Pelvic Girdle Shape Predicts Locomotion and Phylogeny in Batoids

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ABSTRACT In terrestrial vertebrates, the pelvic girdle can reliably predict locomotor mode. Because of the diminished gravitational effects on positively buoyant bony fish, the same relationship does not appear to exist. However, within the negatively buoyant elasmobranch fishes, benthic batoids employ pelvic fin bottom-walking and punting as primary or supplementary forms of locomotion. Therefore, in this study, we employed geometric and linear morphometrics to investigate if their pelvic girdles exhibit shape characteristics similar to those of sprawling terrestrial vertebrates. We tested for correlates of pelvic girdle shape with 1) Order, 2) Family, 3) Swim Mode, and/or 4) Punt Mode. Landmarks and semilandmarks were placed along outlines of dorsal views of 61 batoid pelvic girdles (3/3 orders, 10/13 families, 35/72 genera). The first three relative warps explained 88.45% of the variation among individuals ($P < 0.01\%$). Only Order and Punt Mode contained groups that were all significantly different from each other ($P < 0.01\%$). Discriminant function analyses indicated that the majority of variation within each category was due to differences in extension of lateral and prepelvic processes and puboischiac bar angle. Over 60% of the original specimens and 55% of the cross-validated specimens were correctly classified. The neutral angle of the propterygium, which articulates with the pelvic girdle, was significantly different among punt modes, whereas only pectoral fin oscillators had differently shaped pelvic girdles when compared with batoids that perform other swimming modes ($P < 0.01$). Pelvic girdles of batoids vary greatly, and therefore, likely function in ways not previously described in teleost fishes. This study illustrates that pelvic girdle shape is a good predictor of punt mode, some forms of swimming mode, and a species' Order. Such correlation between locomotor style and pelvic girdle shape provides evidence for the convergent evolution of morphological features that support both sprawled-gait terrestrial walking and aquatic bottom-walking. J. Morphol. 275:100–110, 2014. © 2013 Wiley Periodicals, Inc.

KEY WORDS: morphometrics; elasmobranch; punting; swimming

INTRODUCTION

In terrestrial vertebrates, the shape of the pelvic girdle is a reliable predictor of both phylogeny and locomotor mode (Gambarian, 2002; Lovejoy et al., 2009; Romer and Parsons, 1977; Snyder, 1954).

However, in marine vertebrates, gravitational forces typically exerted on terrestrial pelvic girdles are essentially released. This is in part due to teleost fishes being positively buoyant and to the majority of these bony fishes and elasmobranch fishes (sharks, skates, and rays) performing swimming as a primary form of locomotion (Moyle and Cech, 1999). Rather than providing support for the posterior half of the body, as in terrestrial vertebrates, the pelvic girdle of fish is unattached from the vertebrae, and serves as a site of muscle attachment and support for fins in most fishes (Fig. 1c). Harris (1938) concluded that rigid pelvic fins of sharks (Elasmobranchii) are not involved in the primary force production during locomotion, but rather, have extremely limited function and can be removed without affecting overall locomotion of the shark (Harris, 1938). The pelvic fins of more derived teleost fishes stabilize the body and assist in maneuverability, and would likely transmit very low forces to the pelvic girdle (Standen, 2008; Harris, 1938; Fig. 1c). However, some teleost fish (e.g., batfish, flying gurnards, frogfish, and lungfish; (Helfman et al., 1997; Pough et al., 2004; Renous et al., 2000; Ward, 2002) and elasmobranch fish (epaulette and bamboo sharks, horn sharks, and batoids (skates and rays); (Compagno, 1999; Goto et al., 1999; Koester and Spirito, 2003; Lucifora and Vassallo, 2002; Macesic and Kajiura, 2010; Pridmore, 1995; Wilga and Lauder, 2001) perform bottom walking with their pelvic fins (Figs. 1a,b). Within the mostly benthic batoids, the pelvic fins are used to walk (each fin alternately; (Lucifora and Vassallo, 2002) and punt (both fins
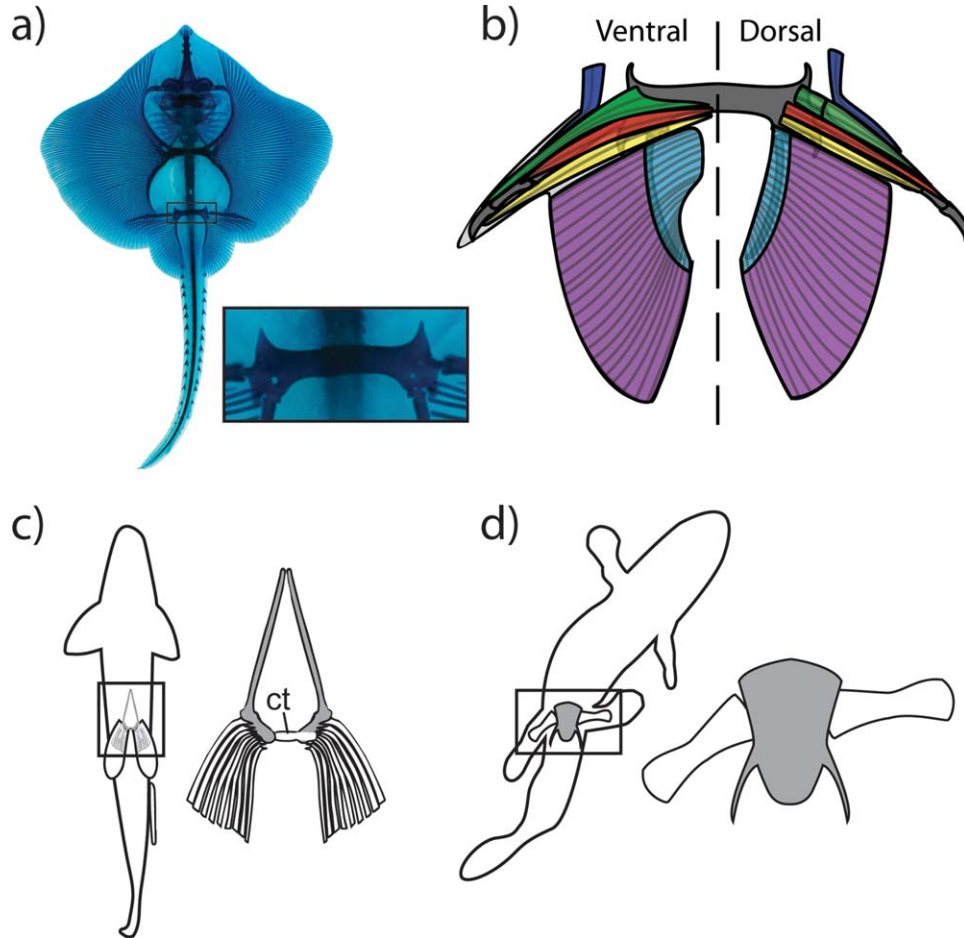
Fig. 1. Morphological variation of pelvic girdles from a batoid (**a**, **b**), illustrating the articulation between the girdle and the propterygia (a) and the musculature associated with the pelvic skeletal elements (b, adapted from Macesic and Kajiura, 2010: Ventral musculature: proximal fin depressor—turquoise, distal fin depressor—purple, distal propterygium depressor—green, proximal propterygium depressor—red; Dorsal musculature: proximal fin levator—turquoise, distal fin levator—purple, proximal propterygium levator—green, distal propterygium levator—red), a rainbow trout [(**c**) adapted from Standen (2008)], and Acanthostega, a primitive sprawled-gait tetrapod [(**d**) adapted from Coates (1996)]. ct = connective tissue.

