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Coevolution of Caudal Skeleton and Tail Feathers in Birds

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ABSTRACT Birds are capable of a wide range of aerial locomotor behaviors in part because of the derived structure and function of the avian tail. The tail apparatus consists of a several mobile (free) caudal vertebrae, a terminal skeletal element (the pygostyle), and an articulated fan of tail feathers that may be spread or folded, as well as muscular and fibroadipose structures that facilitate tail movements. Morphological variation in both the tail fan and the caudal skeleton that supports it are well documented. The structure of the tail feathers and the pygostyle each evolve in response to functional demands of differing locomotor behaviors. Here, I test whether the integument and skeleton coevolve in this important locomotor module. I quantified feather and skeletal morphology in a diverse sample of waterbirds and shorebirds using a combination of linear and geometric morphometrics. Covariation between tail fan shape and skeletal morphology was then tested using phylogenetic comparative methods. Pygostyle shape is found to be a good predictor of tail fan shape (e.g., forked, graduated), supporting the hypothesis that the tail fan and the tail skeleton have coevolved. This statistical relationship is used to reconstruct feather morphology in an exemplar fossil waterbird, *Limnofregata azygosternon*. Based on pygostyle morphology, this taxon is likely to have exhibited a forked tail fan similar to that of its extant sister clade *Fregata*, despite differing in inferred ecology and other aspects of skeletal anatomy. These methods may be useful in reconstructing rectricial morphology in other extinct birds and thus assist in characterizing the evolution of flight control surfaces in birds. J. Morphol. 275:1431–1440, 2014. © 2014 Wiley Periodicals, Inc.

KEY WORDS: birds; axial skeleton; geometric morphometrics; tail; comparative methods

INTRODUCTION

Variation in tail feathers (rectrices) is one of the most conspicuous signs of avian morphological diversity. Tail shape is extremely variable, from the deeply forked, V-shaped tail of the Magnificent Frigatebird to the delicate streamers of the Red-tailed Tropicbird. The tail in all its forms is a key component of the aerial locomotor apparatus. The wings produce flight by generating lift, thrust, and turning moments (e.g., Pennycuick, 1975; Hedenström, 2002). The tail supplements the role of the wings by generating lift, reducing whole-body drag, contributing to static stability, and serving as a rudder for maneuvering (Thomas and Balmford, 1995; Thomas, 1996; Maybury et al., 2001; Sachs, 2007). The aerodynamic properties of the tail, and thus the potential for the tail to perform these functions, is determined by the shape of the fan of rectrices that make up the tail (Thomas and Balmford, 1995). This tight form-function relationship between tail shape and flight performance means that hypotheses grounded in aerodynamic principles have been useful for understanding the evolution of tail feather diversity (e.g., Fitzpatrick, 1999; Park et al., 2000; Clark 2010). Whereas the caudal skeleton similarly exhibits morphological disparity, the evolution of this variation is less well understood (Van Oort, 1904). Previous work has shown that caudal skeletal morphology is related to foraging behavior. For example, birds that forage underwater convergently evolve a characteristic pygostyle morphology, consisting of an elongate, straight shape (Felice and O'Connor, 2014). This study explores a potential alternative source of variation in the caudal skeleton: its association with the caudal feathers it supports. Herein, I test the covariance between integument and bone in this important locomotor module. Furthermore, I evaluate the utility of caudal skeletal morphology for predicting tail fan shape in fossil birds that do not preserve feathers.

The morphology of the rectrices and the caudal skeleton are predicted to covary for several reasons. First, the rectrices exhibit close topological and functional association with the underlying skeleton (Fig. 1). The calami of these rectrices insert within a fibroadipose structure called the

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rectricial bulb, which is in turn supported by the caudal skeleton. Specifically, the rectricial bulb is affixed to the pygostyle, the terminal caudal element (Baumel, 1988; Gatesy and Dial, 1996b). The pygotyle is a laterally compressed, plowshare-shaped bone formed by the co-ossification of the terminal few (5–9) caudal vertebrae (Baumel, 1988). It not only acts as an attachment for the rectricial bulbs (and in turn the rectrices), but also as an attachment for the muscle that facilitates tail fanning (m. bulbi rectricium) and several of those that produce dorsoventral and lateral movements of the tail (e.g., m. depressor caudae, m. lateralis caudae; Baumel, 1988; Gatesy and Dial, 1996b). Together, the muscles, skeleton, and integument function as an integrated whole.

In addition to these functional associations, the early evolution of the avian tail suggests that there is correlated evolution of skeleton between rectrices and pygostyle. The earliest examples of pygostyles are found in stem-group Neornithes such as Confusciusornithidae and Enantiornithidae (e.g., Gatesy and Dial, 1996a; Chiappe et al., 1999; Gatesy, 2001, 2002; Zhou and Zhang, 2003). These taxa exhibit an elongate, rod-like pygostyle that consists of as many as 12 fused caudal vertebrae, typically longer than the combined length of the free caudal vertebrae, and at most two elongate, streamer-like rectrices (Clarke et al., 2006). The evolution of an articulated tail fan capable of spreading and folding is coincident with the first occurrence of a modern plowshare-shaped pygostyle in the stem ornithurine *Yixianornis* (Clarke et al., 2006). For this reason, it is thought that the evolution of the tail apparatus of birds is characterized by coordinated evolution of the caudal integument and the pygostyle.

