



# Polymorphism in Conservative Structures? The Scapulocoracoids in Skates Genus *Psammobatis* (Chondrichthyes, Arhynchobatidae) and the Validity of *P. parvacauda*

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Skeletal structures, especially the claspers, neurocrania, and scapulocoracoids have been widely used to characterize and describe new species of elasmobranchs. Intra and interspecific variation of scapulocoracoids in 3 species of *Psammobatis* ( $n = 94$ ) from the Southwest Atlantic Ocean were analyzed to assess its utility as a diagnostic character in skates. Moreover, based on scapulocoracoids and body morphometric analyses, the validity of *Psammobatis parvacauda* McEachran, 1983 was evaluated. A remarkable sexual dimorphism in scapulocoracoids was observed in all species in accordance with original descriptions, which was also evident in the principal component (PCA) and Discriminant Analyses. The number and arrangement of post-dorsal and post-ventral fenestra were highly variable at intra-specific level, in contrast with original descriptions. Particularly, one of the morphotypes observed in females of *P. normani* was identical to the one reported in *P. parvacauda*. Results showed intraspecific variation in this structure, as was previously observed in *Sympterygia* species. Therefore, this structure should not be used as a diagnostic character in skates, at least for these genera. Regarding body morphometry the PCA showed that *P. parvacauda* grouped with *P. normani* females and the cross-validated analysis showed that *P. parvacauda* was classified in the group of *P. normani* females. *P. parvacauda* is only known from its original description (one female) and a likely second specimen, but our analyses revealed a lack of diagnostic characteristics. Based on observations and measurements of the holotype of *P. parvacauda*, and comparisons with congeners, *P. normani* is regarded a senior synonym of *P. parvacauda*.

**Keywords:** Rajiformes, *Psammobatis*, scapulocoracoids, intraspecific polymorphism, *P. parvacauda*, synonymization

## INTRODUCTION

Skates (Chondrichthyes, Rajiformes), constitute a monophyletic and cosmopolitan group of cartilaginous fishes, with representatives in all oceans. The Order includes approximately 290 species and is composed by two highly diverse families (Rajidae and Arhynchobatidae) and two smaller families (Anacanthobatidae and Gurgesiellidae) (Last et al., 2016a,b; Séret et al., 2016;

Weigmann et al., 2016). The endoskeleton of skates -like all chondrichthyan fishes- is comprised predominantly of a hyaline-like cartilage that persists throughout the entire life and is not replaced by bone (Compagno, 1999; Seidel et al., 2017). During ontogeny the matrix undergoes a distinctive calcification, developing an outer calcified rind of hydroxyapatite or tesserae, located between the cartilaginous core and the outer, perichondrium (Seidel et al., 2017).

Skeletal structures, especially the claspers, neurocrania and scapulocoracoids have been widely used not only to characterize and describe new species of skates (McEachran and Compagno, 1982; Stehmann and Seret, 1983; McEachran and Last, 1994; de Carvalho et al., 2005; Last and McEachran, 2006; Last and Gledhill, 2007; Jeong and Nakabo, 2009), but also for conducting comprehensive systematic studies (Stehmann, 1970; Hulley, 1972; McEachran and Miyake, 1990; McEachran and Dunn, 1998). The scapulocoracoid or pectoral girdle is located just posterior to the branchial arches and is attached to the vertebral column dorsally (Compagno, 1999). The scapulocoracoid consists basically of a ventral and transverse coracoid bar, a dorsolateral scapular process on each side and, in some species an articulated suprascapula above the scapular process. The lateral face of the scapulocoracoid has an articular surface for the pectoral basal cartilages and foramina for blood vessels and nerves (Compagno, 1999). Fenestrae on the lateral face of the scapulocoracoid of primitive batoids include anterodorsal and anteroventral fenestrae between the pro and mesocondyles, and postdorsal and posventral fenestrae between the meso and metacondyles (Compagno, 1999).

McEachran (1982, 1983) conducted a comprehensive review of skate species from the *Sympterygia* and *Psammobatis* genera, and described their skeletal structures including scapulocoracoids. He found a strong sexual dimorphism in this part of the skeleton in *Psammobatis* species, and defined the overall morphological pattern of this structure for each species, endorsing it as a diagnostic character. Recent studies have called into question the usefulness of scapulocoracoids as a diagnostic character at the specific level. Jurado et al. (2017), reported a high variability in this structure at the intraspecific level in *Sympterygia* species, especially in the number of postdorsal and postventral fenestrae. On this basis, it would be relevant to investigate potential morphological variability in scapulocoracoids within *Psammobatis*, a closely related genus (McEachran and Dunn, 1998), to determine whether a similarly non-conservative pattern is observed.

