Variation of the synarcual in the California Ray, *Raja inornata* (Elasmobranchii: Rajidae)

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ABSTRACT:

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Seven juvenile specimens of *Raja inornata* were CT scanned and digitally modeled to examine the variation of synarcual morphology with changing size. The synarcual is a highly variable skeletal element across batoids with great potential for use in phylogenetic studies. Results show that as *R. inornata* increases in body size, the synarcual becomes more elongate and laterally compressed. Projections of the synarcual become more pronounced with increasing size as well. The synarcual of *R. inornata* is narrower than that of *R. erinacea*. There appears to be a correlation between median crest width and synarcual spine size. Also, in the context of higher-level batoid phylogenetics, the morphologically ventral position of the u-shaped lateral stay is considered primitive.

Key words: Fused anterior vertebrae, Computed tomography.

INTRODUCTION

Two relatively unstable characters that unite the batoids with the sawsharks (Pristiophoridae) and the angelsharks (Squatinidae) are the presence of a basioccipital fovea and occipital hemicentra (SHIRAI 1996). Also present in the sawsharks, anglesharks and the batoids are significant modifications to the first several vertebrae, or anterior synarcual in batoids (Compagno 1977; = synarcuum, Lovejoy 1996; = synarchial, McEachran & Aschliman 2004). Thus, in addition to its role in diagnosing Batoidea, I hypothesize that the manor in which anterior synarcual develops will be significant in determining relationships of Batoidea to other elasmobranchs.

The anterior synarcual cartilage is an often long skeletal element, formed by the fusion of the first several vertebrae in batoids. Neural arches contribute to the tube-like portion that transmits the spinal cord and ventral or pleural ribs contribute to the ventral base and

lateral stays. Anteriorly, the anterior synarcual contacts the neurocranium. Posteriorly, it is forked and is closely associated with isolated centra that progress into the vertebral column. In stingrays (Myliobatidae), a second, posterior synarcual is present and separated from the first by two or more intersynarcual centra, depending on the taxon (GARMAN 1913, NISHIDA 1990). Documentation of the general morphology of the anterior synarcuals in stingrays is limited and scored in only a handful of phylogenetic studies about the interrelationship of batoids (e.g. NISHIDA 1990, CARVALHO 1996, LOVEJOY 1996, SHIRAI 1996, McEachran & Aschliman 2004, Carvalho & al. 2004, Gonzáles-Isáis & Domínguez 2004). With few exceptions, non-stingray batoids, such as the skates (Rajidae), were excluded from these studies or treated as single terminal taxonomic units.

Skates are a morphologically conserved clade within Batoidea and they have a substantial species di-

versity. The interrelationships among skates, apart from other taxa, were examined on several occasions (e.g. McEachran & Compagno 1982, McEachran 1983, 1984, McEachran & Dunn 1998). Skeletal characters used in earlier analyses of the skates were heavily focused on the neurocranium, claspers, and scapulocoracoid. This study is an introduction to the variation of the anterior synarcual in the California Ray, *Raja inornata* Jordan & Gilbert, 1881. Character descriptions presented here are relevant for ongoing and future analyses of batoids.

MATERIALS AND METHODS

Seven juvenile specimens of *Raja inornata* from the Seth Eugene Meek Library of the Field Museum of Natural History (FMNH) were scanned at The High-Resolution X-ray Computed Tomography Facility at the University of Texas at Austin (UTCT). All individuals are catalogued under the same specimen number, FMNH2754, and are referred to by letters A-G (Table 1). Specimens A and B were stacked one on top of the other and scanned with their vertebral column parallel to the floor. Specimens C-G were suspended one in front of the other with their vertebral column perpendicular to the floor. Detailed scanning parameters are available in Table 1. Resulting digital thin sections were input into the volume rendering

software, VGStudio MAX (Volume Graphics, Heidelberg, Germany). The anterior synarcuals and associated intersynarcual vertebrae were digitally dissected from the remainder of the dataset using contrast thresholding and opacity optimization (Textfig. 1). Standard straight-line distance measurements followed those described by McEachran & Carvalho (2003).

	I., J., J., J. A. D.	I dii d1- C C		
		Individuals C-G		
	P250D, 419 kV,	II 200 kV,		
	1.8 mA	0.12 mA,		
intensity control	-	on		
high-power mode	-	on		
filter	no	no		
container wedge	air	empty		
offset	130%	none		
slice thickness	0.25 mm	0.06083 mm		
S.O.D.	681 mm	175 mm		
views	1000	1400		
samples per view	1	3		
field of reconstruction	160 mm	56.5 mm		
maximum field of view	179.9645 mm	58.02518 mm		
reconstruction offset	400	5000		
scanner scale	10300	9800		
reconstruction scale	8000	6100		
total final slices	205	1006		

Table 1. Scanning parameters of Raja inornata (FMNH 2754)