Finally, woodpeckers (Picinae) exhibit perhaps the most specialized tail of any bird, an adaptation that is expressed through coevolution of bones and feathers. Arboreal specialist members of this clade utilize the tail as a prop to support the body during vertical climbing (Burt, 1930; Richardson, 1942). These taxa are characterized by a wedge-shaped tail fan with thickened rachises and stiffened vanes on all but the outer two rectrices (Richardson, 1942; Manegold and Töpfer, 2012). This derived feather morphology is accompanied by a pygostyle with an enlarged lateral surface (lamina pygostyli), providing increased area for attachment of the rectrices, and an "enormously enlarged," concave ventral surface (discus pygostyli), increasing the area of attachment for enlarged tail depressor muscles (Burt, 1930; Richardson, 1942; Manegold and Töpfer, 2012). These derived caudal feather and skeletal traits evolved in concert and in a stepwise manner. More stem-ward members of Picinae have only the medial few pairs of rectrices stiffened and lack a enlarged discus pygostyli, but do exhibit the

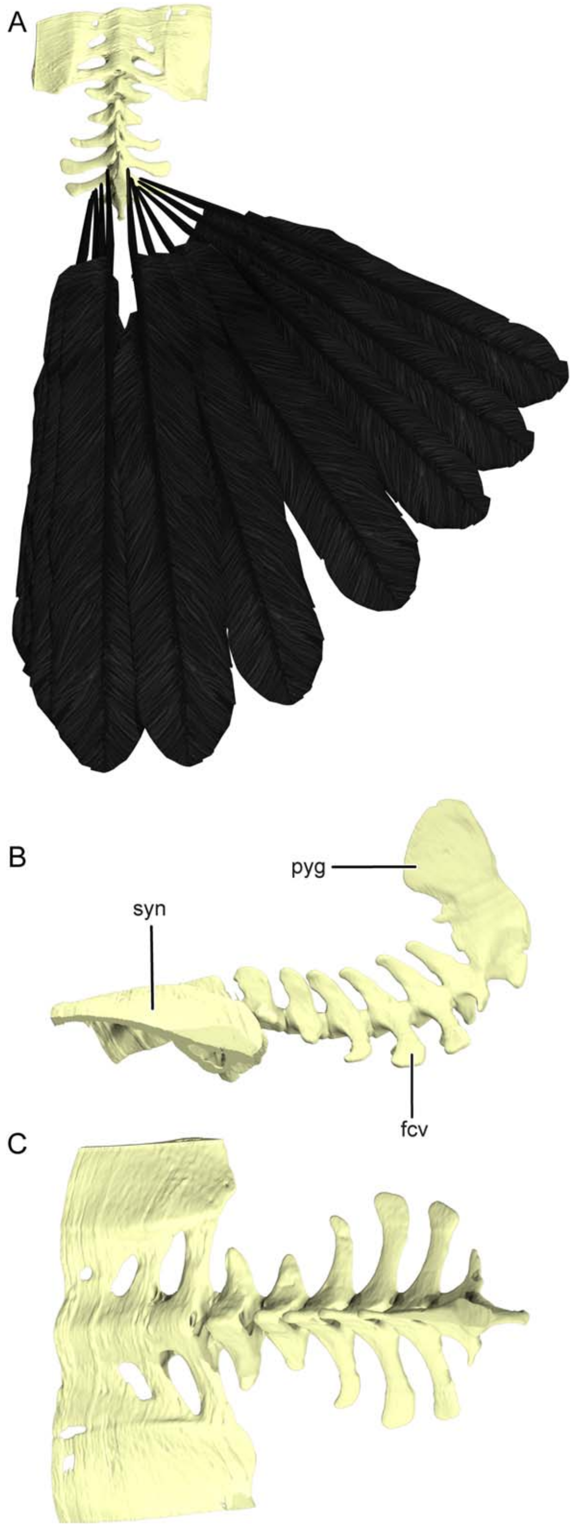

Fig. 1. Digital 3-D Model of Caudal Skeleton and Rectrices. Dorsal view of a generalized avian tail apparatus (**A**) with rectrices folded on the left side and spread on the right side. Isolated caudal skeleton in left lateral (**B**), and dorsal (**C**) views. fcv, free caudal vertebra; pyg, pygostyle; syn, synsacrum. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

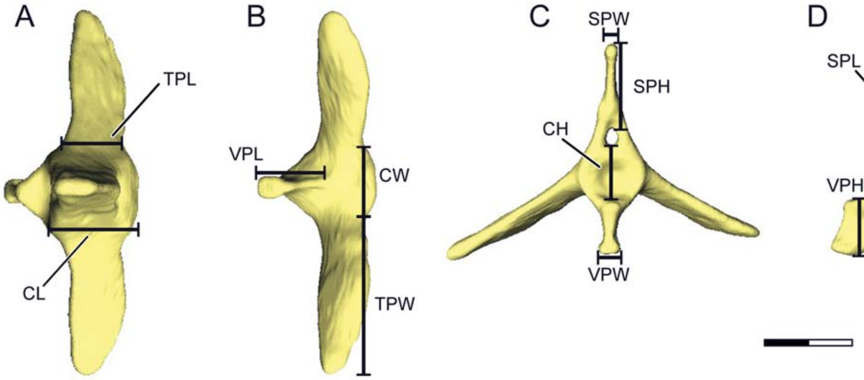

Fig. 2. Free caudal vertebra a generalized bird in dorsal (**A**), ventral (**B**), anterior (**C**), and left lateral (**D**) views. Skeletal metrics collected: Centrum length (CL), centrum width (CW), centrum height (CH), transverse process length (TPL), transverse process width (TPW), spinous process length (SPL), spinous process width (SPW), spinous process height (SPH), ventral process length (VPL), ventral process width (VPW), ventral process height (VPH). Scale bar equals 2 mm. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

expanded lamina pygostyli. This amounts to a stepwise evolution of the tail apparatus for its derived function as part of an arboreal locomotor apparatus, with correlated changes in the tail skeleton and rectrices (Manegold and Töpfer, 2012). The trunk-foraging Brown Creeper (*Certhia Americana*, a member of passeriformes) also uses the tail as a prop during vertical climbing. This taxon similarly exhibits an expanded pygoystyle and stiffened medial rectrices, also thought to be adaptations for arboreal locomotion (Richardson, 1942). These examples are one line of evidence supporting the hypothesis that the components of the avian tail coevolve.