synchronously; (Koester and Spirito, 2003; Macesic and Kajiura, 2010) on the substrate. While this pelvic fin locomotion would require considerably less support of the body by the pelvic girdle than in terrestrial locomotion, small ground reaction forces would exist. In addition to true punting, performed with just the pelvic fins, some batoids perform augmented punting, in which the pectoral fins are also employed and are thought to generate supplemental thrust (Macesic and Kajiura, 2010). Despite this augmented feature, kinematics such as distance and speed per punt are not greater than in the true punters. The pectorals are likely generating thrust, thus reducing the amount of force experienced by the pelvic fins alone during a punt (Macesic et al., 2013). Moreover, several pelagic rays likely do not perform any form of punting. Therefore, the goal of this current study was to determine if the shape of the batoid pelvic girdles vary with punting ability.

We hypothesize that true punters will exhibit traits similar to those of a sprawled-gait terrestrial vertebrates, including a broad, anteroposteriorly expanded pelvic girdle, with exaggerated lateral processes (Boisvert, 2005; Clack and Coates, 1995; Coates et al., 2008, 1980, 1996; Figs. 1a,b,d). Similarly, we also hypothesize that, like the laterally facing acetabula of sprawled-gait terrestrial vertebrates (Fig. 1d), the angle at which the propterygium (the stylopodial element that is primarily used in punting) articulates with the pelvic girdle will vary such that the true punters have the most laterally facing articulations. We employ geometric and linear morphometrics to examine the overall shape of the pelvic girdle and to measure the angle of articulation between the pelvic girdle and propterygium among batoids that are diverse with respect to phylogeny, swimming (Rosenberger, 2001; Webb, 1984), and punting modes. Using the data from extant specimens, we
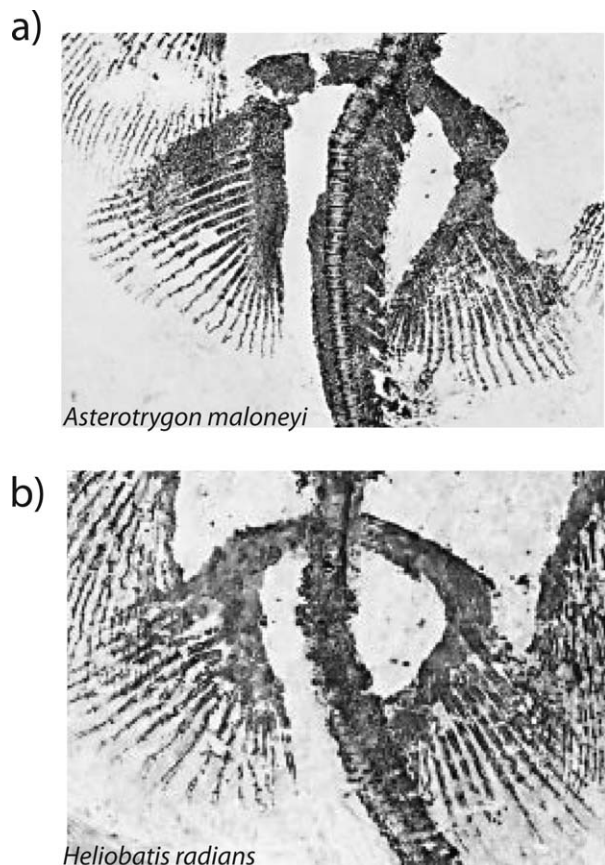
a)

Asterotrygon maloneyi

b)

Heliobatis radians

Fig. 2. Pelvic girdles and fins of the two fossil specimens examined in this study from deCarvalho et al. (2004). (**a**) *Asterotrygon maloneyi* and (**b**) *Heliobatis radians*.

also examine fossil specimens (Fig. 2, deCarvalho et al., 2004) and place them with respect to phylogeny and locomotor mode based on our results from the extant species in this study.

METHODS
Species

We included 61 two-dimensional photographs (dorsal view), radiographs, or scientific illustrations (dorsal view) from peer-reviewed publications of the surface of batoid pelvic girdles (Supporting Information, Table 1). We sampled representatives from three of the four orders of Batoidea (Torpediniformes (1/2 families), Rajiformes (2/2 families), and Myliobatiformes (7/9 families), including 35 of the 72 genera (Fig. 3, Supporting Information, Table 1). Each species' mode of swimming and punting was determined from the literature (Macesic and Kajiura, 2010; Rosenberger, 2001; Webb, 1984). Because the punt mode for the majority of batoids is undescribed, we assigned this ability based on descriptions of general benthic association, prey and habitat preference. True punters are highly benthic, augmented punters are benthopelagic, and non-punters are pelagic. Taxonomic assignments were based on McEachran and Aschliman (2004).

