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Morphological variation in a conservative structure: the scapulocoracoids in *Sympterygia acuta* Garman, 1837 and *Sympterygia bonapartii* Müller & Henle, 1841 (Chondrichthyes: Rajidae)

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Abstract

Scapulocoracoid variation in *Sympterygia acuta* and *S. bonapartii* was analyzed inter- and intraspecifically, and the utility of this structure as a diagnostic character in skates was evaluated. Skeletal pieces were obtained from a total of 85 specimens collected in coastal waters of northern Argentina in 2011 and 2012. Morphometric variation was analyzed using non parametric tests. Morphologic variation was qualitatively and quantitatively evaluated by comparing number, shape and arrangement of posterior fenestrae. Scapulocoracoids of both species are rectangular in shape and expanded anteroposteriorly, but those of *S. bonapartii* were more expanded. Differences in shape, both in males and females, were reflected in the ANOSIM test. Greatest Height and Height of Rear Corner were the variables that most contributed to the differences found between both species. These differences in morphology agree with previous descriptions. No sexual dimorphism was observed regarding scapulocoracoids in *S. acuta*, and only a slight variation between males and females of *S. bonapartii* was found. Number of postdorsal and postventral fenestrae was highly variable. At least five scapulocoracoid morphotypes for *S. acuta* (with two to six fenestrae) and seven scapulocoracoid morphotypes for *S. bonapartii* (with three up to nine fenestrae) were identified. However, patterns of fenestrae arrangement were also very diverse in both species. Therefore, a broad variation in fenestrae number and pattern, especially postdorsal ones, was shown in both species. These results indicate that caution needs to be taken when using the scapulocoracoids not only in phylogenetic studies but also in descriptions of new species.

Key words: scapulocoracoid, systematics, skates, *Sympterygia*

Introduction

Skates (Rajoidei) are the most diverse group of batoids, with ~300 valid species (Naylor *et al.* 2012) constituting 24% of all chondrichthyans and a 43% of all known batoids (Ebert & Compagno 2007; Naylor *et al.* 2012). Despite this diversity, rajoids are not morphologically diverse, and much of the morphological diversity expressed in recent species, rostral morphology and pelvic girdle structure, is also present in fossil specimens of the Upper Cretaceous and Early Paleogene (McEachran & Dunn 1998).

Several skeletal structures (clasper, neurocranium and scapulocoracoids) have been commonly used to describe and characterize new species of skates (McEachran & Compagno 1982; Stehmann & Seret 1983; McEachran & Last 1994; de Carvalho *et al.* 2005; Last & McEachran 2006; Last & Gledhill 2007; Jeong & Nakabo 2009), being clasper anatomy the most useful in systematics (Stehmann 1970; Hulley 1972; McEachran & Miyake 1990; McEachran & Dunn 1998). The scapulocoracoid, or shoulder girdle, is inserted in the body wall just posterior to the branchial arches, and consists of a ventral and transverse coracoid bar and a dorsolateral scapular process on each side. The lateral face of the scapulocoracoid, at the junction of the coracoid bar and scapular processes, has an articular surface for the pectoral basal cartilages and foramina for blood vessels and nerves. There

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are three discrete articular condyles: the procondyle for the propterygium, the mesocondyle for the mesopterygium, and the metacondyle for the metapterygium. Fenestrae on the lateral face of the scapulocoracoid include anterodorsal and anteroventral fenestrae between the pro- and mesocondyles, and postdorsal and postventral fenestrae between the meso- and metacondyles. The anterior bridge is a horizontal bar separating the pro- and mesocondyles laterally, and dorsoventrally it separates the anterodorsal and anteroventral fenestra, although this structure is lost in many skates (Compagno 1999). The presence of an anterior bridge in *Bathyraja*-like rays and stingrays is thought to be a secondary formation, and is directly associated with the necessity to sustain an increased resistance to environmental pressures (Dolganov 2002).

Several scapulocoracoid characters have been used as diagnostic both for describing new species and in phylogenetic analyses, such as shape of lateral face, presence of anterior bridge, height and shape of rear corner, distance from pro- to mesocondyle and from meso- to metacondyle, shape of dorsal and anteroventral margins, and number and shape of postdorsal and postventral fenestrae (McEachran & Compagno 1982; Stehmann & Seret 1983; McEachran & Miyake 1990; McEachran & Last 1994; McEachran & Dunn 1998; de Carvalho *et al.* 2005; Last & McEachran 2006; Last & Gledhill 2007; Jeong & Nakabo 2009). However, Dolganov (2002) stated that the number and shape of postdorsal and postventral fenestrae significantly vary both between the suborders and among representatives of the same genus or even species. They have no direction, and therefore they are not important for phylogenetic analysis. Indeed, Mabragaña (2007), analyzing species of *Psammobatis* from Southwest Atlantic, observed a large intraspecific variability in this structure arguing against its utility as a systematic character.