Thus, coevolution of the skeleton and integument of the tail is in evidence from the gross morphology of the system, its early evolutionary history, and from a specific example of adaptation in trunk-climbing birds. It is therefore reasonable to ask whether this pattern of covariation between rectrices and caudal skeleton can be observed in a broad comparative sample of extant birds.

MATERIAL AND METHODS

Skeletal and rectricial morphology was quantified in 48 taxa, sampled from the waterbird (Aequornithes) and shorebird (Charadriiformes) groups (Supporting Information Table 1). These clades were chosen for study as they exhibit morphological, body size, and ecological disparity (e.g., Smith, 2012). Among the members of these clades are soaring (e.g., albatrosses), flapping (e.g., loons and gulls), and swimming (e.g., penguins and auks) taxa (e.g., Pennycuick 1982; Spear and Ainley, 1997; Shealer, 2002). Body sizes vary greatly among the sampled taxa, from Wilson's storm petrel (*Oceanites oceanicus*, 32 g) to the great albatross (*Diomedia epomorpha*, 8,200 g, Dunning, 1993). Caudal skeletal diversity in these clades is also well documented (Felice and O'Connor, 2014). The diversity represented in these two clades makes this taxonomic sample a good focal group for characterizing evolutionary patterns in caudal morphology. Importantly, sexual dimorphism in rectricial morphology is not present in the taxonomic sample chosen (Coulson, 2002). Even groups such as frigatebirds and tropicbirds that are characterized by elaborate tail feathers are sexually monomorphic for rectricial morphology (Coulson, 2002; Veit and Jones, 2003). Specific taxon sampling within these clades was designed to meet several criteria. First, sampling within Aequornithes was designed to include representatives of all the major groups within the clade and was modeled after related studies of evolutionary morphology in waterbirds (e.g., Simons, 2010; Smith, 2012). Second, selected members of Charadriiformes serve as an outgroup to Aequornithes, with individual taxa exhibiting convergent skeletal morphology and ecology between the two clades (Felice and O'Connor, 2014). Finally, species were selected for analysis if multiple skeletal and study-skin specimens were available in major museum collections.

Skeletal morphology was quantified using two methods (described previously, Felice and O'Connor, 2014). The morphology of the free caudal vertebrae was characterized using linear measurements collected using digital calipers (Mitutoyo Model 573–731, Plymouth, MI). To fully capture the extent of morphological variation of the free caudal vertebrae, the following measurements where used: centrum length, centrum width, centrum height, transverse process length, transverse process width, spinous process length, spinous process width, spinous process height, ventral process length, ventral process width, ventral process height (Fig. 2). Additional skeletal elements (sternal length, sternal width, height of sternal keel, synsacral length, and femur length) were measured and used to calculate a geometric mean to act as a body size proxy for each specimen: (Mosimann, 1970; Mosimann and James, 1979; Simons, 2010). A linear regression reveals a significant relationship ($R^2 = 0.84$, $P < 0.001$) between body size proxy values and published body mass values (Dunning, 1993). This indicates that the proxies calculated from skeletal data suitably approximate the actual body masses of these taxa. Body mass proxies were then used to conduct a phylogenetic least-squares regression using the phylogenetic topology, described below (Fig. 3), under a Brownian motion model, to correct raw measurements for body size. The species' means of the residuals were used as variables for subsequent analyses (Revell, 2009, 2011).

Second, pygostyle morphology was quantified using elliptical Fourier analysis (EFA). EFA is a geometric morphometric method that is useful for describing shape variation in two-dimensional forms, like the pygostyle, that have few clearly defined homologous landmarks (Rohlf and Archie, 1984; Crampton, 1995). Using this method, the outline of a given shape is summarized as a series of harmonically related sine and cosine equations. Taken together, these sets of equations, termed harmonics, may be used to describe an increasing degree a complexity of the original outline shape. The result is a

