**Cetacean pelvic bones are targets of sexual selection, not vestigial structures**

Dines, J. P.1,2, \*, E. Otárola-Castillo3,4, P. Ralph5, J. Alas5,6, T. Daley5,7, A. D. Smith5, M. D. Dean5, \*

1Mammalogy, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007  
2Integrative and Evolutionary Biology, University of Southern California, Los Angeles 90089  
3Department of Human Evolutionary Biology, Harvard University, Cambridge, MA  
4Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA

5Molecular and Computational Biology, University of Southern California, 1050 Childs Way, Los Angeles, CA 90089

6West Adams Preparatory High School, 1500 West Washington Boulevard, Los Angeles, CA 90007  
7Department of Mathematics, University of Southern California, 3620 South Vermont Avenue, Los Angeles, CA 90089  
\*Correspondence: jdines@nhm.org (JPD), matthew.dean@usc.edu (MDD)

**Abstract**

Cetaceans (whales and dolphins) have evolved a diverse set of characteristics considered adaptive for an aquatic lifestyle, including dramatic reduction of the pelvic bones. Although often considered functionally unimportant, these bones anchor muscles controlling the penis, which male cetaceans maneuver with great dexterity. Combining morphometric and phylogenetic approaches, we show that males from species with relatively intense sexual selection have evolved relatively large pelvic bones (and penises) compared to their body size. Similar to size, pelvic bone shape diverges more quickly among species pairs that have diverged in mating ecology. Neither pattern was observed in bones unrelated to genital control, suggesting that sexual selection specifically favors relatively large and novel-shaped pelvic bones, features that may underlie male reproductive fitness.

**Introduction**

Reduced morphological features are often interpreted as vestigial when they lose their original function. For example, reduced eyes and pigmentation of cave-dwelling organisms, or loss of locomotion in parasitic taxa may have evolved to “save costs” associated with developing and maintaining features no longer necessary [**CITES needed** **if you guys like this beginning**]. Since evolving from land-dwelling mammals roughly 40 million years ago, cetaceans (dolphins and whales) have evolved a diverse set of features thought to be adaptive for a fully aquatic lifestyle ([1](#_ENREF_1), [2](#_ENREF_2)), including loss of external hindlimbs and extreme reduction of the pelvic bones (Fig. 1A). Cetacean pelvic bones are often described as vestigial, implying they are non-functional and on an evolutionary trajectory of being lost **[maybe add Drickamer refs].**

Ancestral cetaceans possessed functional pelves and hindlimbs 40 million years ago, and evolved to their reduced state in the span of roughly 5 million years ([1](#_ENREF_1), [2](#_ENREF_2)). If cetacean pelvic bones were non-functional, we would predict that they would be lost through time. Yet in the 35 million years since evolving to their reduced state, pelvic bones have only been lost in two out of 89 extant species (*Kogia sima* and *K. breviceps*), and even these two species appear to have cartilaginous sheets that function like a fully ossified pelvic bone ([3-5](#_ENREF_3)).

In addition to these evolutionary patterns, anatomical evidence argues against the view that cetacean pelvic bones are vestigial. The paired pelvic bones anchor the paired ischiocavernosus muscles, which control the penis ([6](#_ENREF_6), [7](#_ENREF_7)) (Fig. 1B). Males apparently maneuver their penises to overcome female mating resistance behavior ([8](#_ENREF_8)), and penis length varies among marine mammals ([9](#_ENREF_9), [10](#_ENREF_10)). The ischiocavernosus muscles attach to the pelvis in all mammals, but cetacean pelvic bones are unique because they are no longer constrained by hind limb attachment and locomotion, potentially freeing them to diverge according to penis morphology.

Given the evolutionary and anatomical evidence, we hypothesized that cetacean pelvic bones evolve in response to sexual selection, allowing males to control penises of varying size. By combining novel morphometric techniques with phylogenetic methodology, we show that cetaceans with large testes for their body (an indication of intense postcopulatory sexual selection) evolve i) relatively large penises, ii) relatively large pelvic bones, and iii) novel-shaped pelvic bones. None of these patterns were observed in the anterior-most pair of vertebral ribs, suggesting that sexual selection specifically acts on cetacean pelvic bones. In addition to rejecting the notion that cetacean pelvic bones are vestigial, our study demonstrates that sexual selection can act not only on external genitalia, but also on the internal infrastructure that supports and controls them.

**Results**

Specimens were gathered from museum collections, and included if body length and sex were recorded (Table S1). We only included sexually mature males/females, as judged by body length (Table S1).