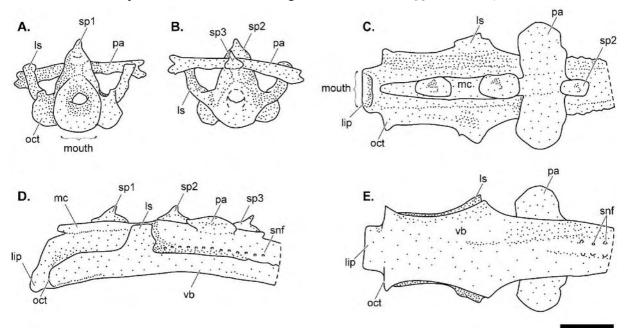


Fig. 1. Line rendering of *Raja inornata* synarcual, FMNH 2754-D. A – Anterior, B – Posterior, C – Dorsal, D – Lateral, E – Ventral. Abbreviations: ls – lateral stay; mc – median crest; oct – occipital cotyle; pa – pectoral arch; snf – spinal nerve foramina; sp1-3 – first through third synarcual spines; vb – ventral base. Scale bar = 5 mm

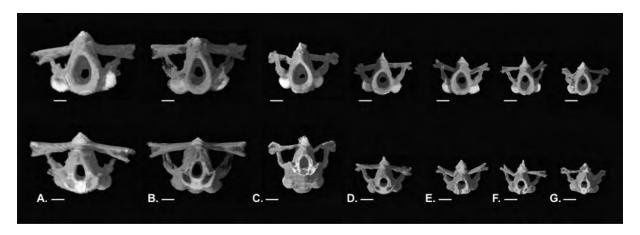


Fig. 2. Raja inornata JORDAN & GILBERT, 1881. Volume rendered 3D images of seven synarcuals, FMNH 2754. A-G – Anterior (top) and posterior (bottom) views. Scale bar = 1 cm

RESULTS

Synarcual description based on CT data

Specimens show minor damage from storage in glass jars but all individuals were in good condition. Individuals B and D had the least amount of damage to the pectoral arch (Text-figs 2, 3). The data sets for individuals A and B are a lower quality than for C-G because of the position that they were scanned in. Thus for finite details, it was difficult to correlate the largest to the smallest specimens. The results discussed here are of gross morphological detail.

Only one synarcual (the anterior synarcual) is present in *Raja inornata* and is referred to as the synarcual from here on. The synarcual of all individuals is an elongate cartilage that incorporates 28-30 vertebral segments into its structure, as indicated by the number of paired spinal nerve foramina present. With increasing body size, walls of the neural canal and ventral base widen, although the relative amount of surface skeletal calcification is unchanged. Also, as body size

increases, the neural canal becomes more dorsoventrally lengthened.

The anterior neural canal opening (mouth) is teardrop shaped, narrower dorsally than ventrally. The walls of the canal are continuous with a ventral synarcual base. The ventral margin of the synarcual mouth projects past the base anteriorly, creating a lip. This lip lies within the foramen magnum. Morphology of the lip varies among the individuals examined. In the smallest individuals, the lip is created by a gradual, anteroventral sloping of the synarcual mouth (Text-figs 2C,E-F). In larger individuals, there is an abrupt outward jut approximately midway down the mouth (Text-fig. 2A, B).

Lateral stays are present midway along the synarcual. Anterior to the lateral stays, the synarcual base curves slightly dorsally and obscures the view of the more dorsally located spinal nerve foramina (Text-fig. 1D). The base also curves slightly medially before widening again at the anteriormost occipital cotyles (Text-fig. 1C, E). Occipital cotyles of the synarcual are tightly articulated with the occipital condyles of the skull and were difficult to render separately for 3D im-

	TL	TaL	DL	DW	SnL	SnL	SynL	SynH	SynW	SA	Sex
				Oral	Orb						
A	41	18.5	22.5	28	6	6.3	5.18	.07	.037	92°	F
В	30	14	16.5	21	4.5	4.5	3.9	.056	.032	94°	F
C	26	12	13	16	3.5	3.5	2.95	.045	.029	100°	F
D	19.5	10	10.1	13.4	3.2	3.2	2.27	.034	.026	97°	M
E	17	9.2	9	12	2.5	2.5	2.05	.034	.026	110	F
F	16	8.5	8.2	10.6	2.3	2.3	1.67	.032	.021	110	F
G	14.3	7.5	7.2	9.9	2.1	2.1	1.34	.027	.019	110	F

Table 2. Measurements of *Raja inormata*, FMNH 2754. Abbreviations: DL=disk length; DW=disk width; F=female; M=male; SA=angle of snout at level of spiracle; SnLOral=length of snout, preoral; SnLOrb=length of snout, preorbital; SynH=height of synarcual mouth aperture; SynL=synarcual length; SynW=width of synarcual mouth aperture; TaL=tail length; TL=total length. Units=cm. Specimens come from a single lot and individuals are identified by a letter throughout the text