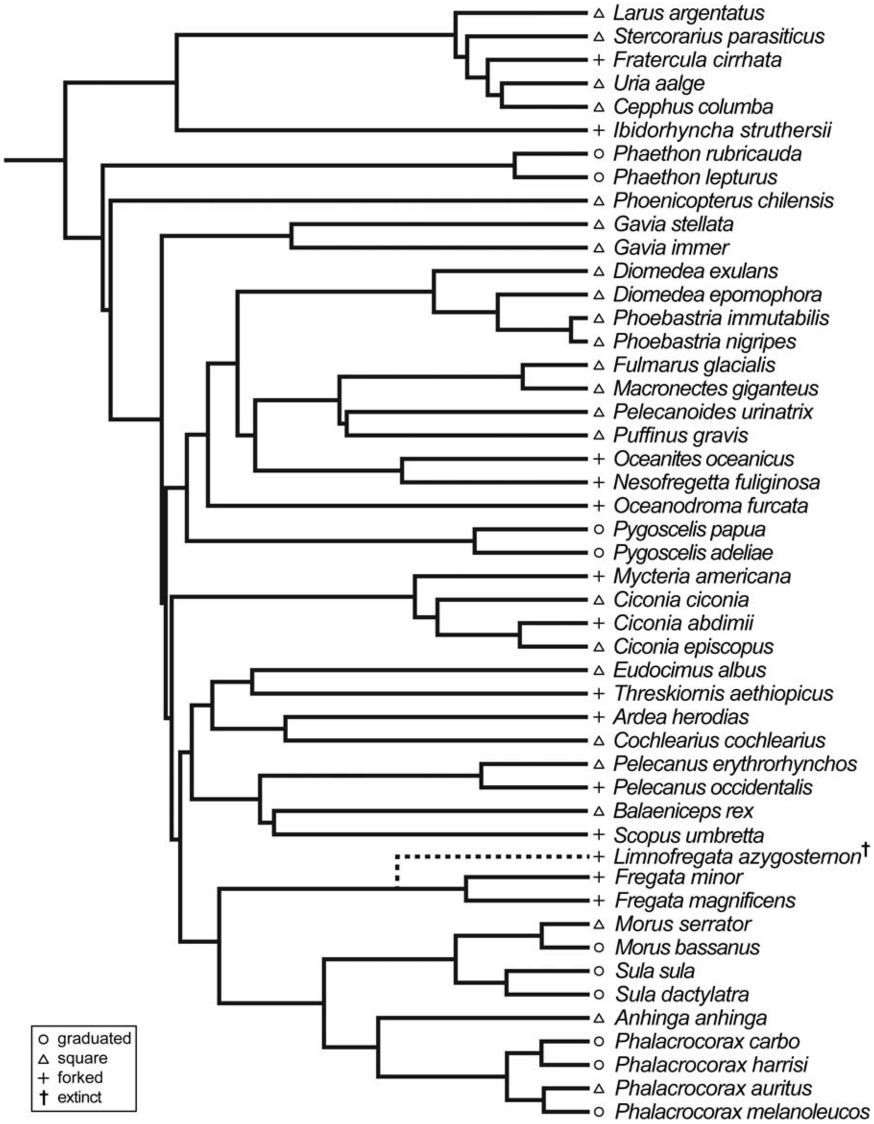

Fig. 3. Phylogenetic tree of 47 extant waterbird and shorebird taxa. Based on (Hackett et al., 2008; Jetz et al., 2012). Extinct taxon *Limnofregata azygosternon* indicated with dotted line.

multidimensional data set containing 4*n* Fourier descriptors for each specimen, where *n* is the number of harmonics used. This dataset is then corrected for the effects of size, rotation, and position, and subsequently can be used in multivariate statistical analyses in the same way that landmark-based morphometric data sets are used (Rohlf and Archie, 1984; Crampton, 1995; Claude, 2008). Each pygostyle specimen was photographed in left lateral perspective. Outline shapes were digitized and EFA was applied using the SHAPE software suite (Iwata and Ukai, 2002). Using the Fourier power equation (Crampton, 1995; Claude, 2008) it was determined that eight harmonics are required to reconstruct 95% of the detail of the digitized outline. Following convention, the first eight harmonics were thus used for subsequent analysis of shape variation.

Finally, tail fan shape was quantified using linear measurements of the rectrices. The length of the outermost and innermost tail feathers were measured from 223 study skin specimens (Collected from the following institutions: American Museum of Natural History, New York, NY; Carnegie Museum of Natural History, Pittsburgh, PA; Field Museum of Natural History, Chicago, IL; National Museum of Natural History, Washington, DC; Ohio University Vertebrate Collection, Athens, OH. Complete list of specimens in Supporting Information Table 1). Feather length was measured from the point that the calamus emerges from the skin to the distal extent of the feather. When the tail is folded, the rectrices are stacked dorsoventrally. To minimize the risk of damage to museum specimens, only the more dorsal of the two innermost rectrices and the more ventral of the two outermost rectrices where measured. Tail fan shape is summarized as the logarithm of the length of the outer rectrix divided by the logarithm of the length of the inner rectrix (Bleiweiss, 2009). Thus, a high tail ratio signifies a deeply forked tail fan and a low tail ratio indicates a graduated tail fan. A tail ratio close to 1.0 indicates that inner and outer tail feathers are nearly the same length. This tail shape is termed "square" as it appears somewhat rectangular when folded, although the fully spread tail fan appears semicircular (Bleiweiss, 2009).

When considering a broad taxonomic dataset such as that assembled herein, it is important to acknowledge the shared evolutionary history of the study species involved and to explicitly address the nonindependence of the data in any statistical

TABLE 1. PGLS regression results

Independent variables	Residual standard error	Multiple R^2	Adjusted R^2	F-statistic	P-value
Free caudal vertebral morphology	0.008983	0.5991	−0.1526	0.7969	0.7132
Pygostyle shape	0.01597	0.7635	0.36	1.892	0.08489

approach (Felsenstein, 1985). To take into account the effects of shared ancestry, I tested for phylogenetic signal utilizing a topology (Fig. 3) based on recent phylogenetic analyses (Hackett et al., 2008; Jetz et al., 2012). A posterior distribution of 5,000 trees was obtained from www.birdtree.org, and a maximum clade-credibility (MCC) tree was constructed from this sample using TreeAnnotator v1.6.2 (Drummond et al., 2012). Using this MCC tree, the strength of phylogenetic signal was tested using two methods. First, the optimal value of the tree transformation parameter lambda (λ) was estimated, a variable that quantifies the extent to which phylogenetic patterns predict variation in the phenotypic data (Pagel, 1999; Freckleton et al., 2002). Optimal lambda values were calculated separately for the two skeletal morphology datasets (pygostyle and free caudal vertebrae). For the geometric morphometric dataset summarizing pygostyle shape, phylogenetic signal was also estimating using an alternative approach referred to as the consistency index (Klingenberg and Gidaszewski, 2010) This method is specifically formulated for the purpose of quantifying the effect of phylogeny on multidimensional data (such as geometric morphometric data) and is thus a more appropriate test in this case. Both methods find significant levels of phylogenetic signal, justifying the use of phylogenetic comparative methods in subsequent analyses. The optimal value of lambda is 0.28 for pygostyle shape and 0.27 for the free caudal vertebra data. The consistency index confirms a moderate level of phylogenetic signal (signal = 0.53, P-value = 0.001, iterations = 999).