**Estimating the intensity of postcopulatory sexual selection across cetaceans.** To test predictions of sexual selection, we first gathered testes mass data from the literature. Males of species with relatively intense postcopulatory sexual selection tend to possess relatively large testes compared to their body size ([11-20](#_ENREF_11)), presumably a costly though adaptive trait as males vie for fertilization under competitive conditions. This pattern has been confirmed within species, among populations that differ in their mating ecology ([12](#_ENREF_12)), or upon experimental exposure to variable mating regimes ([21](#_ENREF_21), [22](#_ENREF_22)).

Maximum testes mass ranged from 10 g ([Franciscana, a species thought to be monogamous, 23](#_ENREF_23)), to 1 ton ([right whale, a species known to engage in male-male competition during and after mating, 8](#_ENREF_8)) (Table S2). Testes mass residuals were calculated using phylogenetic generalized least squares (PGLS, Fig. S1) and served as a proxy for the intensity of postcopulatory sexual selection. All else equal, species with larger testes mass residuals are expected to experience a more promiscuous mating ecology.

**Relative penis length increases with relative testis mass.** Using PGLS in a re-analysis of data from Brownell and Ralls ([9](#_ENREF_9)) revealed that species with large relative testes mass also tended to have large penises compared to their body length (Fig. S2). While the ultimate mechanism behind this correlation is not clear, one possibility is that males with longer penises are favored in promiscuous species because they can overcome female resistance behavior, as observed by Mate et al. ([8](#_ENREF_8)). Or perhaps female reproductive tracts are more convoluted in promiscuous species, favoring males that can deposit sperm closer to the sites of fertilization. Understanding the mechanism is not a goal of the present study, the important point is that species with relatively large testes (and penises) must have relatively large ischiocavernosus muscles to control them, which require relatively large pelvic bones to serve as anchors.

**Relative size of pelvic bones increases with relative testis mass.**  From museum collections, we gathered pelvic bones from 97 sexually mature males (24 species) (Fig. 2, Table S1). Where possible (87 sexually mature males from 20 species), we included the anterior-most pair of vertebral ribs as a negative control as they are not linked to genital musculature (Fig. 2, Table S1). Using a variety of tools in computational geometry, we defined 962 semi-landmarks from digitized versions of the bones for downstream analyses (Fig. 1C, Fig. 1D, Fig. S3, Fig. S4). Centroid size, the square root of the sum of squared distances of the 962 semi-landmarks from their centroid, was used to quantify size.

We took two complementary approaches to test whether relative pelvic bone centroid size was positively correlated with relative testes mass; both account for phylogenetic relationships. First, using PGLS methodology, pelvic bone residuals (log pelvic bone centroid size phylogenetically regressed onto log body length per specimen, averaged per species, Fig. S5) were positively correlated with testis mass residuals calculated above (Fig. S1) (p=0.0005, r=0.60**,** Fig. 3A), a pattern not observed in ribs (p=0.98, r=0.04, Fig 3B, Fig. S6). This pattern held if we excluded *Pontoporia blainvillei* (species #15 in Fig. 3) or if we only analyzed species for which both pelvic bones and ribs were sampled (p=0.0048, r=0.58).

Our application of PGLS ignores several complexities in the data, including missing data (not all target bones are present in museum collections) and uneven sampling of species (Table S1). Therefore, we developed a second, customized phylogenetic model where log body length, testes size, and left and right pelvic and rib centroid sizes evolved as a correlated multivariate Brownian motion on the cetacean phylogeny ([24](#_ENREF_24)). We carried out a Bayesian analysis, similar to ([25](#_ENREF_25)) but modified to include intraspecific data. After removing their common correlation to body length, male pelvic bone centroid sizes were positively correlated to testes mass (correlation *rho*=0.67, 95% credible interval: 0.25 to 0.90, Fig. 4A, Tables S3-S4). In other words, species with relatively large testes have relatively large pelvic bones for their body. There was no correlation between rib centroid size and testes size (correlation *rho*=0.07, 95% credible interval: -0.51 to 0.62, Fig. 4B, Tables S3-S4). Results were qualitatively similar if we only analyzed those individuals represented in both the pelvic and the rib datasets (Fig. S7) although we lose statistical significance for the correlation between pelvic bone centroid size and testes (correlation *rho*=0.58, 95% credible interval: -0.05 to 0.92, Tables S5-S6), as expected given our smaller dataset after subsampling.

