

Revision of the Dermal Tubercles of Rays (Chondrichthyes: Batoidea) from the Parana Basin, Tertiary of South America.*

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[an English version of the abstract is provided within the original article]

Introduction

In 1886 Larrazet described and illustrated “bony bucklers” of rays reported from the Parana Basin, South America and dated as from the Late Miocene. These specimens, attributed to *Dynatobatis paranensis*, *D. rectangularis*, *Raia antiqua*, and *Raja agassizii*, are compared here to the skin coverings of modern chondrichthyans and assigned to the family Potamotrygonidae, a clade endemic to South America.

Unlike marine ray species, which are able to frequent lakes and rivers only for short periods of time, the Potamotrygonidae are exclusive to freshwater and cannot tolerate a saline environment due to the atrophy of the rectal gland and the absence of urea in the blood (Thorson et al., 1967; Thorson et al., 1978; Thorson et al., 1983).

Material and Methods

This work is based on the twelve specimens from the Tertiary of the Parana Basin deposited in the collections of the Paleontology Laboratory of the National Natural History Museum in Paris (AGD). These specimens have been compared to constituent elements of the skin covering of various modern chondrichthyan families (Echinorhinidae, Rhinidae, Rhinobatidae, Rhynchobatidae, Platyrrhinidae, Arynchobatidae, Pseudorajidae, Rajidae, Dasyatidae, Potamotrygonidae, and Urolophidae), belonging to the following ichthyological collections: National Natural History Museum, Paris (M.N.H.N); Smithsonian Institution, Washington D.C. (USNM); California Academy of Sciences, San Francisco (C.A.S; S.U.); University of Bergen (B.M.); Texas A&M University (T.U.); Institute of Natural Resources and Environment, Hobart (C.S.I.R.O.) and the British Museum of Natural History, London (B.M.N.H.).

In the discussion below, the numbers between parentheses following the numbering by the Institute of Paleontology of the M.N.H.N. refer to Larrazet’s original plates (e.g. Lar. No. 00 – pl. XX).

The nomenclature of the different constituent elements of the body covering of batoids follows Bertin (1958), Hubbs & Ishiyama (1968), and Stehmann & Burkel (1984). The terms used in the body of the text are as follows:

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Dermal denticles: structures of dermo-epidermal origin in the tenths of millimeters to several millimeters in length, constituting the primitive skin covering of chondrichthyans. Dermal denticles are made up of an intradermal base separated from a crown or exodermal polymorphic scute by a more or less differentiated peduncle.

Tubercles, bucklers, and spines: hypertrophic denticles with a massive, more or less pointed crown or of an aberrant shape without a differentiated peduncle and generally arranged in a series forming more or less regular rows.

The “groove” refers to a concave longitudinal furrow in a generally radiating pattern, a characteristic of the superficial relief of the tubercles and differentiating itself from the ridge, which is a convex structure.

The “striations” refer to generally parallel fine lines, less marked than the grooves.

The term “stellate” refers to a star-shaped contour outlined by the basal surface.

The term “radiated” characterizes the radiating lines of the spine or the base of the tubercles or dermal denticles.

The “spine” (crown or cusp) is characterized as the superficial, pointed part of the dermal denticles and tubercles.

Fossils of the Tertiary of the Parana Basin

AGD1 to AGD4: Four “bony bucklers” of *Dynatobatis paranensis* Larrazet 1886, Rio Parana Cliff at Uquiza villa, Tertiary Formation. Sizes: 40-50mm in base length.

AGD5: One “bony buckler” of *Dynatobatis rectangularis* Larrazet 1886, same locality and formation as above. Size: 48mm in base length.

AGD6 to AGD12: Seven “bony bucklers” of *Raja agassizi* Larrazet 1886 (not *R. agassizi* Muller & Henle, 1841), same locality and formation as above. Sizes: 18-38mm in base length.

Description

The morphologic study of the tubercles collected by Larrazet allow for their classification into an either discoidal or pyramidal morphotype as seen from a lateral view.

The discoidal morphotype

The ten specimens reported as *Raja agassizi* (AGD5-AGD12) and *Dynatobatis paranensis* (AGD2 and AGD3) exhibit an elliptical profile of discoidal type composed of

two noticeably identical convex parts. The lower part is weakly domed and without distinct relief while the upper part exhibits a more accentuated bulge.

A small spine is positioned at the center of the specimen: its circular and lightly-striated base is set in the center of a shallow cavity or at the top of a more or less pronounced bulge (Lar. 6 – XIII) (Pl. 1, fig. 1,2). This spine is separated from the periphery of the tubercle by a narrow band following the contour of the specimen. Outside of the central spiny region and away from the external border, the surface of the tubercle is deeply incised by radiating grooves giving it a cracked appearance.