McEachran (1982, 1983) conducted an exhaustive review of species from genera *Sympterygia* and *Psammobatis,* and described, among other structures, their scapulocoracoids. He found a strong sexual dimorphism in this part of the skeleton, at least in *Psammobatis* species, and defined the overall morphological pattern of this structure for each species, endorsing it as a specific character.

In the wake of the observations made by Mabragaña (2007) in *Psammobatis*, we set out to investigate if species of *Sympterygia* from the Southwest Atlantic (*S. acuta* and *S. bonapartii*), might also present morphological and morphometric variation in the scapulocoracoid at both inter- and intraspecific levels. Therefore, the aim of this study was to evaluate the utility of this structure as a diagnostic character in these skates.

Materials and methods

Sample collection. Skeletal pieces were obtained from specimens of *Sympterygia acuta* and *S. bonapartii* collected with a 6 m shrimp net (mesh size 50 mm at wings, 20 mm in the cod end) by trawl fishing at the coast near Mar Chiquita coastal lagoon (37° 32’ S, 57° 19’ W), Argentina, in 2011 and 2012.

For each specimen, total length and disc width in millimeter, sex and maturity were recorded in the laboratory. Scapular girdles were extracted by dissection, which were kept in freezer for subsequent study. In order to reveal scapulocoracoid structure (shape, number and fenestrae pattern), dissected material was submerged in water at 90-95°C for easing flesh removal. Once cartilaginous structures were clean, they were stored in ethanol 70%. Morphometric and morphological variables were registered following McEachran & Compagno (Mceachran & Compagno 1979) (Fig. 1).

Number of postdorsal and postventral fenestrae was recorded, as well as greatest length and height, anterior and posterior length to mesocondyle (pre- and postmesocondyle, respectively), and height of rear corner. For each measurement, a digital caliper with a 0.01 mm error was used. For illustrative purposes, digital photographs were taken from the lateral view of scapulocoracoids.

Data Analysis. To obtain independence from body size effect, all measurements were standardized to greatest length of scapulocoracoids. Morphometric variation was analyzed using non parametric tests (Analysis of Similarities, ANOSIM) and ordination techniques (Non-Metric Multidimensional Scaling, nMDS). A Similarity percentages test (SIMPER) was performed in order to assess the morphometric variables of highest contribution to differences between species. Morphologic variation was evaluated qualitatively and quantitatively by comparing number, shape and disposition of posterior fenestrae, both dorsal and ventral. The number of fenestrae was analyzed through a Mann-Whitney test. Statistical analyses and graphics were performed using R software v3.1.1 (R Core Team, 2014).