Geometric Morphometrics

Landmark placement. To analyze the general shape of the pelvic girdle, both Type 1 (discrete homologous biological

structures) and Type 2 (points on local maxima or minima of a curve) Bookstein landmarks (Bookstein, 1991), as well as two sets of semilandmarks, were placed along the outline of each pelvic girdle, both extant and fossil (Fig. 3). To generate semilandmarks, a curve was created and resampled to achieve equidistant demarcation points using the software tpsDig2 2.16 (Rohlf, 2010). These points were converted to semilandmarks using the software tpsUtil 1.46 (Rohlf, 2010). The first set of semilandmarks ($n = 24$) was placed along the curvature of the anterior surface of the pelvic girdle (Fig. 3). The second set was placed along the posterior surface ($n = 29$) (Fig. 3). Landmark and semilandmark coordinates were recorded and digitized using tpsDig2 2.16 (Rohlf, 2010).

In order to determine variation among the pelvic girdles, each girdle shape is compared to a consensus, or averaged, pelvic girdle. To create this consensus girdle, we performed a generalized Procrustes analysis (GPA; Gower, 1975; Rohlf and Slice, 1990) on the coordinates of the landmarks and semilandmarks to remove nonshape variation (size, orientation, location; Rohlf and Slice, 1990) and therefore, obtain data relating strictly to shape of the pelvic girdle alone. Semilandmarks were slid to minimize the Procrustes distance between each girdle and the "consensus" reference girdle generated by the GPA. The software tpsRelw 1.49 (Rohlf, 2010) was used to perform the GPA and to generate the consensus set of landmarks and semilandmarks (Fig. 3). This was performed for both extant and fossil specimens.

Shape variation among all pelvic girdles. Using the consensus girdle as the reference, we then generated partial warp scores for every specimen from the superimposed sets of coordinates. We used these scores in a principal components analysis (PCA) to generate relative warp scores (RWs). These scores relate to changes in specific shape factors, and therefore, allow for the visualization of the distribution of the taxa in morphospace. Changes in pelvic girdle shape were also visualized with deformation grids, termed thin plate splines. The PCA and the generation of thin plate splines were performed using tpsRelw 1.49 (Rohlf, 2010). All specimens were included in this analysis. In all subsequent analyses, average RWs were used when more than one specimen existed for each species.

Variation within categories. For extant specimens only, multivariate analysis of variance (MANOVAs) were used to determine if the groups within each category (Order, Family, Swim Mode, Punt Mode) differed by pelvic girdle shape. A MANOVA with Scheffe's post-hoc tests for unequal group sizes was performed for each category separately. We then performed a discriminant function analysis (DFA) of the RWs to determine factors relating to shape differences [canonical variates (CVs)] for each category. We added an additional "Ungrouped" category for each group to which we assigned the fossil specimens. From this analysis, we visualized the variation of pelvic girdle shape among the groups within each category. The original pelvic girdles within each category were classified by posterior probabilities in the DFA. In addition, all specimens were also classified by means of "leave one out" cross-validation, such that each pelvic girdle was classified by the CVs derived from all specimens other than its own. The MANOVAs and DFAs were performed in SPSS Statistics 18.0.

TABLE 1. *Summary statistics for the four different discriminant functions analyses significance is determined at P < 0.05*

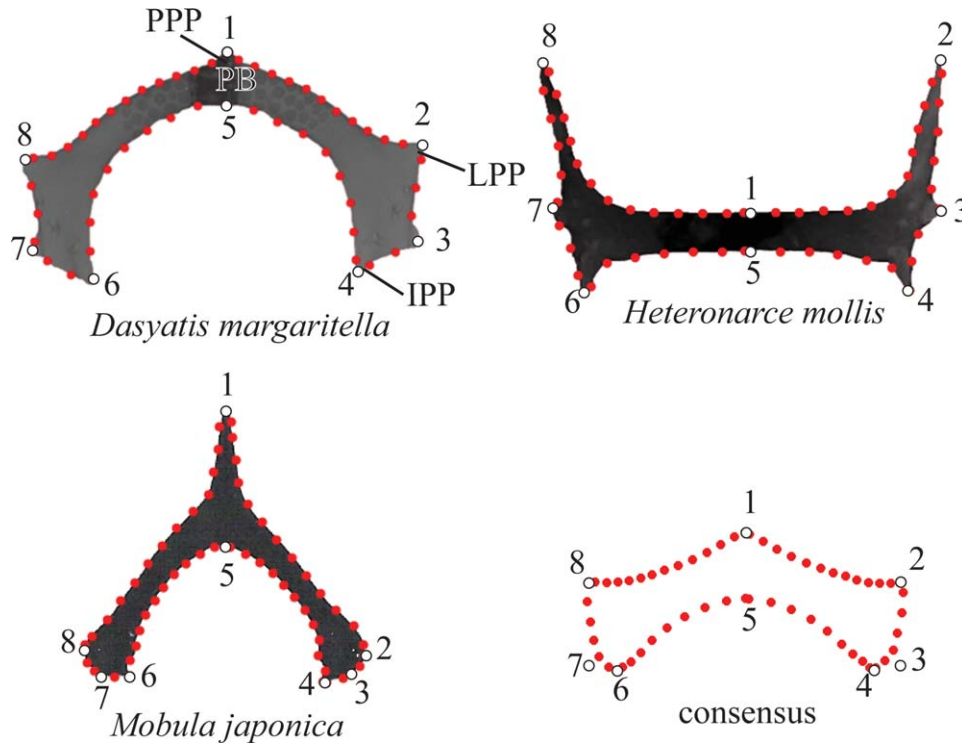| Category Order	CV	% var	Wilk's λ	χ^2	df	p
Order	1	98.71	0.153	124.825	8	<0.01
Family	1	79.57	0.011	277.402	36	<0.01
	2	11.59	0.145	119.541	24	<0.01
	3	7.43	0.394	57.653	14	<0.01
Swim mode	1	82.16	0.227	97.94	12	<0.01
	2	17.65	0.691	24.372	5	<0.01
Punt mode	1	90.36	0.215	101.914	8	<0.01
	2	9.64	0.782	16.384	3	<0.01