The relationship between skeletal morphology and tail fan shape was then evaluated using several statistical approaches. First, a phylogenetic generalized least squares regression (PGLS) was used to test whether skeletal morphology could be used to predict tail fan ratio. Two regressions were calculated: one with the pygostyle shape data as the independent variables and one with free caudal vertebrae data as the independent variables. In both analyses, the dependent variable was tail fan shape and the phylogenetic tree described above was used as the comparative framework.

I also utilized a more general, categorical approach in contrast to the continuous data approach of the PGLS. In this case, each taxon was assigned into one of three tail fan shape categories: the quartile with the highest tail fan ratio was defined as forked-tailed, the quartile with the lowest ratio was defined as graduated-tailed, and the median 50% was defined as square-tailed (Fig. 3). Using this classification scheme, a phylogenetic MANOVA (multivariate analysis of variance) was used to test whether each tail fan group exhibits significantly different caudal skeletal morphology (Garland et al., 1993). Again, separate analyses were performed for the pygostyle and free caudal vertebrae data sets. A phylogenetic flexible discriminant analysis (PFDA) was also used to determine if skeletal morphology can be used to consistently predict gross tail fan shape. PFDA is a multigroup classification method related to linear discriminant analysis that is used to predict group identity (in this case tail fan group) using multivariate continuous data (in this case skeletal morphology) (Motani and Schmitz, 2011; Schmitz and Motani, 2011). PFDA was also used to generate ordination plots to better visualize and interpret differences in skeletal morphology among tail fan groups.

Finally, if there is significant covariation between skeletal morphology and rectrices, skeletal morphology should be able to be used to predict tail fan shape in fossil birds that do not preserve integument. I test this assertion using an exemplar specimen of the extinct bird *Limnofregata azygosternon* (Olson, 1977). *Limnofregata* represents the sister taxon to modern frigatebirds (Smith, 2010). Frigatebirds are pelagic marine waterbirds that are seemingly adapted for efficient aerial foraging in the open ocean, where food resources are patchy and unpredictable (Weimerskirch et al., 2004). Putative adaptations for this foraging strategy include long, narrow wings, feet specialized for perching rather than paddling, and a long tail that is deeply forked (Weimerskirch et al., 2004; Olson and Matsuoka, 2005).

In contrast to the oceanic modern frigatebirds, the middle to late Eocene *Limnofregata* is found in lacustrine sediments (Olson, 1977; Olson and Matsuoka, 2005). Its hindlimb morphology indicates that it exhibited more substantial toe webbing than *Fregata* (the genus of extant frigatebirds), suggesting it was more capable of alighting on water than *Fregata*. This morphological and paleoenvironmental evidence has led paleontologists to interpret *Limnofregata* as exhibiting an ecology more similar to *Larus* (gull) than *Fregata*. That is, *Limnofregata* is thought to be more of an opportunistic predator and scavenger like modern *Larus* than a specialized highly aerial predator like *Fregata* (Olson and Matsuoka, 2005). Indeed, it has been hypothesized that the deeply forked tail of modern frigate birds only evolved in an oceanic context as an adaptation for soaring flight (Olson and Matsuoka, 2005). An alternative hypothesis, supported by aerodynamic models of tail function, predicts that agile aerial foragers benefit from forked tails, as this configuration increases lift to drag ratio and moment-to-drag ratio (efficiency of producing turns; Thomas and Balmford, 1995). Thus, if *Limnofregata* was a generalist/opportunistic forager like a gull, it may be expected to have a "square" tail shape like a gull. If it was an aerial forager like *Fregata*, it would be expected to have a forked tail.

To test whether *Limnofregata* possesses the distinct deep forked tail like *Fregata*, I quantified the shape of the pygostyle of *Limnofregata azygosternon* (specimen FMNH PA 723) using EFA and subjected it to the PFDA analysis described above to predict tail fan shape in this specimen. For this iteration of the PFDA, I constructed an informal phylogenetic tree by starting with the topology described above and grafted *Limnofregata* as the sister to *Fregata* (Fig. 3, dashed line), as recovered by a recent morphology-based phylogenetic analysis (Smith, 2010). This produces an ultrametric tree, meaning that the extinct taxon is represented as being contemporaneous with the extant taxa. I acknowledge that this is not a completely accurate representation of the true evolutionary history of the taxonomic sample. However, this informal tree is an appropriate method to incorporate the extinct taxon into the PFDA analysis given our taxonomic sample and our current knowledge regarding the evolutionary relationships among extinct and modern waterbirds (e.g., Smith, 2012; Zanno and Makovicky, 2013). The alternative, constructing a formal phylogenetic hypothesis using a total evidence method (morphological and molecular data) to include this single extinct taxon is outside of the scope of this study.

RESULTS

Each of the two regions of the caudal skeleton exhibits a different relationship with rectricial morphology. First, there is no covariation between morphology of the free caudal vertebrae and tail fan shape. The results of the PGLS regression using free caudal vertebrae data to predict tail fan

TABLE 2. Phylogenetic MANOVA results

Dataset	Degrees of freedom	Pillai–Bartlett trace	Approximate *F* number	Phylogenetic *P*-value
Free caudal vertebral morphology	2	1.2009	0.80155	0.9986
Pygostyle shape	2	1.6784	3.0589	0.0377

ratio are not significant (Table 1). Additionally, when tail fan shape is treated as categorical, a phylogenetic MANOVA shows that there is not a significant difference in free caudal vertebral morphology among forked-, square-, and graduated-tailed birds (Table 2).