The genus *Psammobatis* (Rajiformes, Arhynchobatidae) is endemic of South America and is comprised of eight small to medium sized skates. Thorough taxonomic revision of the genus was conducted by McEachran (1983) and completed by de Carvalho and Figueiredo (1994). The genus currently includes two amphioceanic species, *P. rudis* Gunther, 1870 and *P. normani* McEachran, 1983, both occurring in the Southwest Atlantic Ocean (SWA) and the South-east Pacific Ocean (SEP), one species exclusively found in the SEP, *P. scobina* (Philippi, 1857), and 5 species exclusively distributed in the SWA, *P. bergi* Marini, 1932, *P. rutrum* Jordan, 1890, *P. extenta* (Garman, 1913), *P. lentiginosa* McEachran, 1983, and *Psammobatis parvacauda*

McEachran, 1983. The latter was described based on a single female collected around Malvinas/Falkland Islands, whose external morphological characteristics and skeletal structures, particularly the scapulocoracoid, were unique (McEachran, 1983). After the revision of McEachran (1983), several studies were conducted on almost all *Psammobatis* species including reproductive biology (Braccini and Chiaramonte, 2002b; Mabragaña and Cousseau, 2004; San Martín et al., 2005, Mabragaña, 2007; Perier et al., 2011; Mabragaña et al., 2012; Martins and Oddone, 2017), feeding ecology (Braccini and Perez, 2005; Mabragaña, 2007; Mabragaña and Giberto, 2007; San Martín et al., 2007; Barbini and Lucifora, 2012), morphology (Braccini and Chiaramonte, 2002a; Mabragaña, 2007), egg cases (Concha et al., 2009; Mabragaña et al., 2011; Vazquez et al., 2016), and their parasites community (Irigoitia et al., 2019). Strikingly, no further studies were conducted in *P. parvacauda*. In fact, no new records of this species were published since McEachran's (1983) original description.

The objectives of this study are (1) to analyze the morphological variability of scapulocoracoids in three *Psammobatis* species from the SWA, (2) to assess the usefulness of scapulocoracoid as a diagnostic character in this genus, and (3) in the light of objectives 1 and 2, to assess the validity of *P. parvacauda* McEachran, 1983 based on morphological and skeletal analyses.

## MATERIALS AND METHODS

### Sample Collection

Skeletal material was obtained from specimens of *P. rudis* (males  $n = 13$ , females  $n = 18$ ) and *P. normani* (males  $n = 18$ , females  $n = 19$ ), collected by trawl fishing during research cruises conducted by the National Institute for Fisheries Research and Development (INIDEP) in southern Patagonian waters (49°28'S, 67°03'W to 52°00'S, 53°49'W, and from 84 to 182 m) in April 2000, and from specimens of *P. lentiginosa* (males  $n = 13$ , females  $n = 13$ ) collected off Buenos Aires Province (36°23'S, 63°59'W to 39°05'S, 58°04'W, from 66 to 99 m depth) in October 2006.

Total length (TL) and disc width (DW) in millimeters, sex and maturity (following Mabragaña and Cousseau, 2004) were recorded for each specimen in the laboratory. Scapular girdles were dissected and kept frozen 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 easy flesh removal. Once cartilaginous structures were cleaned, they were stored in ethanol 70%.

### Scapulocoracoid Morphometric Analysis

Morphometric (linear morphometric measurements; LMM) were taken following McEachran and Compagno (1979). Morphometric variables included greatest length and height, anterior and posterior length to mesocondyle (pre- and postmesocondyle, respectively), and height of rear corner. These variables were taken on the left scapulocoracoid side. Given that in *P. lentiginosa* only 10 scapulocoracoids could be measured, the total of observations was 78. A digital caliper with a

0.01 mm error was used for taking each measurement. Digital photographs were taken from the lateral face of scapulocoracoids for illustrative purposes.

Statistical and mathematical procedures for the LMM analysis followed González-Castro et al. (2012, 2016). The morphometric characters were organized by sexes and species. A normalization technique to scale the data that exhibit allometric growth was employed following Leonart et al. (2000). Scapulocoracoid length (ScL) was used as the independent variable. ScL0 represents a reference value of ScL (23 mm) to which all scapulocoracoids were either reduced or amplified (Lombarte and Leonart, 1993). After transformation, a principal component analysis (PCA) was performed using MULTIVARIADO® software (Salomón et al., 2004). Finally, principal component scores (PCs) were submitted to cross-validated discriminant analysis (DA) using SPSS® vers. 13.0 (Nie et al., 2004), in order to build a predictive model of group membership based on the observed characteristics of each case. This procedure generates a set of discriminant functions based on linear combinations of the predictor variables that provide the best discrimination between groups.