To limit the ecological variation across the full phylogeny, and to specifically focus on species where intraspecific variation could be estimated, we re-analyzed two independent species pairs with relatively large sample sizes: *Phocoena phocoena* (N=6 sexually mature males) vs. *Phocoenoides dalli* (N=8) and *Delphinus capensis* (N=24) vs. *D. delphinus* (N=8). For both species pairs, residual pelvic bone centroid size was significantly larger in the species with the larger residual testes size (*t*=8.69, 3.40; df=10, 29; p<10-5, 0.002 for the two species pairs, respectively), a pattern not observed in ribs (t=0.88, 1.08; df=7, 26; p=0.41, 0.29, respectively). The two *Delphinus* species are so closely related that they were only recognized as separate species approximately 20 years ago ([26](#_ENREF_26)); even this species pair showed significant covariation of pelvic bone and testes size.

In sum, cetaceans with relatively large testes have relatively large pelvic bones, but not ribs. Relatively large pelvic bones provide more surface area for attachment of the ischiocavernosus muscles, offering one mechanism by which males could achieve enhanced maneuverability of relatively large penises.

**Pelvic bone shape diverges more rapidly among species that have diverged in inferred mating ecology.** In addition to size, sexual selection may also favor divergence in shape, which could lead to evolutionary innovation in the forces that ischiocavernosus muscles impart on the penis. We quantified pairwise shape divergence within and between species in a Generalized Procrustes framework (see Materials and Methods)

Among 9 independent species pairs for which both pelvic bones and rib bones could be analyzed, pelvic bone shape divergence significantly increased with divergence of inferred mating ecology (Fig. 5A). As with the analyses of size presented above, such a relationship did not hold for ribs (Fig. 5B), confirming a unique link between inferred mating ecology and pelvic bone shape evolution. Although the mechanism driving this pattern remains unknown, it is possible that sexual selection favors males that control their penis in novel ways, which could drive pelvic shape divergence.

**Sexual dimorphism.** There are no straightforward predictions about how female pelvic bones should evolve, but there are least three possibilities. First, female pelvic bones may show no relationship to relative testes mass of their species, if female pelvic bones are non-functional for example. Second, even if female pelvic bones are non-functional, they may follow the patterns observed in males simply through shared developmental programs. Third, females may experience their own unique selective pressures associated with pelvic bones if they are functional. To begin teasing apart these hypotheses, we repeated the above analyses on female pelvic (33 sexually mature females from 17 species) and rib (27 females from 12 species) bones (Fig. 2, Table S1).

Interestingly, pelvic bone centroid size residuals were positively correlated with residual testes mass of their species, in both the PGLS and the customized phylogenetic models described (PGLS: p=0.002, r=0.68, Fig. S8; customized model: *rho*=0.77, 95% credible interval: 0.30 to 0.99**,** Fig. S9, Tables S7-S8) a pattern not observed in ribs (PGLS: p=0.90, r=-0.10, Fig. S8; customized model: *rho*=0.20, 95% credible interval: -0.58 to 0.80**,** Fig. S9, Tables S7-S8), just as observed in males. The similarity of male and female patterns could be due to shared developmental programs. However, both pelvic bones and ribs were sexually dimorphic in both size and shape, after accounting for species differences (distance-based ANOVA [27, Tables S9-S12, also see](#_ENREF_27) , [28](#_ENREF_28)), suggesting that pelvic bones function in unique aspects of male and female reproductive ecology. As in males, female ischiocavernosus muscles originate on the pelvic bone, but insert instead on the clitoris. It is possible that clitoral movements play a role in female choice, potentially placing the female pelvic bone in the arena of sexual selection, but at the moment this hypothesis remains speculative.

**Discussion**

Male genitalia often evolve more rapidly than any other morphological feature ([29](#_ENREF_29), [30](#_ENREF_30)), especially in promiscuous species ([30-32](#_ENREF_30)). There are multiple hypotheses for the forces driving this divergence, including male-male competition and/or male-female interactions. In addition to genitalia, reproductive tract morphology also evolves rapidly ([11](#_ENREF_11)), and can exhibit plasticity ([33](#_ENREF_33)). Interestingly, female reproductive tract morphology has been shown to covary with male genitalia over evolutionary time ([34](#_ENREF_34)). Some studies have suggested that shifts in female reproductive tract morphology induce reciprocal changes in male genitalia and/or gametes, as would be expected if selection favors females that make it difficult for males to fertilize their ova and males that overcome these defenses ([35](#_ENREF_35), [36](#_ENREF_36)). Importantly, the shapes of male genitalia can underlie real differences in fertilization success ([37-40](#_ENREF_37)). In the context of cetacean mating evolution, it is possible that female anatomy and/or behavioral resistance to mating favors males with relatively long penises to overcome female defenses.