The discoidal specimen AGD9 (Lar. 4 – XIII) (Pl. 1, fig. 3,4) comes from the fusion of two distinct sub-units. The weakly convex upper surface of this specimen is marked by pronounced relief. Its lower surface is uneven and marked by deep perpendicular grooves along its longitudinal axis.

The largest sub-unit constitutes an ovoid base and possesses a deep central invagination concealing two short broken spines with a widened and radiated base. At the periphery of this cavity the surface of the tubercle exhibits a porous appearance.

The second sub-unit, composed of a circular base, possesses at its center a blunt yet prominent spine. The spine base is expanded and covered with about twelve radiating ridges. A smooth narrow zone is distinct within the outer region of this tubercle. Specimen AGD9 was born from the union of two discoidal bucklers, considered by Larrazet to be a transitional form between simple bucklers and those derived from the inflation of a pre-formed element (a compound buckler).

The rectangular shape of the specimen reported as *Dynatobatis rectangularis* (AGD5, Lar. 1 – XV) resulted from lateral fractures on an originally circular form as evidenced by concentric striations on the upper surface of the specimen which are abruptly interrupted by truncated sides. The base of a weak spine is discernible at the bottom of a small central cavity.

Specimen AGD8 (Lar. 3 – XIII), which is longitudinally broken, exhibits a laterally compressed basal surface, ovoid in outline and marked by superficial ridges and grooves. Two large spines are visible on its upper surface. Their radiated base shows a sub-circular outline. This specimen was characterized by Larrazet as a compound buckler “resulting from the union of several simple bucklers.”

The pyramidal morphotype

This morphotype corresponds to two of four specimens described by Larrazet under the name *Dynatobatis paranensis*.

AGD4 (2 – XIV) (PL. 1, fig. 7,8): it is a specimen of which the roughly ovoid base is composed of a lower part, rather thin and coarse at its extremities and a bulky and quite

convex upper part marked by a flattening of its top and the presence of two distinct, smooth spines. The largest part of this piece is incised by deep radiated grooves.

AGD1 (1 – XIV) (Pl. 1, fig. 5, 6): this roughly conical specimen is composed of a well-developed ovoid base, of which the lower part is rather thin while the upper part is more developed. The top is marked by two smooth spines. The off-center one is larger. Deep grooves appear from the base of the specimen to the top while the lower part presents a distinct natural median concavity that Larrazet interpreted as a break.

Comparative analysis

By their significant size (between 18 and 55mm in base length), their undifferentiated peduncle, their circular base, and their discoidal or pyramidal morphology, the studied specimens reveal themselves to be spiny tubercles or bucklers like those defined above. The comparison with modern species of chondrichthyans allows us to offer the following details:

Some tubercles, bucklers, or spines distinguish themselves among sharks in the family Echinorhinidae and are used in the taxonomic separation of two living species. These tubercles, of large size in *Echinorhinus brucus* (Bonnaterre 1788), have a more or less dorso-ventrally compressed base (fig. 1a, b) marked by a prominent bulge on the larger specimens.

The bases are sometimes coalescent in *E. brucus* whereas they are radiated, present a stellate margin, and never fused in *E. cookei* Pietschmann 1928 (Cadenat & Blache, 1981; Compagno, 1984; Deynat, 1990) (fig. 1c). In the latter species, the base is topped by a short spine, erect or slightly inclined to the rear without a differentiated peduncle.

Tubercles and dermal denticles of these two shark species differ from the Tertiary Parana Basin specimens by the flattened form of their base, the erect off-center spine not housed in a cavity, pronounced and less-numerous grooves (*E. brucus*), and the stellate, coarsely-serrated contours of the base (*E. cookei*).

Some bucklers, spines, and spiny tubercles of variable shape are found in most species of batoids belonging to the orders Rajiformes and Myliobatiformes (Table 1).

In the “Rhinobatoidei” sensu Compagno (1973) some large tubercles are distinguishable mainly in *Rhina ancylostoma* (Bloch & Schneider, 1801). This species possesses large spiny tubercles, which are more or less juxtaposed and aligned in longitudinal rows (tubercular crests).

These tubercles possess a large triangular laterally constricted cusp, slightly inclined to the rear and covered with numerous striations along nearly its entire length but looks nothing like the short erect spines of our specimens (fig. 1d, e). Lacking distinct relief, the ovoid base bears no resemblance to the studied material.

Within the “Rajoidei” (rays in the strict sense) the tubercles are modified into spines and bucklers. The Rajidae, the Pseudorajidae, and the Arynchobatidae possess series of aligned or isolated spines of which the ovoid base may or may not be covered with deep grooves and include a more or less pronounced spine. The interspecific morphology shows only slight variations in the shape of the spine or the base (fig. 1j, k, l, m). The general morphology of the examined fossil specimens in this article do not exhibit characteristics of spines typical of the Rajoidei.