### Scapulocoracoid Morphological Analysis

Morphological variables were taken following McEachran and Compagno (1979). The variables included number of postdorsal and postventral fenestrae, and were taken in both left and right sides of scapulocoracoids. Therefore the total of observations arise to 188. Morphological variation was quantitatively and qualitatively evaluated by comparing number, shape and arrangement of posterior fenestrae, both dorsal and ventral. The number of fenestrae was analyzed through a Mann–Whitney test. Statistical analyses were performed using Statistica 7.0 (Stat. Soft. Inc). For illustrative purposes, digital photographs were taken from the lateral face of scapulocoracoids.

### Morphological and Morphometric Analyses of *P. parvacauda*

To assess the validity of *P. parvacauda*, the holotype was examined. The specimen is stored at Zoologisches Museum Hamburg [ZMH 25234 (ex ISH 1671-1966 ISH Aussenstelle Ichthyologie des Instituts für Seefischerei)] Germany. Morphological features as well as body morphometric LMM of the specimen were taken.

For comparison purposes, 12 morphometric variables LMM were selected and measured on dorsal and ventral sides of specimens of *P. normani* ( $n = 81$ ), *P. rudis* ( $n = 34$ ) and *P. lentiginosa* ( $n = 35$ ) following Last et al. (2008), and compared to those of *P. parvacauda*. The variables were: DW, disc length, snout length, preoral length, prenasal length, orbit diameter, interorbital distance, mouth width, distance between first gill openings, distance between fifth openings, distance snout to cloaca, and distance cloaca to caudal tip. As in scapulocoracoid analysis, a normalization technique to scale the data that exhibit allometric growth was employed following Leonart et al. (2000). In this case, DW was used as the independent variable and DW0 represents a reference value of DW (230 mm) to which all specimens were either reduced or amplified. Even though TL

was also measured in all individuals, this variable was removed from the analysis because of the damage tail of the holotype of *P. parvacauda*.

## RESULTS AND DISCUSSION

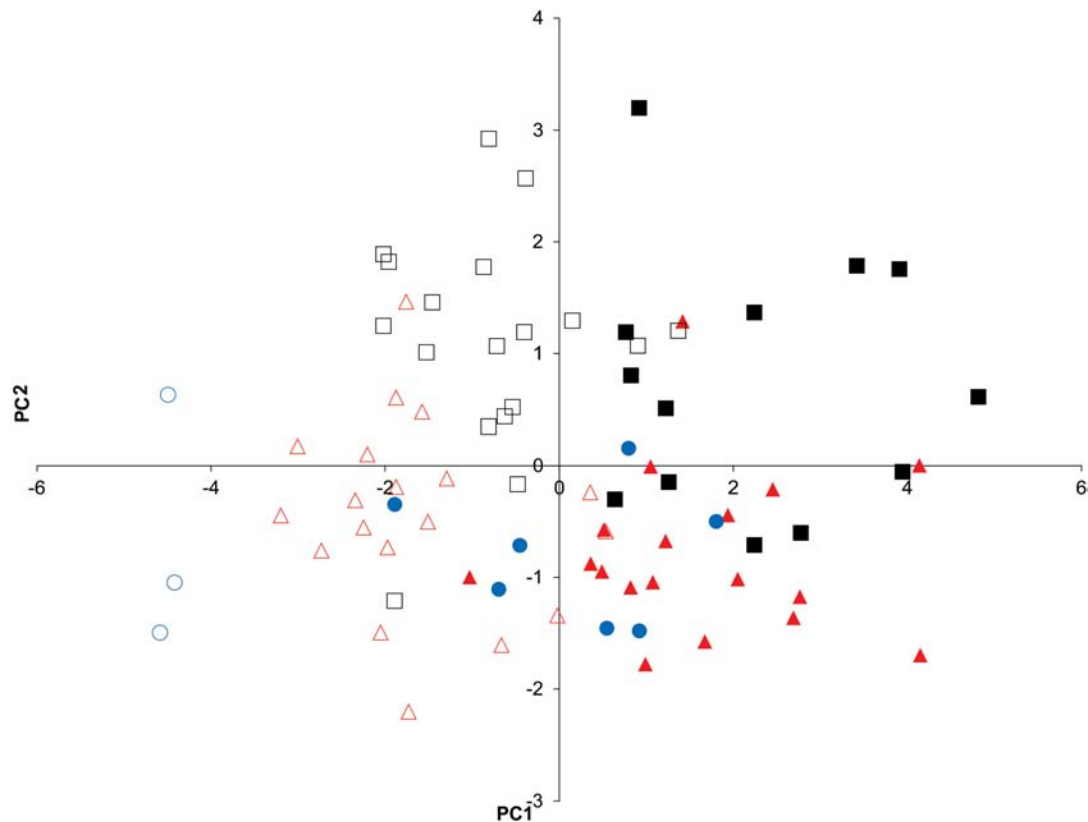
### Scapulocoracoid Morphometric Analysis