Pygostyle shape, however, is more closely related to tail fan morphology. Although PGLS regression finds that the relationship between pygostyle fan shape and tail ratio is not significant (Table 1), the statistical approaches classifying tail shape more generally as a categorical variable do recover a strong relationship between caudal skeleton and integument. Forked-, square-, and graduated-tailed birds indeed exhibit significantly different pygostyle shape (Table 2).

To visualize the differences in pygostyle shape among these groups, I calculated average pygostyle shape for each group and constructed outlines for each using inverse EFA (Claude, 2008; Bonhomme et al., 2013). Taxa with graduated tails (e.g., gannets and cormorants) exhibit a pygostyle that is craniocaudally elongate and that tapers to a point caudally (Fig. 4a). In contrast, the pygostyle of forked-tailed birds (e.g., storm petrels, frigatebirds) is rounded caudally and deflected caudodorsally (Fig. 4c) compared to the straight configuration observed in the graduated-tail group. The pygostyle of this group also has well-defined ventral processes and exhibits distinct craniodorsal and caudoventral concavities at midlength, generating the hourglass shape in lateral view (Fig. 4c). Finally, the pygostyle shape of square-tailed birds is somewhat intermediate between that of the forked and graduated groups (Fig. 4b). It shows the pronounced ventral process of the forked group. The hourglass shape is also present in the square-tailed group, but it is less strongly defined. The pygostyle in the square-tailed group is less dorsally deflected than that of the forked-tail group but not as straight as in the graduated-tail group. The pygostyle shape of forked-tailed and graduated-tailed birds therefore represent two extremes, with the square-tailed taxa exhibiting an intermediate condition.

Given that pygostyle shape differs among these groups, I subjected these data to a PFDA to assess whether pygostyle shape can be used to predict the tail fan category to which a species belongs. The results indicate that pygostyle shape is an excellent predictor of tail fan shape with just 2.1% misclassification error (Fig. 5). The first discriminant axis explains 55% of the between-group variance. This axis describes the change in height of the pygostyle along its length. Taxa that score high on axis one (forked tailed taxa, e.g., *Nesofregetta fuliginosa*, *Oceanodroma furcata*) exhibit a pygostyle with a defined hourglass shape, with a narrowing midway along its length followed by an expansion at the caudal extent (e.g., Fig. 4c). Those that score low on this axis (square tailed taxa, e.g., *Ardea herodias, Cochlearius cochlearius)* exhibit a pygostyle that is taller at midlength and tapers slightly at the caudal margin, thus lacking the hourglass shape. The second discriminant axis explains the remaining 45% of the between group variance. This axis separates the graduated-tailed taxa from the other groups and describes the extent to which the pygostyle is deflected dorsally. Graduated-tailed taxa (e.g., *Phaethon rubricauda, Pygoscelis papua*) score very high on axis two exhibit a straight pygostyle (e.g., Fig. 4a). Forked- and square-tailed taxa score low on axis two and exhibit a dorsally deflected pygostyle (e.g., Fig. 4b,c).

Of the 48 taxa measured, only *Eudocimus albus* (American White Ibis) was not accurately classified by the PFDA model: it belongs to the square tail fan group, but was predicted to have a forked

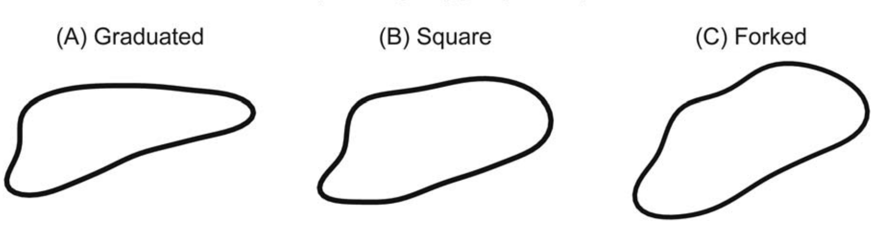

Fig. 4. Group average pygostyle shape. Average pygostyle shapes of (**A**) Graduated-, (**B**) Square-, and (**C**) Forked-tailed taxa as reconstructed by inverse EFA.

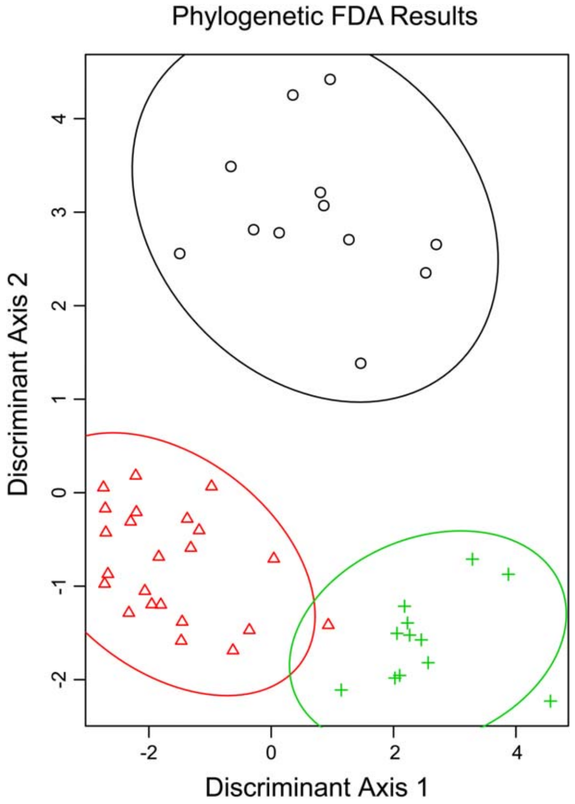

Fig. 5. Results of PFDA. Circles: graduated-tailed taxa, triangles: squared-tailed taxa, crosses: forked-tailed taxa. Misclassification rate = 2.1%. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

tail fan. Taken together, these results suggest that there is a relationship between pygostyle shape and caudal feather configuration. This relationship is not strong enough to predict precise tail fan ratio (as in PGLS) but can be used to predict general tail fan shape (as in PFDA).