Fig. 3. Sample pelvic girdles from three batoids (*D. margaritella*: an augmented punter, pectoral intermediate swimmer; *H. mollis*: a true punter, axial undulator; and *M. japonica*: a nonpunter, pectoral oscillator swimmer) illustrating positioning of landmarks and semilandmarks. Eight landmarks (white) and two curves of semilandmarks (red) were positioned along the outline of the dorsal view of each pelvic girdle (anterior at top, posterior at bottom). The landmarks were defined as: 1) tip of the prepelvic process (when PPP absent, landmark was positioned at the anterior midpoint of the PB); 2 and 8) tips of LPPs; 3 and 7) tip of joint that articulates with the first radial; 4 and 6) tip of iliac pelvic processes (IPP); 5) posterior midpoint of the PB. The first curve consisted of 24 equidistantly spaced semilandmarks along the anterior curve of the pelvic girdle (from landmark 8 to 2). The second curve consisted of 29 equidistantly space semilandmarks along the posterior curve of the pelvic girdle (also from landmark 8 to 2). Landmarks and semilandmarks are shown on three representative pelvic girdles and as the consensus girdle (bottom right) for all of the species in this study.

Pelvic Fin Angle

In addition to landmark-based geometric morphometrics, we also measured the neutral angle at which the socket of the first radial, the propterygium, articulates with its condyle on the pelvic girdle (Fig. 3, at Landmarks 3 and 7). Using the software ImageJ (Rasband, 1997), we drew a line perpendicular to the base of the condyle and measured the angle between this line and the horizontal. Average angles were used when more than one specimen existed for each species. Using SPSS Statistics 18.0, we determined differences in pelvic fin angle among assigned groups for each of the four categories by using analysis of variance (ANOVAs) with Scheffe's post-hoc tests for unequal group sizes.

RESULTS
Geometric Morphometrics

Shape variation among all pelvic girdles: PCA-RWA analysis. All specimens were analyzed in the PCA-RWA to determine variation in shape among all pelvic girdles, regardless of category. The PCA revealed that the first three RWs explained 88.45% of the shape variation (RW1: 70.69%, RW2: 13.07%, RW3: 4.69%). The thin plate splines illustrate that RW1 corresponds to changes of the lateral and prepelvic processes

(LPPs and PPPs, respectively), whereas RW2 corresponds to changes in the height and length of the puboischiac bar (PB, Fig. 4). The values of RW3 correspond with the curves of the most lateral edges of the pelvic girdle, both on the anterior and posterior surfaces. Consensus shapes for each family are shown in Figure 5.

Variation of RWs within categories: MANOVA analysis. Using the first three RWs as dependent variables and each category as an independent variable in MANOVA, we found that the groupings within each category were significantly different based on pelvic girdle shape (Order: Wilk's $\lambda = 0.222$, $F_{(6, 132)} = 24.69$, $P < 0.01$; Family: Wilk's $\lambda = 0.021$, $F_{(30, 167.98)} = 15.44$, $P < 0.01$; Punt Mode: Wilk's $\lambda = 0.244$, $F_{(6, 132)} = 22.52$, $P < 0.01$; Swim Mode: Wilk's $\lambda = 0.250$, $F_{(9, 158.34)} = 13.52$, $P < 0.01$). Whereas all three RWs had a significant effect on differences among members of the Family category (RW1: $F_{10} = 52.55$, $P < 0.01$; RW2: $F_{10} = 8.47$, $P < 0.01$; RW3: $F_{10} = 5.41$, $P < 0.01$), only RW1 had a significant effect on Order (RW1: $F_2 = 98.28$, $P < 0.01$), and both RW1 and RW3 had significant effects on the two locomotory mode
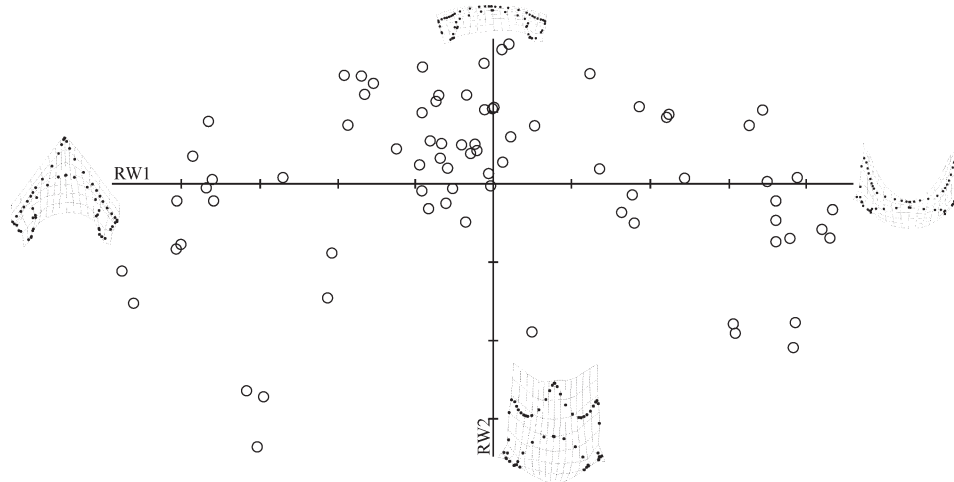
Fig. 4. RWs illustrate the variation in pelvic girdle shape among the 61 species analyzed. RW1, which accounts for 70.69% of the variation, relates to the presence (−) and absence (+) of PPPs, the presence (+) and absence (−) of LPPs, and the angle of the PB. RW2 (13.07% variation) relates to the thickness of the PB and the curvature of the anterior surface of the pelvic girdle. Thin plate spline grid deformations show the extreme negative and positive values for each of the RWs.

categories (Punt mode: RW1: $F_2 = 80.80$, $P < 0.01$ and RW3: $F_2 = 3.97$, $P < 0.01$; Swim mode: RW1: $F_3 = 40.22$, $P < 0.01$ and RW3: $F_3 = 7.99$, $P < 0.01$). The three Order categories were distinctly different from one another (Scheffe's post-hoc tests, $P < 0.05$). Within the Family category, only the Myliobatidae, Platyrhinidae, and Narcinidae families were distinctly different from the other families; all other families were grouped into at least two subsets (Scheffe's post-hoc tests, all $P < 0.05$). The pectoral oscillators and axial undulators were significantly different from the other swim modes (Scheffe's, $P < 0.01$); pectoral undulation and intermediate pectoral locomotion were not significantly different from each other (Scheffe's, $P = 0.084$). All modes of punting were significantly different from each other (Scheffe's, $P < 0.01$ for all) based on RWs.