Here we have shown that both size and shape of pelvic bones are evolutionary correlated to relative testes mass, a strong indication that sexual selection is an important force affecting them ([11-18](#_ENREF_11)). One unifying hypothesis in this study is that cetaceans with relatively large testes, an indication of strong sexual selection, have relatively large penises, which require relatively large muscles and anchor sites for their control. Sexual selection may also favor divergence in shape if that allows males to maneuver their penises in novel ways. Importantly, our study rejects the common assumption that cetacean pelvic bones are nonfunctional vestiges, and instead suggest they are a critical component of male, and possibly female, reproductive fitness.

**Materials and Methods**

All original laser scans and the associated code for imposing landmarks has been made available on the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.[NNNN]).

**Estimating the intensity of postcopulatory sexual selection across cetaceans.** In the modern era, most cetacean specimens come from beached animals in various states of degradation, so testes mass cannot be reliably measured per individual. Furthermore, testes regress outside of breeding season. Therefore, we gathered maximum testes mass and body length from the literature (Table S2). Similarly, body mass cannot be reliably measured per individual so in all our analyses we rely on body length as a measure of size.

Using the phylogeny of McGowen et al. ([24](#_ENREF_24)), maximal recorded testes mass was regressed onto maximal recorded body length using the gls procedure in the R package nlme, with a correlation structure that accounted for phylogenetic relatedness ([41](#_ENREF_41)), using the corPagel procedure in the R package ape ([42](#_ENREF_42)). The phylogenetic residuals of testes mass (Fig. 2, Fig. S1) were used as a proxy of postcopulatory sexual selection.

**Relative penis length increases with relative testis mass.** Using the same phylogenetically controlled methods just described, we regressed penis length onto body length, using the data from Table 2 of Brownell and Ralls ([9](#_ENREF_9)). We then regressed the residuals of penis length onto testes mass residuals calculated above. We note that this analysis includes only baleen whales but any uncertainty about the relationship in toothed whales will only make our conclusions conservative.

**Defining semi-landmarks on bones.** Pelvic bones are devoid of distinguishing landmarks, hampering traditional morphometric techniques. To overcome these challenges, we first scanned bones with a NextEngine 3-dimensional Laser Scanner, which returns tens of thousands of x; y; z points per bone. A pipeline was developed to sub-sample 962 evenly spaced and ordered points. The pipeline is graphically illustrated for pelvic bones (Fig. S3) and ribs (Fig. S4) separately.

**Estimating size of bones.**  Bone size was estimated with centroid size, the square root of the sum of squared distances of the 962 semi-landmarks from their centroid. We quantified technical replication by randomly choosing 41 bones (21 pelvic bones, 20 ribs) to scan more than once. One bone was scanned 11 times, the rest scanned twice, each time removing the bone from the scanner and reloading it. The median coefficient of variation (unbiased standard deviation/mean) for centroid size was 0.0094 for pelvic bones, 0.0090 for ribs, indicating high repeatability of our methods.

Two different analyses were performed to test whether bone size evolved in a correlated manner with residual testes mass. First, we calculated the phylogenetic residuals of species-averaged centroid size regressed onto species-averaged body length, then tested whether those residuals were correlated to testes mass residuals, all using PGLS methodology.

Due to complexities in the data such as missing bones uneven sampling across species, we felt averaging centroid size per species might oversimplify the dataset prior to PGLS. Therefore, we developed a second, customized phylogenetic model where log body length, testes size, and left and right pelvic and rib centroid sizes evolved as a correlated multivariate Brownian motion on the cetacean phylogeny ([24](#_ENREF_24)). The mathematical details appear in S1 Materials and Methods.

**Estimating shape differences among bones.** Using the same semi-landmarks just described, we quantified shape difference between all pairs of pelvic bones, or between all pairs of rib bones in a Generalized Procrustes framework, which standardizes each set of 962 semi-landmarks to a common size, translates them to a common origin, then optimally rotates semi-landmark coordinates to minimize their Procrustes distance, the square root of the sum of the squared distances between corresponding landmarks following alignment ([43](#_ENREF_43), [44](#_ENREF_44)). During Procrustes superimposition, our semi-landmarks were allowed to “slide” along the bones’ surfaces using the function gpagen in R package geomorph ([45](#_ENREF_45)). Sliding semi-landmarks is a well-established morphometric technique to improve alignment of regions that are hypothesized to share homology while maintaining structural integrity ([46-49](#_ENREF_46)). Left-sided bones were “mirror-imaged” prior to aligning.

Technical replication was estimated using the same re-scans described above. The median coefficient of variation for shape differences between each re-scan and all the other bones in the sample was 0.0194 for pelvic bones, 0.0342 for ribs, indicating high repeatability in our methods.