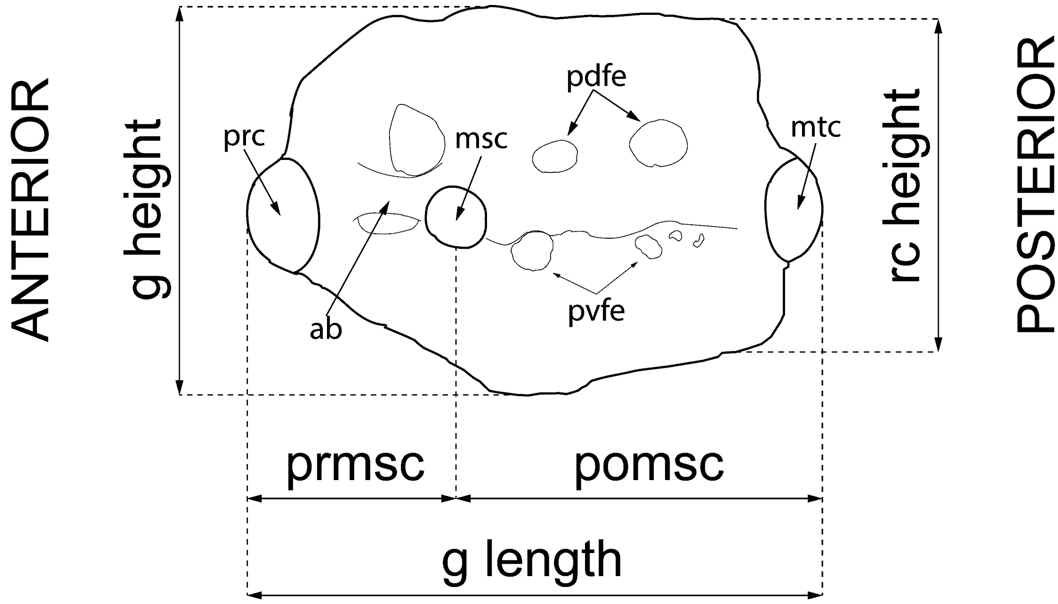


FIGURE 1. Lateral view (left) of a skate scapulocoracoid showing measurements proposed by McEachran & Compagno (1979). Abbreviations: g length = greatest length; g height = greatest height; prmsc = premesocondyle; pomsc = postmesocondyle; RC height = height of rear corner; prc = precondyle; msc = mesocondyle; mtc = metacondyle; ab = anterior bridge; pdfe = postdorsal fenestrae; pvfe = postventral fenestrae.

Results

A total of 43 *Sympterygia acuta* (22 males and 21 females) and 42 *S. bonapartii* (14 males and 28 females) were analyzed. Considering that the scapulocoracoid is a symmetrical structure, the total of observations arises to 170.

Shape analysis. Scapulocoracoids of both species are rectangular in shape and expanded anteroposteriorly, but those of *S. bonapartii* were more expanded (Fig. 2). Differences in shape were reflected in the ANOSIM test, both in males ($R = 0.963$, $p = 0.001$) and females ($R = 0.999$, $p = 0.001$), and are represented in the nMDS graphics (Fig. 3).

SIMPER analysis revealed that Greatest Height (0.624) and Height of Rear Corner (0.812; left and right ones) were the variables that most contributed to the differences found between both species.

Given the fact that no differences were observed in shape from left and right sides in neither of the studied species ($p > 0.05$), both sides were grouped for sexual comparisons. ANOSIM test revealed no differences in shape between males and females in *S. acuta* ($R = 0.077$, $p = 0.018$; Fig. 4a). Conversely, *S. bonapartii* showed a slight sexual dimorphism ($R = 0.183$, $p = 0.001$; Fig. 4b).

SIMPER analysis revealed that height of rear corner (0.141), postmesocondyle (0.529) and greatest height (0.647) were the variables that most contributed to the differences between sexes in *S. bonapartii*. Both heights are slightly greater in males, and the postmesocondyle was slightly greater in females. However, these differences are not evident at first glance.

Fenestrae Analysis. Number of postdorsal and postventral fenestrae in both species was highly variable. This variation was also shown when comparing left and right sides. In *S. acuta*, about 70% of specimens showed differences in the number of postdorsal fenestrae on each side, and 58% in *S. bonapartii*.

Sympterygia acuta showed differences between males and females in number of postdorsal fenestrae ($p = 0.018$ left side, $p = 0.029$ right side) and right postventrals ($p = 0.048$). On the other hand, *S. bonapartii* showed differences between males and females in number of postdorsal fenestrae ($p = 0.005$ left side, $p = 0.008$ right side) and left postventrals ($p = 0.002$).

Overall, *S. bonapartii* presented more fenestrae than *S. acuta*, both postdorsals and postventrals, and these differences were significative ($p < 0.05$), except for left postventral fenestrae in males ($p = 0.082$).