Category specific shape variation—CVA and DFA. The first six RWs were used to generate significant CVs for each category. Shape variation among groups in the Order category was attributable to one significant CV (98.71% of variance; Table 1; Fig. 6a). For this category, the CV corresponds with the presence or absence of LPPs and PPPs, and with the PB angle (Fig. 6a). Within the Family category, three significant CVs were generated (CV1: 79.57% of variance, CV2: 11.59% of variance, CV3: 7.43% of variance; Table 1, Fig. 6b). In the Family category, CV1 corresponds with the LPPs and the angle of the PB; CV2 largely corresponds with the presence of the prepelvic process and the height of the PB (Fig. 6b). Both the Swim Mode (CV1: 82.16% of variance, CV2: 17.65% of variance; Table 1) and Punt Mode (CV1: 90.36% of variance, CV2: 9.64% of variance; Table 1) categories generated two significant CVs. Again, most of the variance among groups within these categories is attributed to CV1, which correlates to

the presence or absence of LPPs and PPPs (Fig. 6c,d). CV2 also provides information regarding the angle of the PB for both swim and punt mode locomotory categories (Fig. 6c,d).
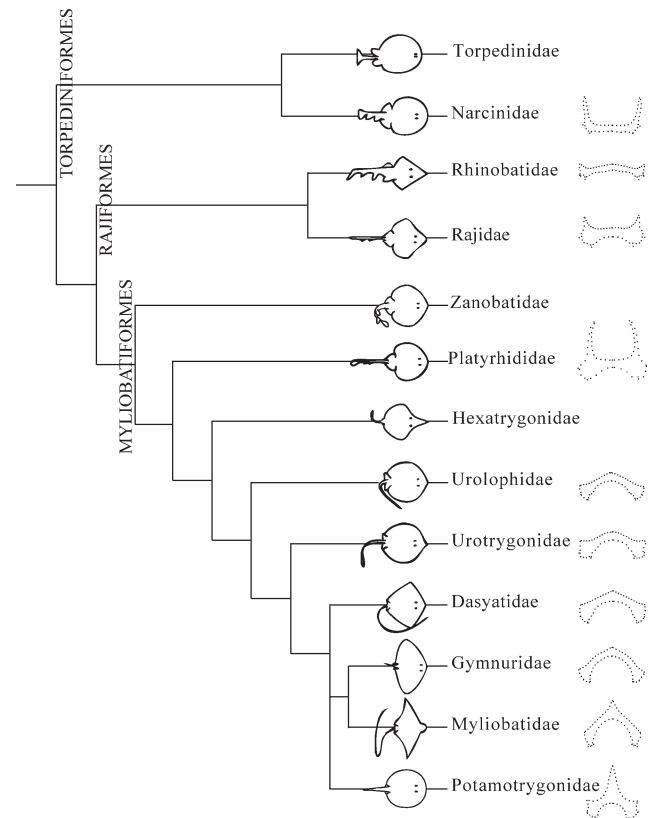

Fig. 5. Phylogeny of Batoidea, after McEachran and Aschliman (2004), Landmark consensus diagrams of the pelvic girdles from families analyzed in the current study are shown to the right of the tree.
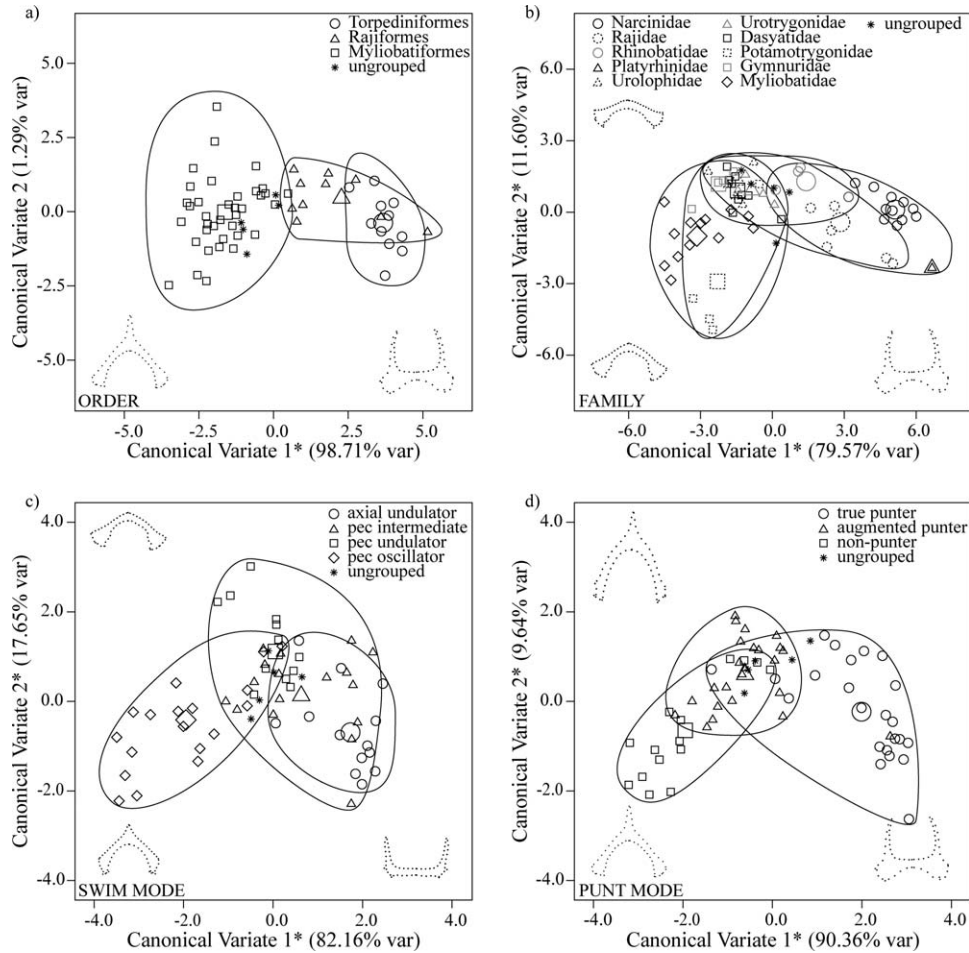
Fig. 6. Morphological groupings of pelvic girdles of batoids based on (**a**) Order, (**b**) Family, (**c**) Swim Mode, and (**d**) Punt Mode based on discriminant Function analyses. Each circle represents one individual; enlarged shapes represent the centroid for each group. Axis titles indicate significance (*) of a CV and the percent shape variation summarized by each CV. Variation in morphology of the pelvic girdle is mostly due to the presence/absence of the LPPs and PPPs and the angle of the PB. Outlines of pelvic girdles show the variation in shape along significant CV axes.