When the fossil bird *Limnofregata* was subjected to the PFDA, it was predicted to have exhibited a forked tail fan, a phenotype often found in agile aerial foragers. A qualitative examination of the pygostyle morphology of *Fregata* and *Limnofregata* reveals some similarities (Fig. 6). Both are characterized by the distinctive dorsally deflected orientation associated with a forked tail fan. Additionally, both have a well-defined ventral process, although it is more expanded in *Fregata*. Both show slight craniodorsal and caudoventral concavities, characteristic of forked-tailed birds. The caudoventral concavity is positioned more proximally in *Limnofregata* than in *Fregata*. The dorsal margin is craniocaudally expanded in *Fregata*, but not in *Limnofregata*. Although pygostyle shape of these two genera are distinct from one another, they both exhibit the characteristic pygostyle morphology indicative of a forked tail fan.

DISCUSSION

The caudal apparatus of birds is an important part of the aerial locomotor apparatus, yet the evolution and diversification of its component parts has until now been understudied. Evidence from the fossil record (Clarke et al., 2006) and from birds with highly specialized tail structure and function (Manegold and Töpfer, 2012) suggests that the fan of tail feathers coevolves with the caudal skeleton that supports it. The results of this phylogenetic comparative analysis of caudal morphology in waterbirds and shorebirds support the hypothesis of coevolution of caudal feathers and the pygostyle. Birds with different tail fan shapes (forked, graduated, or square) have significantly different pygostyle shapes. Moreover, pygostyle shape can be used to accurately predict tail fan shape using PFDA. In several instances, common pygostyle shape and tail fan shape evolve in distantly related taxa. For example, the various fork-tailed taxa (e.g., African sacred ibis, *Threskiornis aethiopicus*; frigatebirds, *Fregata*; great blue heron, *Ardea Herodias;* hydrobatids, *Nesofregetta*, *Oceanites*, *Oceanodroma*; tufted puffin, *Fratercula cirrhata*) all exhibit a characteristic dorsally deflected, hourglass-shaped pygostyle. These taxa are somewhat dispersed across the phylogeny (Fig. 3), suggesting that feathers and skeleton independently coevolved in each of these lineages. Likewise, distantly related graduated-tailed taxa (e.g., cormorants, *Phalacrocorax*; penguins, *Pygoscelis*; tropicbirds, *Phaethon*) exhibit a common long, straight pygostyle shape. This convergent evolution of both tail fan shape and pygostyle shape supports the hypothesis that these components of the caudal apparatus coevolve. Interestingly, many of the graduated-tailed taxa are underwater foraging birds (e.g., Shealer, 2002). The straight, tapered pygostyle shape that is correlated with this tail fan shape is also characteristic of underwater foraging taxa (Felice and O'Connor, 2014). This suggests that that an interplay of functional demands and covariation among traits serves to generate the diversity of caudal morphology observed among birds.

Another notable finding is the discordance between the results of continuous (PGLS) and categorical (MANOVA and PFDA) approaches. Whereas no significant relationship was found between tail feathers and pygostyle using PGLS, a correlation was recovered using MANOVA and PFDA. The difference in results could be due to the structure of the data. The geometric morphometric dataset describing pygostyle shape does not meet one of the assumptions of MANOVA and PGLS. Mardia's tests of multinormality (Mardia, 1974; Korkmaz and Goksuluk, 2014) were used to determine that this dataset exhibits