A sexual dimorphism has been observed in the three *Psammobatis* species analyzed, according to the original descriptions (McEachran, 1983), being the scapulocoracoids of females more rectangular than those of males, which were more triangular shaped. The PCA of the correlation matrix of LMM of scapulocoracoid, generated by the normalization procedure, produced 2 eigenvalues of  $>1$  (data not shown) and 8 PCs. Correlations between variables and components  $>0.59$  were considered significant (data not shown). The PCA based on LMM allowed a clear differentiation along the PC1 of the females from the males of the three species analyzed (Figure 1). Males showed higher loadings for pre-mesocondyle, greatest height, height of rear corner, and pre-dorsal fenestrae height, whereas higher loadings of variables, post-mesocondyle, and post-dorsal fenestrae length characterized females of the three species analyzed (data not shown). Moreover, the characterization of the species by sexes was only partial, because some overlap between them was detected (Figure 1). The DA on the variations in the 78 individuals of *Psammobatis* classified by sexes and species were explained by 5 canonical discrimination functions, of which the first 2 explained 93.4% (63.3 and 30.1%, respectively) of the total variance in the data, (Wilks' lambda = 0.076,  $p < 0.000$ ). The DA correctly classified 74.4% of the original grouped cases, whereas the cross-validated analysis correctly classified only the 59.4% of the fishes according to their LMM of scapulocoracoid. Moreover, the cross-validated analysis showed that misclassifications varied from 5.3 to 33.3%, depending on the group analyzed (Table 1A). Again, the sexual dimorphism was evidenced as a variable equal, or even stronger than species influence in the group discrimination.

### Scapulocoracoids Morphological Analysis

The number of pre-dorsal and pre-ventral fenestra observed were identical to those described by McEachran (1983). However, a high variability in the number and arrangement of post-dorsal and post-ventral fenestra (pdf and pvf, respectively) was observed, in contrast with original descriptions. This variation was also shown when comparing left and right sides. Both, in *P. rudis* and *P. normani*, about 16% of specimens showed differences in the number of postdorsal or postventral fenestrae on each side, and 31% in *P. lentiginosa*.

*Psammobatis rudis* showed no differences between males and females in number of pdf and pvf. On the contrary, *P. normani* showed sexual differences in number of left pvf ( $p = 0.013$ ). On the other hand, *P. lentiginosa* showed differences between males and females in both, number of pdf ( $p = 0.015$  left side,  $p = 0.006$  right side), and pvf ( $p = 0.003$  left side,  $p < 0.001$ ).



**FIGURE 1** | Principal component (PC) analysis (PC1 vs. PC2) based on linear morphometric measurements of scapulocoracoids. The first 2 PCs explained 71.3% of the variance in the data. *Psammobatis rudis* males (black squares); *P. rudis* females (white squares); *P. normani* males (red triangles); *P. normani* females (white triangles); *P. lentiginosa* males (black circles); and *P. lentiginosa* females (white circles).

Overall, no differences in the number of pdf between males of the three species were observed. Similarly, no differences in the number of pvf between males of *P. rudis* and *P. normani* were observed. On the contrary, females of *P. rudis* presented more pvf than those of *P. normani* ( $p = 0.015$  left side,  $p = 0.035$  right side). On the other hand, males of *P. lentiginosa* presented more pvf than those of *P. rudis* ( $p < 0.001$  left side,  $p = 0.013$  right side). Similarly, females of *P. lentiginosa* had more pdf ( $p < 0.001$  left side,  $p < 0.001$  right side) and pvf ( $p < 0.001$  left side,  $p = 0.013$  right side) than those of *P. rudis*. Finally, males of *P. lentiginosa* had more pvf ( $p = 0.001$  left side,  $p = 0.007$  right side) than those of *P. normani*, and females of *P. lentiginosa* presented more pdf ( $p = 0.003$  left side), and pvf ( $p < 0.001$  left side,  $p < 0.001$  right side) than those of *P. normani*.

Regarding arrangement of fenestrae, in males of *P. rudis*, three different morphotypes were observed. Twenty-three percent of the samples were identical to those reported by McEachran (1983), (i.e., with one pdf and two pvf), 73% of the samples possessed 1 pdf and 1 pvf, whereas 4% had 1 pdf and 3 pvf (Figure 2A). In females of *P. rudis* two morphotypes were observed, 67% were coincident with original description, (i.e., with one pdf and one pvf), and 33% presented 2 pvf (Figure 2A).

In males of *P. normani*, three morphotypes were observed, 72% of the samples were identical to those described by

McEachran (1983), having one pdf and one pvf, but 22% possessed 2 pvf and the remaining 6% possessed 3 pvf (two bigger and between them a third little foramina; Figure 2B). In females of *P. normani* three morphotypes were also observed. 71% of the samples were identical to those described by McEachran (1983), 21% possessed 1 pvf, and 8% (3 specimens) possessed two pdf and one pvf (Figure 2B).