**Sexual dimorphism.**  Four different distance-based ANOVA’s were performed to test the contribution of sex to differences in pelvic or rib bones by size or shape, using the function adonis in the R package vegan ([50](#_ENREF_50)), with significance determined with 10,000 permutations. In addition to these ANOVA’s, all analyses performed for sexually mature males were repeated using sexually mature females, using residual testes mass estimated from their respective species.

**References**

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**Figure 1.** Skeletal anatomy of the bottlenose dolphin (*Tursiops truncatus*). (A) Hindlimbs have been lost, and the pelvic girdle reduced to a pair of small bones that no longer articulates with the skeleton. Artwork: Carl Buell. Used with permission from John Gatesy. (B) A closeup of the pelvic bone (P), showing one of the paired, coiled ischiocavernosus muscles (IC), the retractor penis muscle (R) that holds the penis (PEN) internal, and the genital slit (GS) of a male dolphin. (C) Laser scans from paired pelvic bones (grey points), followed by subsampling of 962 semi-landmarks (green) (Figs. S3-S4). (D) Laser scans and landmarks from the anterior-most pair of ribs.

**Fig. 2.** Phylogeny of cetacean species included in this study. Only species for which maximum testes size and body length could be gleaned from the literature are included. Numbers to the left of parentheses indicate residual testes mass (Fig. S1). Numbers in parentheses indicate the number of individuals sampled for male pelvic, male rib, female pelvic, and female rib bones, respectively. Images indicate representative body morphology (left column, artwork from Carl Buell, used with permission from John Gatesy), paired pelvic bones (middle column), and paired rib bones (right column) from a subset of species. N/A=rib bones could not be sampled from all museum specimens. Phylogenetic relationships taken from ([24](#_ENREF_24)).

**Fig. 3.** Among sexually mature males, residual centroid size (species-average centroid size regressed onto body length) was positively correlated with residual testes mass (maximum species testes mass regressed onto maximum body length) in (A) pelvic bones, but not (B) ribs. The results held if we excluded *Pontoporia blainvillei* (#15) or if we only analyzed species for which both pelvic bones and ribs were sampled. 1-*Balaenoptera acutorostrata*, 2-*Balaenoptera musculus*, 3-*Delphinus capensis*, 4-*Delphinus delphis*, 5-*Eschrichtius robustus*, 6-*Eubalaena glacialis*, 7-*Feresa attenuata*, 8-*Grampus griseus*, 9-*Inia geoffrensis*, 10-*Lagenorhynchus acutus*, 11-*Lagenorhynchus obliquidens*, 12-*Lissodelphis borealis*, 13-*Phocoena phocoena*, 14-*Phocoenoides dalli*, 15-*Pontoporia blainvillei*, 16-*Pseudorca crassidens*, 17-*Stenella attenuata*, 18-*Stenella coeruleoalba*, 19-*Stenella frontalis*, 20-*Stenella longirostris*, 21-*Steno bredanensis*, 22-*Tursiops truncatus*, 23-*Ziphius cavirostris*.

**Fig. 4.** The results of a Bayesian model of correlated evolution between traits. (A) All 1000 correlation coefficients sampled from the marginal posterior distributions showed that shifts in relative testes mass positively predicted shifts in pelvic centroid size (correlation *rho*=0.67, 95% credible interval: 0.25 to 0.90). (B) In contrast, shifts in testes size did not predict shifts in rib centroid size (correlation *rho*=0.05, 95% credible interval: -0.38 to 0.48).

**Fig. 5.** (A) Among nine independent species pairs (numbers), pelvic bone shape divergence was positively correlated with divergence in testes residuals (p=0.008, r=0.81). (B) In contrast, rib shape divergence was not correlated with divergence in testes size residuals (p=0.72, r=-0.14). For completeness, the data for all pairwise contrasts, including non-independent contrasts, is shown in gray circles in; only sexually mature males for which both pelvic and rib bones could be sampled were included; 1=*Delphinus capensis* vs. *Delphinus delphis*, 2=*Feresa attenuata* vs. *Pseudorca crassidens*, 3=*Grampus griseus* vs. *Steno bredanensis*, 4=*Inia geoffrensis* vs. *Pontoporia blainvillei*, 5=*Lagenorhynchus acutus* vs. *Ziphius cavirostris*, 6=*Lagenorhynchus obliquidens* vs. *Lissodelphis borealis*, 7=*Phocoenoides dalli* vs. *Phocoena phocoena*, 8=*Stenella attenuata* vs. *Stenella longirostris*, 9=*Stenella coeruleoalba* vs. *Stenella frontalis*.

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