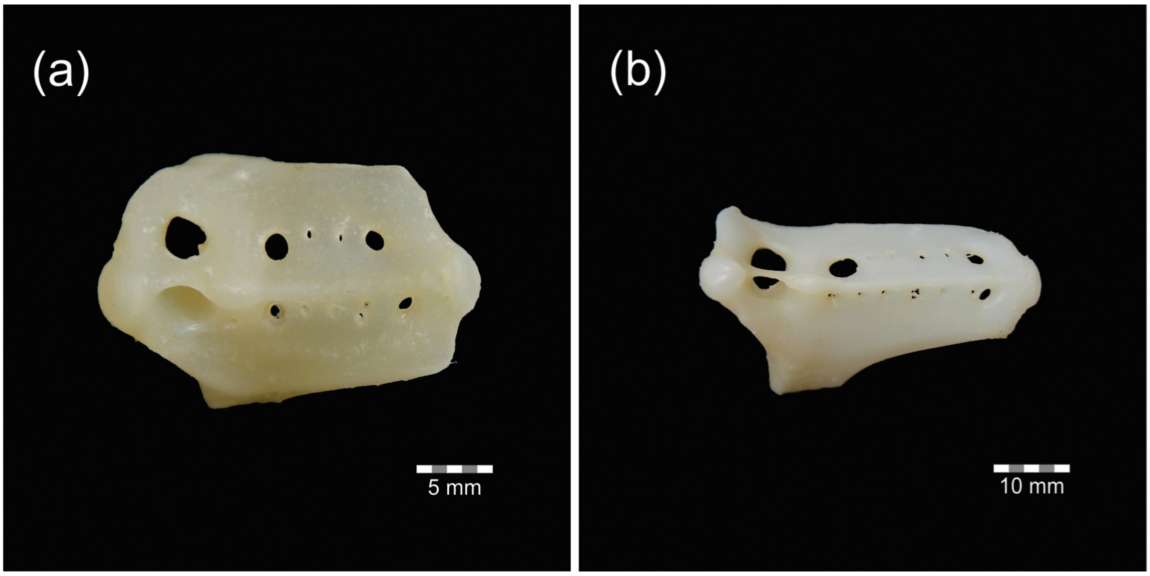


FIGURE 2. Lateral left side view of scapulocoracoids of (A) *Sympterygia acuta* and (B) *S. bonapartii*.

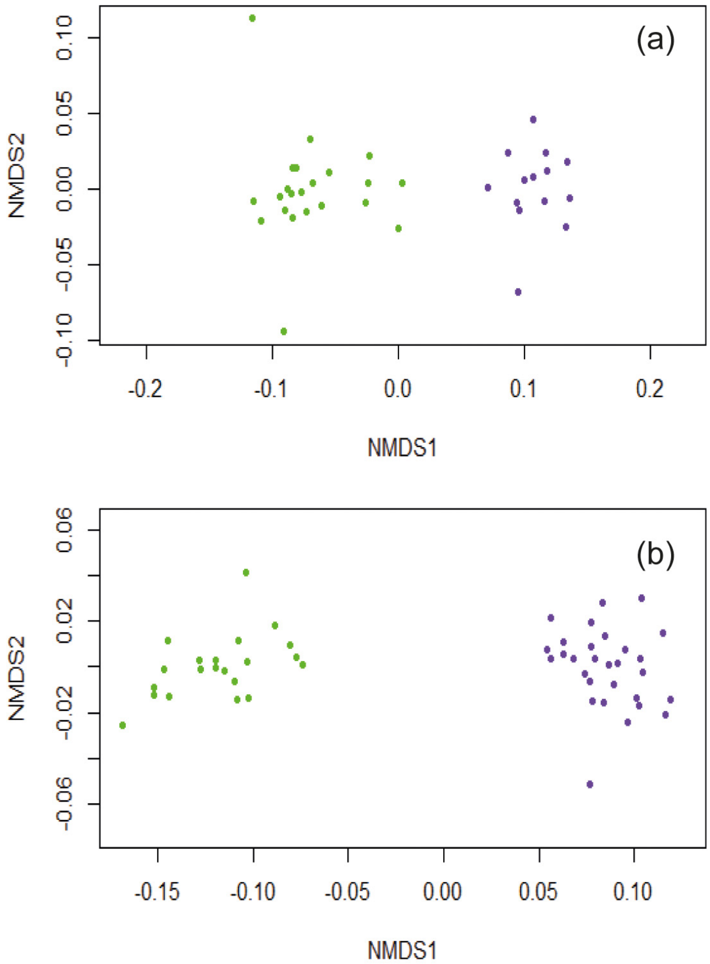
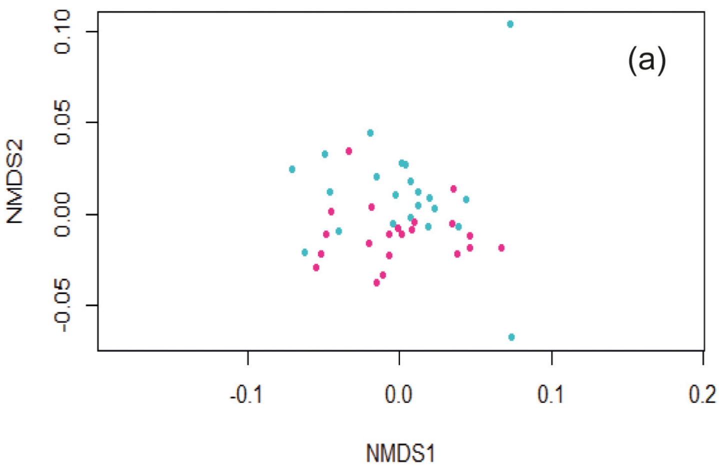


FIGURE 3. NMDS (non-metric multidimensional scaling) graphic from four standardized morphometric variables of scapulocoracoids of (A) males (n = 36) and (B) females (n = 49) of *Sympterygia acuta* (green; n = 43) and *S. bonapartii* (purple; n = 42).