In males of *P. lentiginosa* three morphotypes were observed, 27% of the specimens are coincident with original descriptions made by McEachran (1983), with one pdf and three pvf, whereas 58% possessed 2 pvf, and 15% had only one pvf (Figure 2C). Finally, in females of *P. lentiginosa* at least 5 fenestrae arrangement patterns were observed, and only 20% of the samples were coincident with original descriptions, with one large pdf and 4 pvf. The remaining morphotypes were distributed as follows: 38% has one large pdf and 3 pvf, 27% had 2 pdf and 3 pvf, 12% possessed 2 pdf and 4 pvf, and 4% possessed 3 pdf and 3 pvf (Figure 2C).

The aforementioned results showed a high variability in fenestrae arrangement at intraspecific level at least within the genus *Psammobatis*, similar to what have been observed in *Sympterygia* spp. (Jurado et al., 2017). Both results call into question the conservative character of this structure and also indicate the lack of taxonomic value, at least in this skates'

**TABLE 1 |** Percent values of the cross-validated discriminant analysis, based on the principal component (PC) scores of: (A) Scapulocoracoid linear morphometric measurements, (B) Body linear morphometric. Group codes are: Pru = *Psammobatis rudis*, Pno = *P. normani*, Ple = *P. lentiginosa*, Ppa = *P. parvacauda*, M = males, F = females.

Species	Predicted group membership (%)						
	Pru_M	Pno_M	Ple_M	Pru_F	Pno_F	Ple_F	
<b>(A)</b>							
Pru_M	53.85	30.77	7.69	7.69	0	0	
Pno_M	11.11	55.56	27.78	5.56	0	0	
Ple_M	0	28.57	57.14	0	14.29	0	
Pru_F	16.67	0	0	61.11	22.22	0	
Pno_F	0	0	10.53	21.05	63.16	5.26	
Ple_F	0	0	0	0	33.33	66.67	
Note: 59.0% of the cross-validated grouped cases were correctly classified.							
Species	Pru_M	Pru_F	Pno_M	Pno_F	Ple_M	Ple_F	Ppa_F
<b>(B)</b>							
Pru_M	0	92.3	0	7.7	0	0	0
Pru_F	76.2	9.5	14.3	0	0	0	0
Pno_M	17.1	0	80.5	2.4	0	0	0
Pno_F	0	7.5	2.5	90	0	0	0
Ple_M	0	0	0	0	100	0	0
Ple_F	0	0	0	0	4.8	95.2	0
Ppa_F	0	0	0	100	0	0	0
Note: 86.8% of the cross-validated grouped cases were correctly classified.							

genera. In this respect, one of the morphotypes observed in females of *P. normani* (with two pdf and one pvf, **Figure 2B**) was identical to the one reported in *P. parvacauda* by McEachran (1983) who stated “scapulocoracoids of *P. parvacauda* are derived in possessing: two postdorsal foramina and an expanded postventral fenestra.”