Categorical *classification* of *specimens* based on *shape*. All of the categories (Order, Family, Swim Mode, Punt Mode) classified more than 60% of the original specimens and more than 55% of the cross-validated specimens correctly (Tables 2–5). Only 10% of the specimens were misclassified in the Order category (Table 2). However, at the Family level, misclassified specimens tripled. The families Urolophidae, Urotrygonidae, and Dasyatidae were commonly misclassified amongst themselves. These three families use various forms of pectoral swimming, but all share the same augmented punting mode. The fossil specimens were equally classified amongst these three families. Rhinobatids (100%), platyrhinids (100%), narcinids (90.9%), and gymnurids (100%) had the most correct reclassifications within the category (Table 3). Two of the families with the most distinct modes of locomotion, the Narcinids, which axially undulate and are true punters, and the Myliobatids, which are

mostly pectoral oscillators and nonpunters, exhibit different classification trends. The Narcinids show approximately 9% misclassification, whereas the Myliobatids show almost 25% misclassification. Overall, groups were correctly classified at a higher rate by Punt mode (80.3%) than by Swim mode (63.4%). Although axial undulation (75.0%), pectoral fin oscillation (85.7%), and pectoral fin undulation (76.2%) were well classified, the overall percentage of correct classification for the Swim Mode category was much lower as a result of poor classification for the intermediate pectoral fin locomotion group (25%; Table 4). Within the Punt Mode category, nonpunters (70.6% correct) were the most likely to be misclassified (Table 5). With the exception of the Order category, in which classifications of originals were equal to the cross-validation classifications, correct cross-validation classification was approximately 5% lower than the correct classification of originals.

TABLE 2. *Leave-one-out classification results based on canonical shape variates for the phylogenetic categories for Order*

	Predicted group membership (n/%)			
	Torpediniformes	Rajiformes	Myliobatiformes	Total
Torpediniformes	**10/90.9**	1/9.1	0	11
Rajiformes	2/20.0	**7/70.0**	1/10.0	10
Myliobatiformes	0	0	**39/100**	39
Ungrouped cases	0	0	5/100	5

Ungrouped specimens represent fossil specimens.
93.3% of original specimens and cross-validated specimens correctly classified.

Pelvic Fin Angle

The angle at which the anterior edge of the pelvic fin articulates with the pelvic girdle was significantly different among groups for all four categories (Order, Family, Swim Mode, Punt Mode; Fig. 7). Within the Order category ($F_{(2,67)} = 23.264$, $P < 0.01$), the Rajiformes (mean = $12.71° \pm 2.812$ standard error (SE)) and Torpediniformes (mean = $13.19° \pm 3.220$ SE) both have fin angles that are significantly less than the Myliobatiformes (mean = $39.96° \pm 3.723$ SE; Scheffe's post-hoc: $P < 0.05$). Although there were significant differences among groups within the Family category ($F_{(10,59)} = 15.37$, $P < 0.01$), most of the families were not significantly different from one another. Similarly, with the exception of pectoral fin oscillation (ANOVA: $F_{(3,66)} = 16.12$, $P < 0.01$; Scheffe's post-hoc: $P < 0.05$), all swimming modes were not significantly different from each other. In contrast, each mode of punting (True Punt mean = $15.05° \pm 2.715$ SE; Augmented Punt mean = $29.54° \pm 2.907$ SE; NonPunt mean = $54.01° \pm 2.991$ SE) exhibited a significantly different fin angle (MANOVA: $F_{(2,67)} = 38.90$, $P < 0.01$; Scheffe's post-hoc: $P < 0.05$ for each).

DISCUSSION

This study supports the hypothesis that batoid pelvic girdle shape correlates with locomotor mode. The geometric morphometric analyses illustrate that the majority of variation among species and within the four categories examined in this study (Group, Family, Swimming Mode, and Punting Mode) is due to the variation in height and/or presence of anterior pelvic processes, the angle of the PB, and the height and width of the PB. Although all four groups exhibit some level of significant correlation with pelvic girdle shape, the strongest correlations are with Punt and Swim Mode. This locomotor mode signal, rather than the phylogenetic signal, appears to have a greater influence on pelvic girdle shape as most pelvic girdles were not correctly classified by family (Table 3).