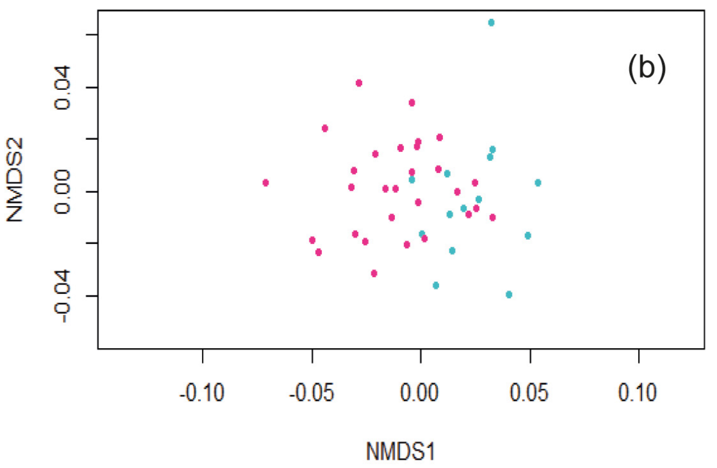


FIGURE 4. NMDS (non-metric multidimensional scaling) graphic from four standardized morphometric variables from scapulocoracoids of males (blue; n = 36) and females (pink; n = 49) of (A) *Sympterygia acuta* (n = 43) and (B) *S. bonapartii* (n = 42).

Scapulacoracoids of each species were grouped based on the number of postdorsal fenestrae: at least five scapulocoracoid morphotypes for *S. acuta* (with two to six fenestrae) and seven scapulocoracoid morphotypes for *S. bonapartii* (with three to nine fenestrae) were identified. However, patterns of fenestrae disposition were also very diverse in both species.

Sympterygia acuta. Morphotypes with two (males 15.9%, females 7.1%), three (males 40.9%, females 23.8%), four (males 29.5%, females 42.9%), five (males 6.8%, females 21.4%), and up to six (males 6.8%, females 4.8%) postdorsal fenestrae were observed (Fig. 5).

Sympterygia bonapartii. Morphotypes with three (males 20%, females 9.3%), four (males 23.3%, females 11.1%), five (males 33.3%, females 11.1%), six (males 13.3%, females 42.6%), seven (males 10%, females 22.2%), eight (males 1.9%) and up to nine (females 1.9%) postdorsal fenestrae were observed (Fig. 6). A single female specimen with eight and nine postdorsal fenestrae was observed for each morphotype.

Discussion

The relatively high specific diversity combined with a conservative morphology makes skates a peculiar group within chondrichthyans. Within skates, several skeletal structures such as neurocranium, clasper and scapulocoracoids, show significant variation and have been used for taxonomic studies as well as to infer phylogenetic relationships (McEachran & Miyake 1990; McEachran & Dunn 1998).