### Morphological and Morphometric Analysis of *Psammobatis* spp.

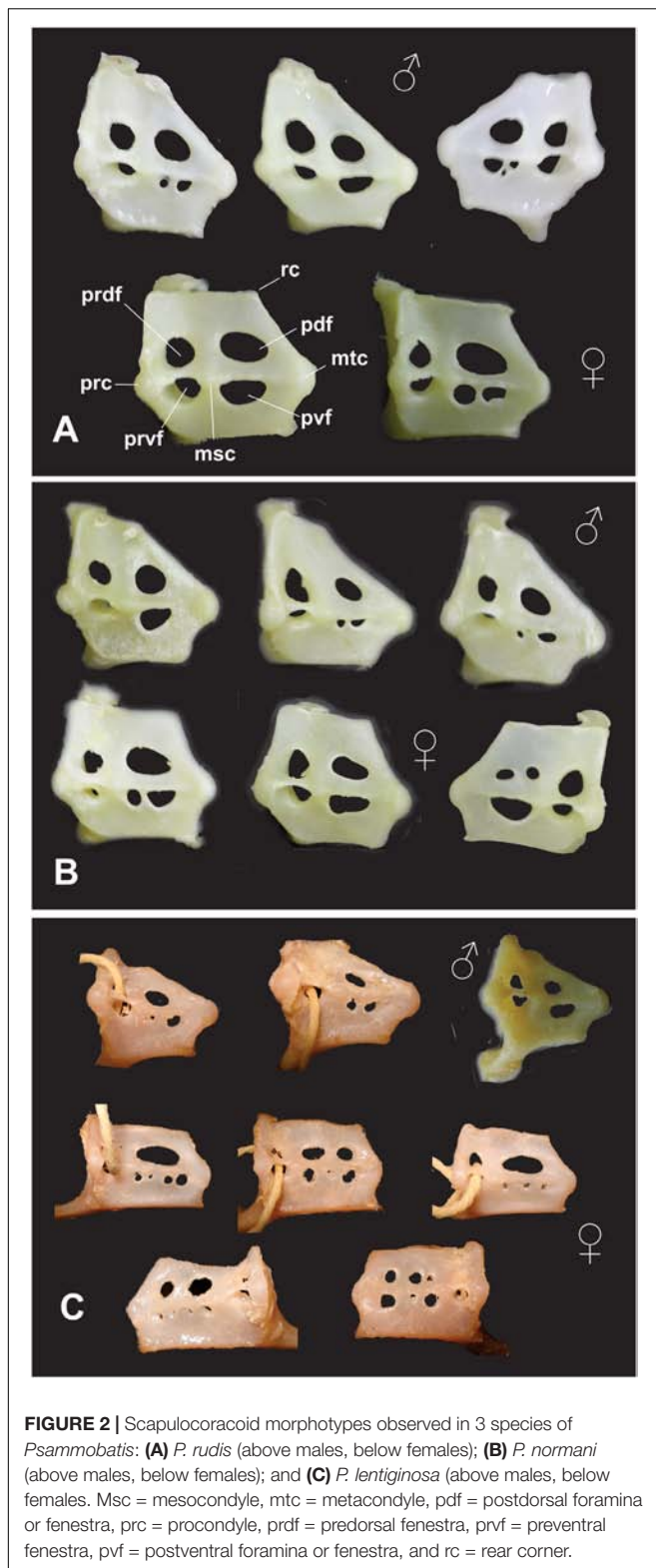
The morphometric analysis of the holotype of *P. parvacauda* and specimens of *P. normani*, *P. rudis*, and *P. lentiginosa* (present study) yielded the following results: the PCA of the correlation matrix of LMM of body, generated by the normalization procedure, produced 3 eigenvalues of >1 (data not shown) and 11 PCs. Correlations between variables and components of >0.59 were considered significant (data not shown). As in the scapulocoracoid morphometric analysis, differences between sexes but also species were recorded. Notably, the PCA showed that *P. parvacauda* (a female) grouped with *P. normani* females in the PC1-PC2 plot, denoting higher loadings of distance between first gill openings and distance between fifth openings, variables. The characterization of the species by sexes was only partial, because some overlap between them was detected (**Figure 3**). The DA on the variations in the 151 individuals of *Psammobatis* classified by sexes and species were explained by 6 canonical discrimination functions, of which the first two explained 84.4% (58.6 and 25.8%, respectively) of the total variance in the data, (Wilks’ lambda = 0.007, *p* < 0.000). The DA correctly classified 94.7% of the original grouped cases, whereas the cross-validated

analysis correctly classified 86.8% of the fishes according to their LMM of body. Moreover, the cross-validated analysis showed that the specimen of *P. parvacauda* was classified by cross validation analysis in the group of *P. normani* females (**Table 1B**).

### Is *Psammobatis parvacauda* a Valid Species?

*Psammobatis parvacauda* was described based on a single female collected around Malvinas/Falkland Islands (McEachran, 1983). According to the author, “*P. parvacauda* most closely resembles *P. rudis* and *P. scobina*, but can be distinguished from the latter by morphometrics, in addition to skeletal structures. In *P. parvacauda* the preorbital length is less than the preoral length (preorbital snout length is equal to or greater than preoral snout length in *P. rudis*), the tail length is less than the distance from tip of the snout to the center of the cloaca (the tail length is greater than the distance from the tip of the snout to the center of the cloaca in *P. rudis* and *P. normani*, and in all other known species of *Psammobatis*.” McEachran (1983) also reported 37 tooth rows in the upper jaw and described its spinulation pattern: two suprascapular and two scapular thorns, not forming distinct triangular patch; tail with three irregular rows of thorns on dorsal and dorsolateral surfaces. Finally, coloration was described as dorsal surface tan and scattered with small, faint, white blotches. However, none of these features are diagnostic for *P. parvacauda*, indeed, the only character used in the key of species provided by McEachran (1983, p. 50) was the length of the tail.