Punting

As hypothesized, true punters share morphological traits with early, sprawled-gait tetrapods, including: prominent LPPs, a lack of PPPs, a broad, anteroposteriorly expanded, straight PB, and laterally facing propterygia joints. As is true for the sprawled-gait tetrapods, these morphological characteristics function to increase the thrust generated during locomotion on the substrate (Coates et al., 2008). The prominent LPPs seen in true punters are origin sites for protractors and adductors of the anterior edge of the pelvic fin (Macesic and Kajiura, 2010; Fig. 1b). Likewise, the ilia of early tetrapods are origin sites for protractors and adductors of the femur (Emerson, 1979;

TABLE 3. *Leave-one-out classification results based on canonical shape variates for the phylogenetic categories for Family*

	Predicted group membership (n/%)										
	Narc.	Raji.	Rhino.	Platy.	Urolo.	Urotry.	Dasy.	Potam.	Gymn.	Mylio.	Total
Narc.	**10/90.9**	1/9.1	0	0	0	0	0	0	0	0	11
Raj.	0	**4/66.7**	1/16.7	1/16.7	0	0	0	0	0	0	6
Rhino.	0	0	**3/100**	0	0	0	0	0	0	0	3
Platy.	0	0	0	**1/100**	0	0	0	0	0	0	1
Urolo.	0	0	0	0	**3/60**	0	1/20	0	1/20	0	5
Urotry.	0	0	0	0	1/25	**2/50**	1/25	0	0	0	4
Dasy.	0	0	0	0	2/22.2	1/11.1	**6/66.7**	0	0	0	9
Potam.	0	0	0	0	0	1/25	0	**3/75**	0	0	4
Gymn.	0	0	0	0	0	0	0	0	**4/100**	0	4
Mylio.	0	0	0	0	0	2/15.4	1/7.7	0	0	**10/76.9**	13
Ungroup	0	0	0	0	1/16.7	3/50	2/33.3	0	0	0	6

Ungrouped specimens represent fossil specimens.
76.7% of original specimens and 70.0% of cross-validated specimens correctly classified.

TABLE 4. Leave-one-out classification results based on canonical shape variates for the locomotive categories for Swim mode

	Predicted group membership (n/%)				
	Axial	Pec Interm.	Pec. Und.	Pec. Osc.	Total
Axial	**11/84.6**	2/15.4	0	0	13
Pec. Interm.	4/23.5	**7/41.2**	3/17.6	3/17.6	17
Pec. Und.	1/8.3	4/33.3	**7/58.3**	0	12
Pec. Osc.	0	2/11.1	3/16.7	**13/72.2**	18
Ungroup	0	4/80	1/20	0	5

Ungrouped specimens represent fossil specimens.
63.3% of original specimens and 56.7% of cross-validated specimens correctly classified.

TABLE 5. Leave-one-out classification results based on canonical shape variates for the locomotive categories for Punt mode

	Predicted group membership (n/%)			
	True	Augmented	Non	Total
True	**20/95.2**	1/4.7	0	21
Augmented	1/4.2	**19/79.2**	4/16.7	24
Non	0	5/33.3	**10/66.7**	15
Ungroup	0	5/100	0	5

Ungrouped specimens represent fossil specimens.
81.6% of original specimens and 76.6% of cross-validated specimens correctly classified.

Manzano et al., 2008; Reilly and Jorgensen, 2011). These analogous sets of muscles are responsible for the swing phase of the punt and sprawl, respectively (Macesic and Kajiura, 2010; Manzano et al., 2008). It is hypothesized for both sets of muscles that anterior attachment sites result in less force wasted laterally during each punt or sprawl cycle; rather, more thrust, or, the force to propel the organism forward can be generated (Keith, 1923; Macesic and Kajiura, 2010; Manzano et al., 2008). In true punters, these lateral
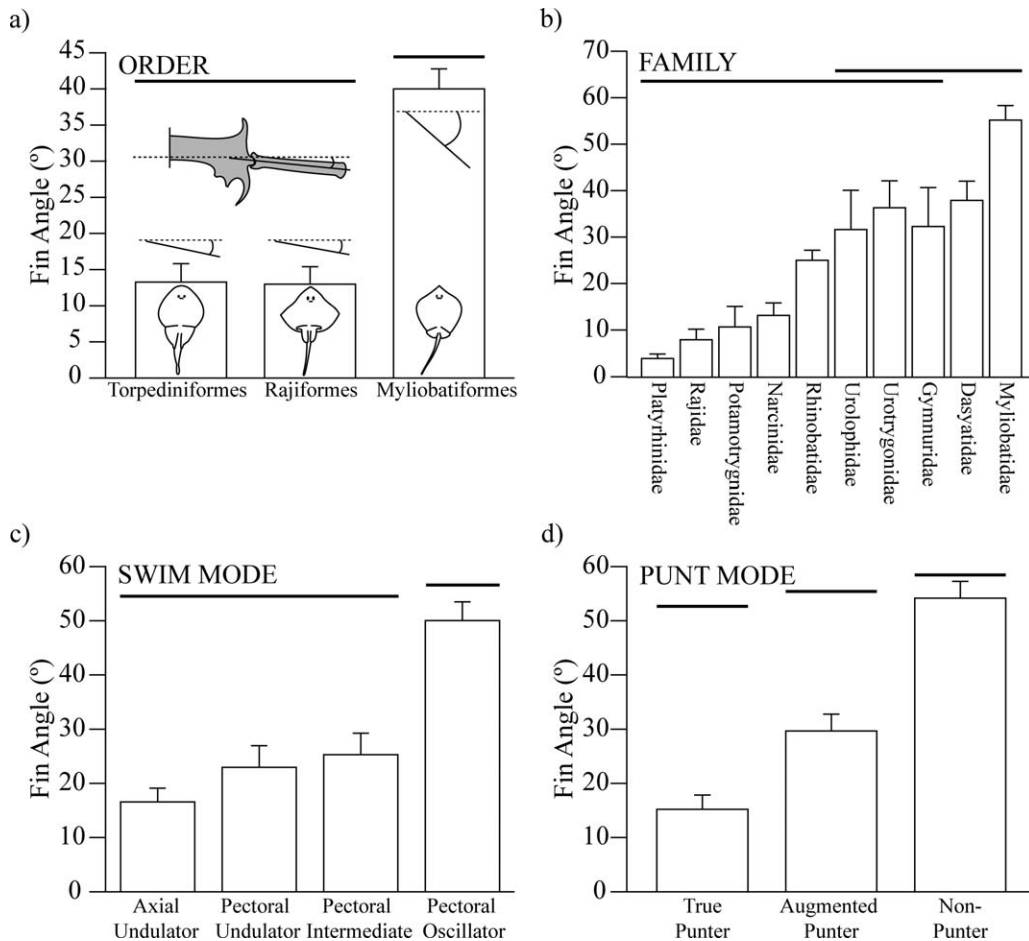