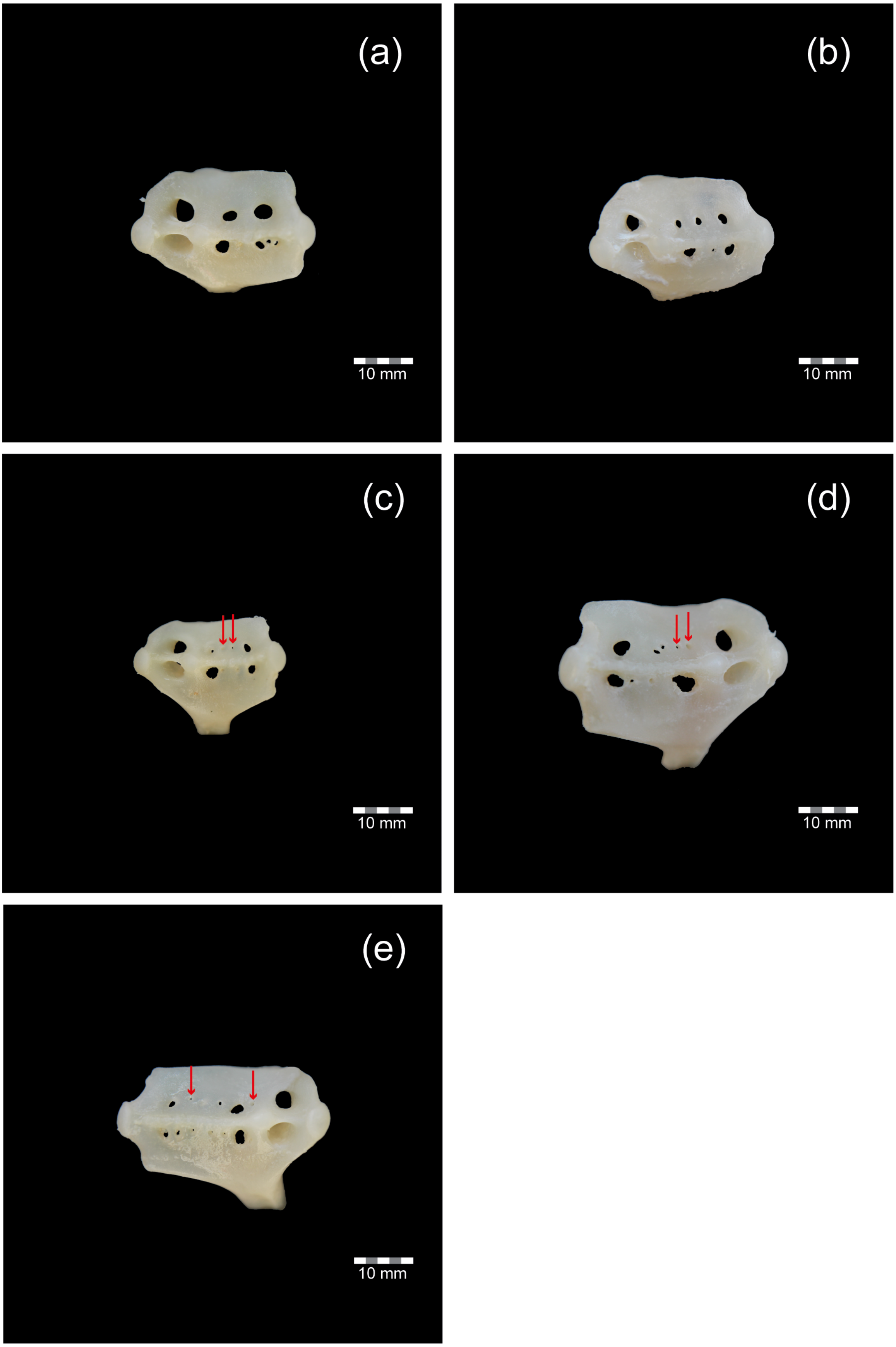


FIGURE 5. Scapulocoracoid morphotypes observed in *Sympterygia acuta*. With (A) two, (B) three, (C) four, (D) five, and (E) six postdorsal fenestrae. Arrows indicate small fenestrae not clearly seen in the image.