Table 1 – Comparison of the dermo-epidermal covering of extant batoids. (1) small “partly spiny” structures have been described in *Torpedo mackayana* Metzelaar, 1919 but these structures appear to be sensitive papillae (Bigelow & Schroeder, 1953: 92).

	Dermal denticles and spinules	Bucklers,
spines, and tubercles		
Torpediniformes spines, nor tubercles	no denticles	no bucklers,
Pristiformes spines, nor tubercles	small, densely-distributed denticles	no bucklers,
Rajiformes		
Rhinidae	small deeply overlapping dermal denticles	tubercular crests
Rhynchobatidae	small, densely-distributed denticles	aligned tubercles
Rhinobatidae	small, densely-distributed denticles	aligned tubercles
Platyrrhinidae	small, densely-distributed denticles	aligned tubercles
Arhynchobatidae	small, densely-distributed denticles	aligned tubercles
Anacanthobatidae mature males	no denticles	alar spines in
Pseudorajidae	sharp denticles variably distributed on both sides	aligned spines
Rajidae bucklers	sharp denticles variably distributed on both sides	aligned spines and
Myliobatiformes		
Dasyatidae lanceolate, spiny denticles	heart-shaped and/or stellate denticles	pearl-like,
Potamotrygonidae tubercles	tricuspid denticles and stellate tubercles	bucklers and spiny
Urolophidae tubercles	small spiny tubercles	aligned lanceolate
Hexatrygonidae spines, nor tubercles	no denticles	no bucklers,
Gymnuridae nor tubercles	no denticles	no bucklers, spines,
Myliobatidae nor tubercles	no denticles or very localized	no bucklers, spines,
Rhinopteridae spines, nor tubercles	no denticles or very localized	no bucklers,

Mobulidae densely distributed denticles on both sides no bucklers,
spines, nor tubercles

In the thornback skate, *Raja clavata* Linnaeus 1758, mature individuals possess large bucklers on both sides of the disk which are composed of a massive globular and ovoid base topped by a small curved spine (fig. 1n, o). Such bucklers also distinguish themselves on the ventral side of the disk of *Sympterygia bonapartei* Muller & Henle 1841. The examined specimens show neither the globular and smooth qualities of these bucklers nor the more or less curved and inclined spine.

Among the Myliobatiformes the tubercles are differentiated only in a very small number of taxa (Tab. 1). Most of the species of the Dasyatidae possess a mediadorsal line of spiny tubercles with a flattened and lanceolate cusp, aligned from the scapular region to the base of the spine – ex. *Dasyatis guttata* Bloch & Schneider 1801 (fig. 1f, g).

In *Dasyatis centroura* Mitchill 1815 supernumerary spiny tubercles with circular dorso-ventrally constricted bases appear along the entire length of the tail and scattered across the dorsal side of the disk. The more or less circular base includes a prominent central spine from which about ten radiating ridges diverge, reaching the edges of the tubercle. The spine is not in a cavity but rests on an elevated base. It is erect without a marked separation from the base and of a size nearly equivalent to the length of the tubercle (fig. 1h, i). There is no granular, differentiated band and the perimeter of the base is generally serrated on the larger specimens. The tubercles can be distinctly juxtaposed.

Within the Dasyatidae the skin covering of the various taxa differ from the examined fossil specimens in their morphological characteristics, such as the constricted spiny tubercles of *Dasyatis* and *Taeniura*, the pearl-like [shiny and rounded] tubercles of *Himantura* and *Dasyatis*, and the heart-shaped denticles of *Dasyatis*, *Himantura*, *Hypolophus*, and *Urogymnus*.

Among the Potamotrygonidae the skin covering is particularly well-developed in the genus *Potamotrygon*, distinguished by the discal bucklers and large caudal tubercles. The discal bucklers have a circular to subcircular base without a distinct peduncle and can be more or less fused in the larger specimens. Their centers are armed with a short, erect spine positioned in the hollow of a small cavity or on a protuberance depending on the maturity of the animal. The region situated between the central spine and the edges of the tubercle is granular, featuring grooves directed towards the center of the tubercle (Pl. 1, fig. 11, 12). This type of buckler approaches the form of specimens AGD2, AGD3, and AGD5 through AGD12.

Among the modern Potamotrygonidae the spiny caudal tubercles have a pronounced pyramidal shape. Their concave base is topped with a short spine. From the base deep grooves appear along nearly the entire height of the tubercles (Pl. 1, fig. 9, 10). The caudal tubercles of this type resemble specimens AGD1 and AGD4.