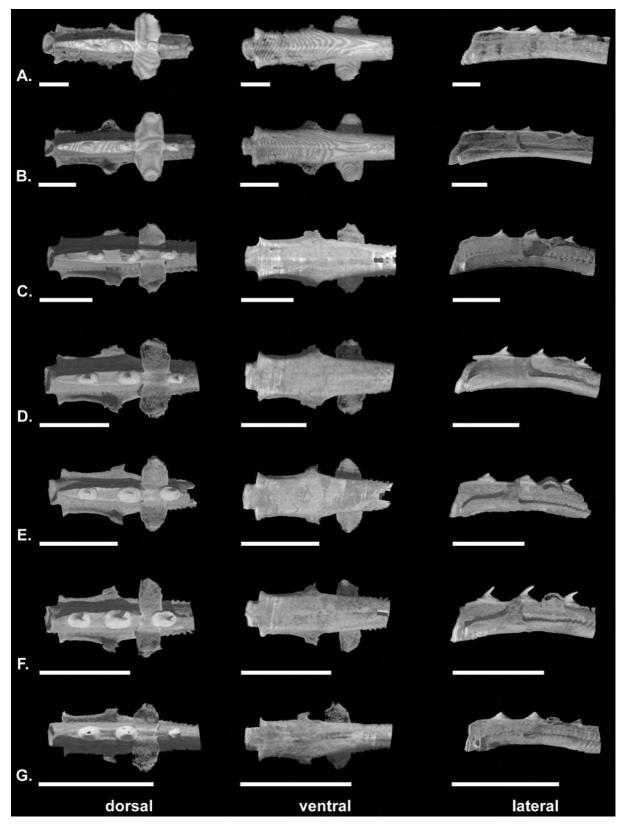


Fig. 3. Raja inornata JORDAN & GILBERT, 1881. Volume rendered 3D images of seven synarcuals, FMNH 2754. A-G – Dorsal (left), ventral (center), and lateral (right) views. Anterior faces left. Scale bar = 1 cm

aging. Cross sectional images show that occipital cotyles are shallow regardless of size. Posterior to the lateral stays, the base narrows more drastically, becoming streamlined. Spinal nerve foramina are visible laterally (Text-fig. 1D). The base is widest between the paired lateral stays. Lateral stays are strongly curved dorsolaterally and are u-shaped in axial cross section. The distal ends of the lateral stay reach at least the same level as the ventral margin of the suprascapula (Text-fig. 1A, B).

The pectoral arch is the widest structure on the dorsal surface of the synarcual. In anterior and posterior views, the pectoral arch is narrowest proximally and expands dorsoventrally towards the distal scapulocoracoid articular surface (Text-fig. 3). The pectoral arch in different individuals is approximately the same. In all individuals, the anterior margin of the pectoral arch is fairly straight and tapers distally forming a narrow articulation with the scapulocoracoid (Text-fig. 1C). The tapering occurs at different distances from the proximal attachment of the pectoral arch in different individuals. Individuals F and G were poorly calcified along the pectoral arch and were not confidently digitally isolated. The posterior margin is not symmetrical with the anterior margin. In some, but not all individuals, the median posterior surface of the pectoral arch is obscured by spines (e.g. Text-fig. 2D-F).

Three spines are situated dorsal to the median crest of the synarcual. The median crest is not tall. Anteriorly, it is narrow and continuous with the dorsal margin of the synarcual mouth. Between the mouth and the first synarcual spine, the crest widens and supports the full diameter of the spine. As body size increases, the relative width of the crest decreases and becomes more elongate. The entire width of the crest is relatively narrowest in the largest specimens. In individuals B and G, the third spine is much smaller than the second spine and it does not overlap with the posterior margin of the pectoral arch. In individual B the proximal attachment of the posterior margin of the pectoral arch is perpendicular to the synarcual tube. In individual G, the posterior margin is at an acute angle to the synarcual tube.

DISCUSSION AND PHYLOGENETIC IMPLICATIONS

Individuals examined for this study demonstrate that as *Raja inornata* increases in body size, the anterior synarcual becomes more elongate and laterally compressed. This is reflected in the external morphology of the taxon as well as the synarcual. In more derived stingrays, the height and width of the synarcual are relatively equal, thus the primitive state for adult

individuals could be a narrow and tall anterior synar-

The synarcual of *Raja inornata* is similar to *Leucoraja erinacea* (see Garman 1913) with a few exceptions. The ventral base and median crest in *R. inornata* at all sizes are narrower than in *L. erinacea*. Also, the occipital cotyles in *R. inornata* are not convex like in *L. erinacea*. Additionally, the pectoral arch of *L. erinacea* curves ventrally, where in *R. inornata* it is perpendicular to the axis of the body. These three characters are potentially informative for rajid systematics. Synarcual spines were not depicted by Garman (1913) but there is evidence from my study that the median crest could be wide enough to support the base of each spine. The variation in position of the spines is of note and should be scored as polymorphic in future phylogenetic analyses.

In the context of higher level analyses, LOVEJOY (1996) proposed that lateral stays that lie dorsal to the spinal nerve foramina could be a derived state and indicated the need to include more outgroups. Observations in *Raja inornata* show that the lateral stay and ventral base are curved dorsolaterally, and obscure the spinal nerve foramina, lending support to that hypothesis.

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