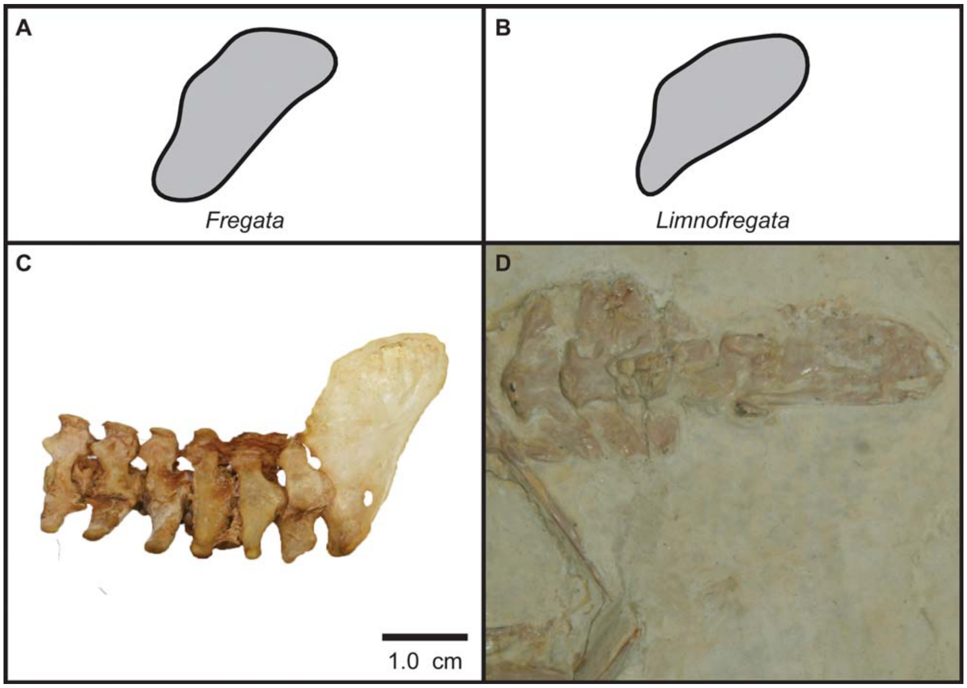

Fig. 6. Comparison of Pygostyle Shape in *Fregata* and *Limnofregata*. Average pygostyle shape of (**A**) *Fregata minor* ($n = 3$) and *Fregata magnificens* ($n = 3$) and (**B**) *Limnofregata azygosternon* ($n = 1$) as reconstructed by inverse EFA. Photographs of the caudal skeleton of (**C**) *F. magnificens* (FMNH 375503), and (**D**) *L. azygosternon* (FMNH PA 723). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

significant kurtosis, deviating from multivariate normality. Conversely, the assumption of homoscedasticity is met (Anderson, 2006; Oksanen et al. 2013). MANOVA using the Pillai–Bartlett trace test statistic has been shown to be somewhat robust to such a departure from normality (Olson, 1974). PFDA, as a nonparametric analysis, is also robust to departures from normality. The nonsignificant results of the PGLS analysis could represent Type II error resulting from the failure of the data to meet the assumptions of the method. Alternatively, the difference in the results of the various analyses could be related to the resolution of each test. Whereas the MANOVA and PFDA analyses evaluate the relationship between pygostyle shape and general tail fan shape (forked, square, and graduated), the PGLS analysis tests the relationship between pygostyle shape and the exact tail fan ratio of each taxon. It is possible that the phenotypic covariation between the pygostyle and the rectrices is simply strong enough to allow for a prediction of gross tail fan shape but not the exact dimensions of the fan.

Using the categorical approach, the sole misclassified taxon was the white ibis (*Eudocimus albus*), a square-tailed species which was predicted to have a forked tail fan. The white ibis scores higher on discriminant axis one than any other square tailed taxon and also lower on axis one than any forked-tailed taxon (Fig. 5). This intermediate position indicates that the white ibis lacks the distinguishing features of either the forked or graduated groups (i.e., it lacks both the “hourglass” shape and a caudal tapering). This serves to illustrate that whereas feather morphology and pygostyle morphology are closely linked, other factors influence the morphology of each of these tissues, complicating the relationship. For example, the correlation between foraging behavior and caudal skeletal morphology is an additional source of skeletal variation (Felice and O’Connor, 2014). White ibis forages while standing in deep water (Frederick and Bildstein, 1992). As such, it exhibits pygostyle morphology characteristic of terrestrial foraging birds (i.e., hind limb based stalking and standing, Felice and O’Connor, 2014). This ecological signal could be overwhelming the feather-bone variation signal and causing the misclassification error.

The predictive power of the PFDA was used to determine that the extinct frigatebird *Limnofregata* probably exhibited a forked tail similar to that of its extant relatives. It has been proposed that *Limnofregata*, found in lacustrine deposits, was a generalist akin to *Larus*, and that the frigatebird linage only evolved specializations for aerial foraging in the context of a marine habitat (Olson and Matsuoka, 2005). These results, however, suggest that *Limnofregata* had already acquired one characteristic of aerial foragers, a forked tail fan. Therefore, it is possible that *Limnofregata* and

Fregata share this foraging style in common. Importantly, this example illustrates that this method for reconstructing rectricial morphology on the basis of pygostyle shape has potential for use with other fossil birds (e.g, *Baptornis*, *Gansus*) with known pygostyle morphology (Martin and Tate, 1976; You et al., 2006). The accuracy of soft tissue reconstructions in stem Neornithes will depend on a more comprehensive taxonomic sampling than what is presented here.

In contrast to the relationship between pygostyle shape and tail fan shape, no relationship is found between the morphology of the free caudal vertebrae and the tail feathers. Variation in free caudal vertebrae is also not associated with locomotor behavior (Felice and O'Connor, 2014). Additional work is needed to determine the drivers of free caudal vertebral evolution. One possibility is that the proportions of free caudal vertebrae are less influenced by their association with the pygostyle and tail fanning apparatus than by other factors, such as whole-body trends in axial skeletal morphology.

Whereas these findings indicate that there is a relationship between the pygostyle and the tail fan, it is still unclear exactly what mechanistic or functional linkage underlies this relationship. Different gross tail fan shapes may exhibit different configurations of the calami relative to the pygostyle. For example, birds with long medial rectricies (graduated tail fans) may have longer calami on the medial rectrices, necessitating an elongate pygostyle. As the pygostyle is also the site of attachment for many of the muscles associated with tail fanning and mobility, differences in pygostyle shape may be attributed to different muscular demands among the tail fan groups. For example, the orientation or size of the tail fanning muscle (m. bulbi rectricium) may vary with tail fan shape, in turn influencing pygostyle shape. These hypotheses require an in-depth investigation of soft tissue anatomy across a variety of taxa.

The results presented here provide evidence that the morphology of the pygostyle and the rectrices are related to one another and may indeed coevolve. Additionally, both tail fan shape (Thomas and Balmford, 1995) and pygostyle shape (Felice and O'Connor, 2014) have been shown to be correlated with locomotor behavior. Taken together, these findings reinforce the tail as a complex, interconnected system that plays an important role in avian locomotion.

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