Regarding skeletal structures, as no males are known from this species, the claspers features and their components are obviously

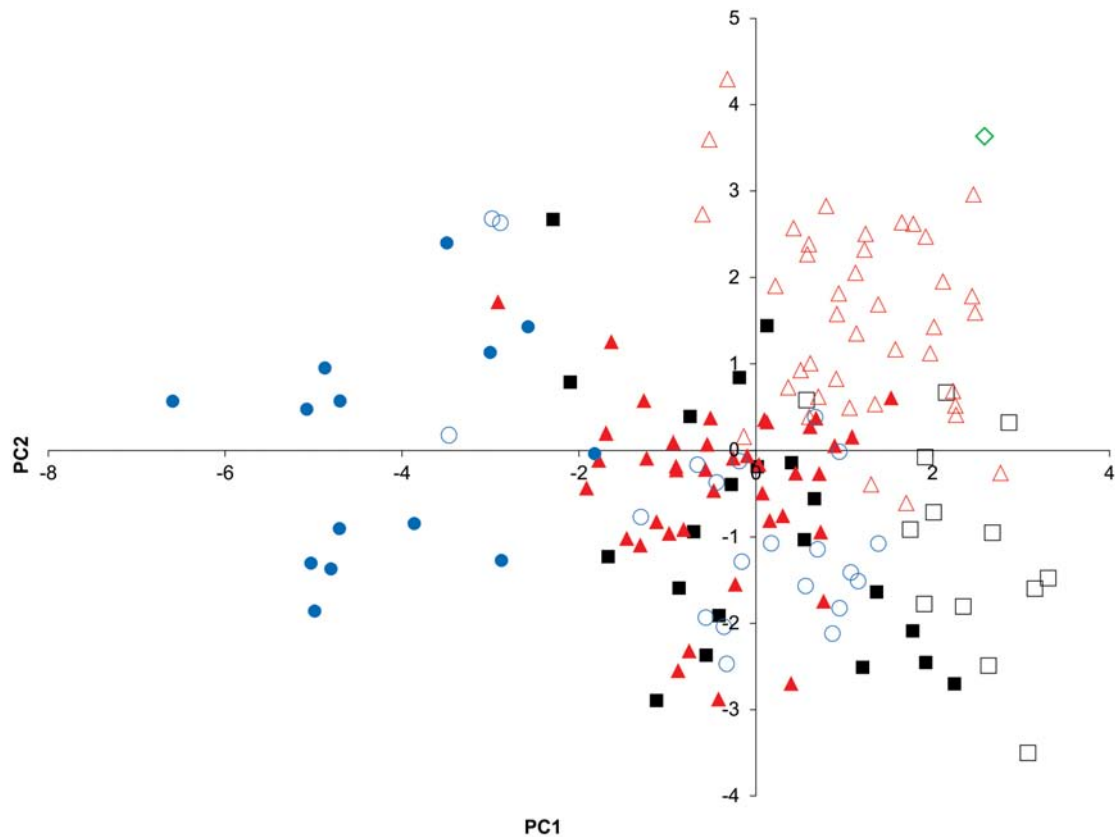


unknown. The neurocranium and the scapulocoracoid are the only skeletal structure available for this species. As noticed by McEachran (1983, p. 42) neurocrania of *P. parvacauda* and

*P. normani* are similar, but, the scapulocoracoid of *P. parvacauda* is distinct from the other *Psammobatis* species in possessing two pdf and an expanded pvf (McEachran, 1983). However, as previously demonstrated, the scapulocoracoid in *Psammobatis* species is highly variable not only among species but also within species. Moreover, as previously indicated the scapulocoracoid pattern of *P. parvacauda* was observed in three specimens of *P. normani* (present study). Interestingly, the spinulation pattern and morphometrics of these specimens were in accordance with original descriptions and the remaining *P. normani* analyzed in the present study. Particularly, they did not have a short tail (length from tip of snout to center of cloaca was similar to length from center of cloaca to tail tip), and eye diameter was not large (4.4% of TL). Therefore, there is no skeletal structures with exclusive characteristic of *P. parvacauda*.

With respect to *P. parvacauda*, Weigmann (2016) stated “Possibly an aberrant specimen of another *Psammobatis* species as the postdorsal tail section of the holotype is apparently incomplete and, despite precise registrations of catches in this area, only one further specimen has been found (Stehmann, 2014, pers. comm.) Nevertheless, the apparently undamaged tail of the second specimen and the very large eyes of the species indicate that the species indeed might be valid despite its close similarity to *P. rudis* and *P. scobina* (Weigmann, unpubl. data).” In the present work, the holotype was examined by one of the co-authors and in fact, the tail section is incomplete (the caudal fin base measured 1.8 mm). Indeed, McEachran (1983) mentioned that epicardial lobe of caudal fin was barely developed in *P. parvacauda*. There is no reliable record of the second specimen reported, because it was not published. Therefore, no information regarding this specimen is available (photos, measurements, meristic, and genetics), only a personal communication by Stehmann to Weigmann is offered. Weigmann highlighted “the very large eyes of the species.” However, McEachran (1983) did not regard this feature as a diagnostic characteristic for the species. He only reported its value as 5.6% of TL (TL 347 mm, OD 19.4 mm).