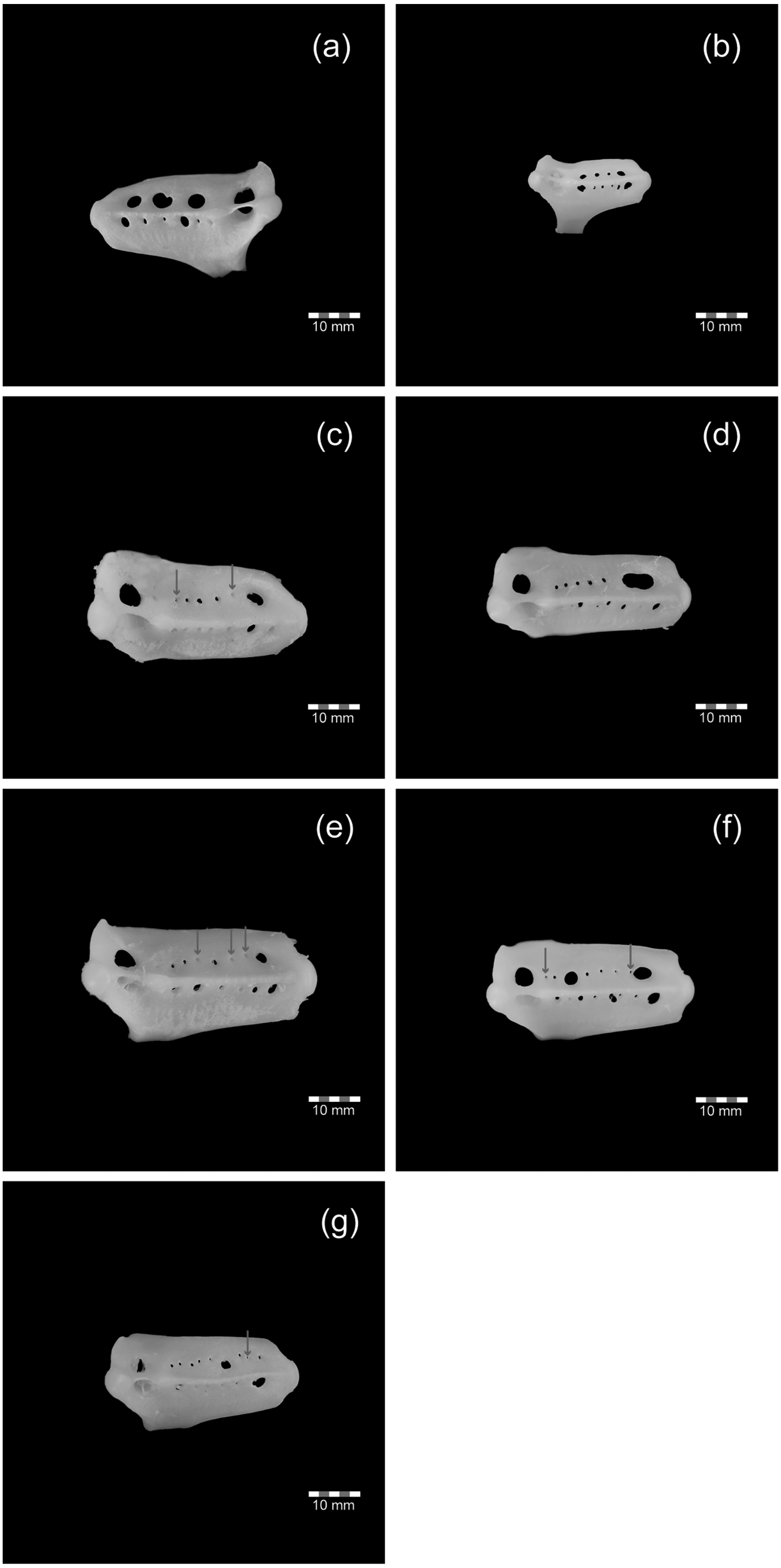


FIGURE 6. Scapulocoracoid morphotypes observed in *Sympterygia bonapartii*. With (A) three, (B) four, (C) five, (D) six, (E) seven, (F) eight, and (G) nine postdorsal fenestrae. Arrows indicate small fenestrae not clearly seen in the image.

McEachran & Dunn (1998) performed a comparative phylogenetic analysis of skates using several structures, including the scapulocoracoids. From this structure, the following characters were taken into account in suprageneric phylogenetic studies: postdorsal and postventral fenestrae, anterior bridge, distance between pro- and mesocondyle and between meso- and metacondyle (McEachran & Miyake 1990; McEachran & Dunn 1998). These authors highlighted that scapulocoracoids are laterally expanded in all Arhyncobatinae (used as a subfamily by these authors, now a family, that includes *Sympterygia*) except in some species of *Psammobatis*; and within Rajinae, in all genera of the Rajini tribe, and in half of the genera of the Amblyrajini and Gurgesiellini. However, it was not possible to define if this expansion occurred separately within each subfamily or just once with reversions in *Psammobatis*, *Rajella* and *Breviraja* (Amblyrajini), *Malacoraja* and *Neoraja* (Gurgesiellini) (McEachran & Dunn 1998).

McEachran (1982) defined the scapulocoracoids of *Sympterygia* as having a lateral face with rectangular shape, anteroposteriorly expanded between meso- and metacondyle, and with a stout anterior bridge. He specifically characterized the scapulocoracoids of *S. bonapartii* as being widely expanded between meso- and metacondyle, with its height equal to half its length, and possessing around 10 postdorsal and 10 postventral fenestrae; whereas scapulocoracoids of *S. acuta* are less expanded, with three postdorsal and four postventral fenestrae (McEachran 1982). On the other hand, in the phylogenetic analysis of the relationships among the genera, McEachran (1982) used six characters (from a total of 26) corresponding to scapulocoracoids. These were: scapulocoracoid rectangular and expanded between meso- and metacondyles, multiple postdorsal foramina or expanded fenestra, ratio of scapulocoracoid height to length <75%, postdorsal and postventral fenestrae ≥3, ratio of scapulocoracoid height to length <55%, and postdorsal and postventral fenestrae >5. From this analysis he established that *Sympterygia brevicaudata* is the sister group of the other three species of *Sympterygia* and that *S. lima* is the sister group of the clade composed of *S. bonapartii* and *S. acuta* (Fig. 7).