The ornamentation on the dorsal surface is also different from one type to another (Table II). On the discal bucklers the upper surface is composed of a maze of deep, radiating grooves giving an overall cracked-radiated appearance. The spine itself is crossed by less numerous but more marked grooves to its base. The surface of the mediodorsal caudal tubercles is marked by deep grooves from the base of the exodermal part to the tip. This differentiation is also observable in the fossil specimens in this article.

Table II. Morphological characteristics of extant potamotrygonid tubercles

		discal tubercles (bucklers)	caudal tubercles
crown	spine	conical and erect	conical and erect
	localization	bottom of the cavity	top of a bulge
peduncle		undifferentiated	undifferentiated
base	dorsal view	circular	ovoid
	lateral view	discoidal	pyramidal
	ventral surface	convex with grooves	concave without
grooves			
coalescence		often	sometimes

Conclusion and Biogeographical problems

The morphological and comparative study allows us to assign the Parana Basin specimens to the family Potamotrygonidae. These specimens can be separated into ten discal bucklers and two spiny caudal tubercles, of which the morphological characteristics belong to those of the hypertrophied dermo-epidermal covering of modern species of the genus *Potamotrygon* (Tab. II).

The genus *Dynatobatis*, erected by Larrazet (1886) for some ray fossils characterized by “some bucklers of which the base is extraordinarily well-developed while the spine is very reduced,” had been previously placed in synonymy with the genus *Potamotrygon* by Garman (1877, 1913) and later by Jordan (1923). Fowler (1970) in his world catalogue of fishes lists five species within the genus *Dynatobatis*: *D. africanus* Arambourg 1947; *D. gaudryi* Larrazet 1886; *D. gotoi* Matsumoto 1836; *D. paranensis* Larrazet 1886 and *D. rectangularis* Larrazet 1886. Many other fossil remains from Africa previously assigned to *Potamotrygon* (Arambourg, 1947) were recently reassigned to the genus *Dasyatis* (Feibel, 1993).

[The author, Feibel, is misspelled at the end of the paragraph above in the original text but spelled correctly in the reference list.]

Taking into account some problems in dating and recovering some of the specimens studied by Larrazet (1886), Thorson & Watson (1975) expressed their doubts about referring these remains to the family Potamotrygonidae.

This study demonstrates the validity of placing the genus *Dynatobatis* into synonymy with the genus *Potamotrygon* and the invalidity of the species *Dynatobatis rectangularis*, erected on the basis of a broken discal buckler. This study also suggests that the species *D. paranensis* and *R. agassizii*, described by Larrazet, are attributable to the modern species *Potamotrygon motoro* as they bear similar bucklers. However, the synonymy will be established only after a study of the variability within the dermal covering of the Recent species of *Potamotrygon*.

The Potamotrygonidae represents South American freshwater rays localized in the major river systems with the exception of the Chilean river system (Castello, 1975) and probably the Sao Francisco River system in the eastern part of Brazil (Brooks et al., 1981). The family includes about twenty species across three valid genera: *Potamotrygon* Garman 1877; *Paratrygon* Dumeril 1865 and *Plesiotrygon* Rosa, Castello, and Thorson 1987 as well as a fourth genus considered a nomen dubium, *Elipesurus* Schomburgk 1943 (Rosa, 1985). The species belonging to the genera *Paratrygon*, *Plesiotrygon*, and *Elipesurus* lack discal bucklers and spiny caudal tubercles at all stages of development as they were described above.

Brooks et al., (1981) proposed four hypotheses for the origin and evolution of the Potamotrygonidae using a cladistic analysis and a vicariance study based on the parasitic worm fauna. The most widely-accepted hypothesis suggests that the Potamotrygonidae represents a monophyletic group derived from a non-dasyatid marine ancestor isolated in South America by the Andean orogeny.

The question of the origin of the group remains open, however, due to the absence of the Isthmus of Panama during much of the Tertiary and the occurrence of successive transgressions of epicontinental seas during the Cretaceous and Tertiary. These transgressions came more from the Atlantic than the Pacific (Uliana & Biddle, 1988), favoring the arrival and interchange of faunas.

The re-identified specimens in this article represent the oldest members of the Potamotrygonidae (Miocene). Other batoid remains are known from the Mesozoic and Cenozoic of South America (Cappetta, 1987; 1992; Brito and Seret in press) but these remains belong to taxa unrelated to the Potamotrygonidae. The identification of the potamotrygonid remains shown here allows us to postulate an origin of the group well before the Miocene. However, only a systematic study stating the phylogenetic relationships of the Potamotrygonidae within the Myliobatiformes as well as a better understanding of South American geodynamic events would allow the formulation of a more precise biogeographic model regarding the origin and evolution of this group. This study now under way is part of a project on the systematics, biogeography, and chronostratigraphy of South American terrestrial vertebrates.

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