Fig. 7. The angle at which the first radial articulates with its corresponding condyle of the pelvic girdle differs significantly within each category. Groups that share a horizontal bar at the top of the graph are not significantly different from each other. Graph (**a**) contains additional diagrams illustrating the location of measurements made on a representative radial and girdle (inset) ii) pelvic fin angles for the three Orders, and iii) an illustration of the neutral position for the pelvic fins in a representative species from each group. The majority of the families (**b**) do not significantly differ in their fin angle. Similarly, within the swim mode (**c**), only the pectoral oscillator group has a significantly greater fin angle than the other three swimming modes. In contrast, (**d**) all three modes of punting exhibit different pelvic fin angles.

processes are tightly associated with the axial musculature, which may contribute additional rotation of the pelvic girdle, thus moving the propterygia farther anteriorly than would be possible with a stationary pelvic girdle. The long ilia of frogs allow for similar movements during walking (Emerson, 1979; Keith, 1923; Koehl, 1996).

To further maximize the amount of forward thrust, the neutral angle of a true punter's propterygium is nearly parallel to the transverse plane (Fig. 7d). This angle of articulation is also seen between the pelvis and femur of early tetrapods (Clack and Coates, 1995; Shubin, 1995; Wake, 1970; Fig. 1c). In contrast, the propterygia of nonpunting batoids are neutrally held at more than 50° from the transverse plane, and therefore, would result in a large wasteful lateral component during punting (Fig. 7d). Typical, nonpunting teleost fishes also possess highly angled pelvic fins and pelvic girdles, which position the fins closer to the body (Standen, 2010; Fig. 1c). Often the pelvic girdle is not even fused, but rather exists as two bones joined with connective tissue (Standen, 2010; Fig. 1c). Nonpunting batoids also possess narrow, anteroposteriorly compressed pelvic girdles, and use the single PPP as the attachment site for muscles that originate on the two LPPs in true punters. This overall reduction in surface area may not be sufficient for attachment of muscles required for punting or for withstanding forces incurred during punting. In contrast, the broad, anteroposteriorly expanded PB seen in true punters and in early tetrapods provides space for the attachment of larger muscles required to support body mass, and thrust generation during punting or sprawled walking (Keith, 1923; Clack, 2002; Macesic and Kajiura, 2010; Fig. 1a,c).

Augmented punters possess pelvic girdles that appear intermediate between the true and non punters. Macesic and Kajiura (2010) found that the pelvic fins and musculature of the augmented punters are relatively smaller and less specialized than the true punters. The additional pectoral fin movements performed during punting may generate supplementary forward thrust which results in punts of similar distance and speed between the two types of punters (Macesic and Kajiura, 2010).

Swimming

Some of the variation in pelvic girdle shape is more highly correlated to specific swimming, rather than to punting, modes. Although the presence of LPPs is indicative of true punters, only axial undulators possess extremely long LPPs. These processes are tightly associated with the axial musculature and may assist the transmission of muscular force throughout the caudal portion of the ray during swimming (Keith, 1923; Macesic and Kajiura, 2010). Moreover, the near-transverse articulation between the pelvic girdle and the propterygia may enhance the swimming mode by enhancing gliding ability. Unlike sharks that perform continuous axial undulation, electric rays perform axial undulation, often in small bursts, followed by a glide (Roberts, 1969; Waite, 1909). The pelvic fins, like the hypertrophied, spread pelvic fins of the four-winged flying fish (*Cypsilurus spp.*) may enhance gliding ability during swimming (Davenport, 1992; Park and Choi, 2010).

In contrast, the pectoral fin oscillator's highly angled PB and highly angled articulations with the propterygia reduce the profile of the pelvic fins. These fins resemble typical, streamlined teleost pelvic fins (Standen, 2008). Therefore, the pelvic fins of pectoral fin oscillators may be utilized to perform teleost-like maneuvering and body stabilization (Harris, 1938; Standen, 2008). These reduced-profile pelvic fins may also function similarly to an avian tail to control vortex shedding and reduce overall body drag during swimming, or, 'aquatic flight' (Maybury and Rayner, 2001). Birds that are agile, maneuverable aerial fliers (e.g., swifts, hummingbirds), like the "aquatic fliers," possess shorter, lighter tails and a narrower tail base (Gatesy and Dial, 1993, 1996).

CONCLUSIONS

The pelvic girdles of early tetrapods resemble those of true punters and pelvic girdles of typical teleost fish resemble those of nonpunters, suggesting the convergent evolution of morphological traits that are functionally advantageous for these two locomotor modes. In this study, we have also highlighted some overlap between phylogeny and locomotor mode, which may provide evidence that in addition to the swimming continuum previously described in batoids (Rosenberger, 2001), there may also be a punting continuum, with true punting being the basal form.

The morphological variation illustrated in this study can now be used as a reliable predictor of both punting and swimming modes and to a broad extent, phylogeny. The fossil specimens included in this study, *Heliobatis radians* and *Asterotrygon maloneyi*, were classified as Mylibatiformes that employ a pectoral intermediate swimming mode and an augmented punting mode. They both were classified as Urolophids, Urotrygonids, or Dasyatids, the three families that were often misclassified amongst themselves. Previous descriptions of these species place them as closely related to Urolophids and Urotrygonids, but not to Dasyatids (deCarvalho et al. 2004). Our example demonstrates that pelvic girdle morphology alone could be sufficient to determine the swimming and punting mode of an unknown specimen, the Order to which it belongs, and in many cases, even the classification of Family.

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