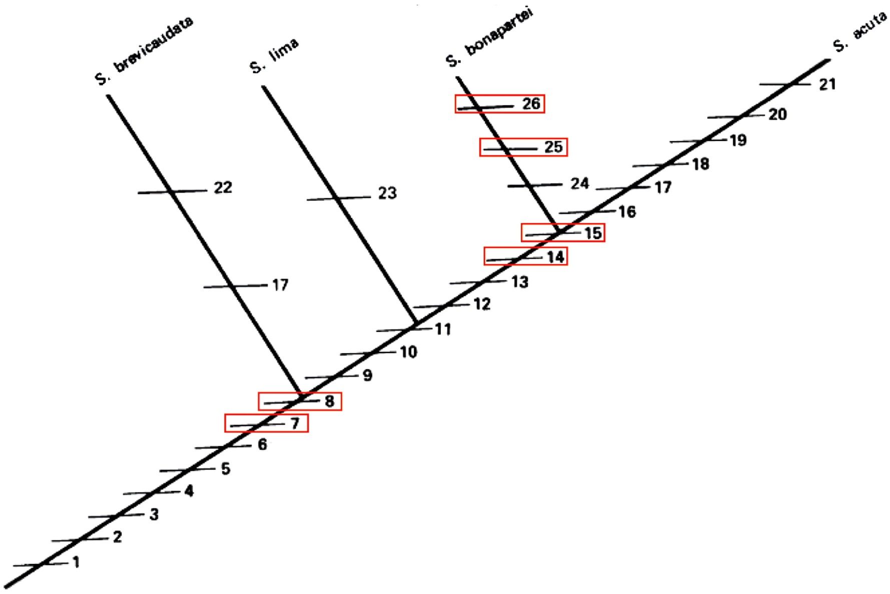


FIGURE 7. Phylogenetic analysis of *Sympterygia* species from McEachran (1982). Scapulocoracoid characters are shown within boxes. [7] = scapulocoracoid rectangular and expanded between meso- and metacondyles; [8] = multiple postdorsal foramina or expanded fenestra; [14] = ratio of scapulocoracoid height to length <75%; [15] = postdorsal and postventral fenestrae ≥3; [25] = ratio of scapulocoracoid height to length <55%; [26] = postdorsal and postventral fenestrae >5.

Morphology of the scapulocoracoids of *S. acuta* and *S. bonapartii* observed in this study agrees with previous descriptions made by McEachran (1982) (Fig. 2). However, a broad variation in fenestrae number and disposition, especially in postdorsal fenestrae (Table 1, Figs. 5, 6) was found. Remarkably, scapulocoracoids with three postdorsal fenestrae in *S. acuta* (Fig. 5a) were similar to those described by McEachran (1982), where the most frequent morphotype observed was in males but not in females. Coversely, scapulocoracoids of *S. bonapartii* that were similar to those described by McEachran (1982) were the rarest morphotype: only one specimen had nine fenestrae (Fig. 6g). Taking into account the observations from this study, the characters used by McEachran (1982) postdorsal and postventral fenestrae ≥3, interpreted as a synapomorphy of *S. acuta* and *S. bonapartii*, and postdorsal and postvenral fenestrae >5, an autapomorphy of *S. bonapartii*, would not be valid. In the present study, specimens of *S. acuta* were observed with a range from two to six postdorsal fenestrae, while *S. bonapartii* had a range from three to nine. Therefore, some specimens of *S. acuta* would share character states with *S. lima* and *S. brevicaudata*, and some specimens of *S. bonapartii* would share character states with *S. acuta*. In addition, if we consider the fact that the number of fenestrae from left and right sides did not always match, the futility of this character for systematic use becomes even more clear.

As opposed to *Psammobatis* (McEachran 1983; Mabragaña 2007), no sexual dimorphism was observed regarding scapulocoracoids in *S. acuta* (Fig. 4a), and only a slight variation between males and females in *S. bonapartii* was found (Fig. 4b). It would be interesting to analyze if this dimorphism is present in other skate species and if this could weaken their use as relevant phylogenetic information. However, intraspecific variation observed in this study in the number of scapulocoracoid fenestrae in species of *Sympterygia*, has also been registered in species of *Psammobatis* (Mabragaña 2007). These facts show that restraint is needed when using the scapulocoracoids not only in phylogenetic studies but also in descriptions of new species.

TABLE 1. Number of fenestrae registered in scapulocoracoids of *Sympterygia* spp. Number of specimens analysed (n), mean (X), standard deviation (SD), median (m), and minimum and maximum ranges is shown.

	Sympterygia acuta								*Sympterygia bonapartii*							
	males n =22				females n =21				males n =14				females n =28			
No. Fenestrae	X	SD	m	Min–Max	X	SD	m	Min–Max	X	SD	m	Min–Max	X	SD	m	Min-Max
Left Postdorsals	3.41	1.03	3	2–6	3.86	0.77	4	2–5	4.79	1.26	5	2–7	5.79	1.54	6	3–9
Left Postventrals	4.23	0.85	4	3–6	4.81	1.01	5	3–7	6.21	1.08	6	5–9	7.04	0.91	7	5–9
Right Postdorsals	3.55	1.03	4	2–6	4.19	0.91	4	3–6	4.64	1.29	5	3–7	5.89	1.05	6	3–7
Right Postventrals	4.18	0.65	4	3–5	4.76	0.81	5	4–6	6.43	0.98	7	3–7	7.25	0.69	7	6–9

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