, *Latimeria chalumnae* Smith, exhibits a similar proportion of tiny brain in a capacious cranium (Milot & Anthony, 1965).

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