In addition, Last et al. (2016b) pointed out that “*P. parvacauda* is very poorly known and its distinction from some sandskates has been questioned. However, based on its relatively large eyes (5.6–6.7% of TL), compared to other members of the genus, we provisionally consider it to be valid.” The authors also indicated that the species is distributed in northeast Malvinas/Falkland Islands (type locality) and in northern Patagonian waters (130 m). However, no record of the latter specimen has been published. On the other hand, the features observed in the “new” sample are not totally in accordance with the holotype. Indeed, Last et al. (2016b) mentioned “Tail rather slender and short, tapering strongly, its length ~0.9–1 times precloacal length.” Therefore, in the “new specimen” tail length is equal to precloacal length and no shorter as was diagnosed in the first description made by McEachran (1983). Regarding the eye diameter, the values reported by McEachran (1983) for the holotype was 5.6% of TL, slightly higher than those reported for the holotype of *P. normani* (5.4% TL; McEachran, 1983, table 3, p. 53), whereas for *P. rudis* and *P. scobina* the author provided only the mean values and those were lower than 4.5%. From 152 specimens of *P. normani* analyzed, Mabragaña (2007) showed that this



**FIGURE 3 |** Principal component (PC) analysis (PC1 vs. PC2) based on linear morphometric measurements of body. The 1st 2 PCs explained 55.6% of the variance in the data. *Psammobatis rudis* males (black squares); *P. rudis* females (white squares); *P. normani* males (red triangles); *P. normani* females (white triangles); *P. lentiginosa* males (blue circles); and *P. lentiginosa* females (white circles). Holotype of *P. parvacauda* (white diamond).

characteristic could reach 5.6% of TL, a value observed in the holotype of *P. parvacauda*. Therefore, there would be no diagnostic characters for the species.

It is suspicious that after almost 40 years from its original description, no novel specimens from this species were reported so far, and a likely second specimen quoted by Last et al. (2016b) and Weigmann (2016) would be another report of the species, even more if we consider that species from this genus are conspicuous and abundant in the Patagonian shelf (Cousseau et al., 2007). Furthermore, Mabragaña (2007) in spite of revising more than 600 specimens of its congeners *P. rudis* and *P. normani* along their entire distribution in the SWA, only found males with clasper morphology typical of *P. rudis* or *P. normani*.

The morphological features of the holotype of *P. parvacauda*, specially the spinulation pattern of tail with 3 irregular rows of tail thorns and no dermal denticles or minute spines on dorsolateral aspects of tail, resemble that of *P. normani* more than *P. rudis* (McEachran, 1983; Mabragaña, 2007). In the same way, the number of tooth rows on upper jaw (37) is within the range of both *P. rudis* (31–37, mean = 34, and  $n = 34$ ) and *P. normani* (33–44, mean = 39, and  $n = 46$ ; Mabragaña, 2007). Orbital nuchal and scapular thorns are also large and visible as in

*P. normani*, and similarly the dorsal surface of disk is not covered with coarse dermal denticles as it happens in *P. rudis* (McEachran, 1983; Mabragaña, 2007). Also, as was already demonstrated, the specimen of *P. parvacauda* was statistically classified (cross-validated analysis of DA) in the *P. normani* female group. The external similarities between *P. parvacauda* and *P. normani*, as well as the presence of that particular fenestrae arrangement in the scapulocoracoid of some *P. normani* similar to that reported for *P. parvacauda*, the lack of a particular diagnostic character in the holotype, and the absence of a reported male for this species, strongly suggest that *P. parvacauda* is a junior synonym of *P. normani*. As Weigmann (2016) stated, this specimen surely constitutes “an aberrant female of other *Psammobatis* species.” Both, *P. rudis* and *P. normani* are sympatrically distributed in the SWA, and although *P. rudis* is more abundant in the southern south-west Atlantic Ocean, *P. normani* inhabits also in Patagonian waters (Mabragaña and Cousseau, 2004; Mabragaña and Giberto, 2007).

In conclusion our data strongly indicate that *P. parvacauda* and *P. normani* correspond to the same species. Given that both species were described in the same moment, but considering that description of *P. parvacauda* is possible based in an aberrant specimen, *P. normani* McEachran should be the senior synonym.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article are available on Figshare at doi: 10.6084/m9.figshare.12142302.v1.

## ETHICS STATEMENT

Ethical review and approval was not required for the animal study because it was based on specimen collected with bottom trawls, in research cruises conducted more than 10 years ago, and specimens were landed already dead.

## AUTHOR CONTRIBUTIONS

EM conceived the study. EM, VG, DV, and JD process the sample material. MG-C performed the statistical analyses. EM and MG-C interpreted the results and wrote the first draft of

the manuscript. All authors wrote and revised the final draft of the manuscript.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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