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Positive Allometry and the Prehistory of Sexual Selection

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ABSTRACT: The function of the exaggerated structures that adorn many fossil vertebrates remains largely unresolved. One recurrent hypothesis is that these elaborated traits had a role in thermoregulation. This orthodoxy persists despite the observation that traits exaggerated to the point of impracticality in extant organisms are almost invariably sexually selected. We use allometric scaling to investigate the role of sexual selection and thermoregulation in the evolution of exaggerated traits of the crested pterosaur *Pteranodon longiceps* and the sail-backed eupelycosaurs *Dimetrodon* and *Edaphosaurus*. The extraordinarily steep positive allometry of the head crest of *Pteranodon* rules out all of the current hypotheses for this trait's main function other than sexual signaling. We also find interspecific patterns of allometry and sexual dimorphism in the sails of *Dimetrodon* and patterns of elaboration in *Edaphosaurus* consistent with a sexually selected function. Furthermore, small ancestral, sail-backed pelycosaurs would have been too small to need adaptations to thermoregulation. Our results question the popular view that the elaborated structures of these fossil species evolved as thermoregulatory organs and provide evidence in support of the hypothesis that *Pteranodon* crests and eupelycosaur sails are among the earliest and most extreme examples of elaborate sexual signals in the evolution of terrestrial vertebrates.

Keywords: dinosaur, lizard, reptile, ornament, weapon, condition dependence.

Introduction

The adaptive significance of the exaggerated structures carried by many fossil vertebrates remains to be resolved (Kellner and Campos 2002*a*, 2002*b*; Williams 2002). One of the favored hypotheses for the function these traits has been a role in thermoregulation (Romer and Price 1940; Bramwell and Fellgett 1973; Farlow et al. 1976; Wheeler

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1978; Haack 1986; Tracey et al. 1986; Bennett 1996; Florides et al. 1999; Kellner and Campos 2002*b*). Nevertheless, many of these traits would have been a burden to their bearers, and in extant taxa, such morphology is almost invariably sexually selected (Andersson 1994; Clutton-Brock 2007).

Many pterosaur species possessed elaborate cranial crests (Martill and Naish 2006), the function of which remains controversial. The favored hypotheses for the function of these crests are that they evolved as thermoregulatory organs (Kellner 1989; Kellner and Campos 2002*a*, 2002*b*), aerial rudders (Bramwell and Whitfield 1974; Stein 1975; Czerkas and Ji 2002), feeding aids (Wellnhofer and Kellner 1991; Stechler 2008), muscle attachment sites (Bramwell and Whitfield 1974; Kellner and Campos 2002*b*), a means of species recognition (Kellner and Campos 2002*b*), a counterpoise to the bill (Bramwell and Whitfield 1974; Williams 2002), or ornaments under sexual selection (Bramwell and Whitfield 1974; Bennett 1992; Martill and Naish 2006). Only the Cretaceous *Pteranodon longiceps* is known in sufficient quantity to permit a quantitative analysis of crest form (Bennett 1992). Based on differences in crest length, width of the pelvic canal, and bimodality in other bones, it has been suggested that *Pteranodon* was sexually dimorphic in the head crest and hence that crests were sexually selected (Bennett 1992). Even so, the scarcity of intact specimens means that the pelvic variation, crest lengths, and bimodalities cannot be compared across individuals (Bennett 1992). Hence, the suggested size classes could represent different-aged animals, evolutionary changes through time, or taxonomic differences rather than sexual dimorphism.

The function of the large dorsal "sails" of the famous Permian eupelycosaurs *Dimetrodon* and *Edaphosaurus* has also been the subject of speculation. The orthodoxy is that the sails were an adaptation to thermoregulation (Romer and Price 1940; Bramwell and Fellgett 1973; Haack 1986; Tracey et al. 1986; Bennett 1996; Florides et al. 1999). In

Dimetrodon it is argued that the advantage of the sail was twofold: to enable these poikilothermic predators to warm faster than their prey (Romer 1948; Tracey et al. 1986) and to facilitate the dissipation of excess metabolic heat (Tracey et al. 1986). The evolutionary increase in body mass is hypothesized to be matched by an evolutionary increase in sail area that was proportional to mass and hence positively allometric in relation to body length (Romer 1948; Tracey et al. 1986; and see below). In *Edaphosaurus* a role in cooling has been proposed (Bennett 1996). The idea that eupelycosaur sails might have been sexually selected has received only passing consideration (Bakker 1970; Bennett 1996).

There is renewed interest in the allometric scaling of sexually selected traits (Bonduriansky and Day 2003; Kodric-Brown et al. 2006). Modeling suggests that under sexual selection, positive allometry, where larger individuals carry relatively larger traits, evolves only where there is a net fitness benefit to larger individuals from increased trait expression (Bonduriansky and Day 2003). This pattern is expected under condition-dependent sexual selection where, for the same investment in trait expression, the marginal fitness benefit is greater for individuals in superior condition (Kotiaho 2001). This argument equates large size with a male's ability to hold or acquire resources, which seems reasonable (see also Blanckenhorn 2000; Bonduriansky and Day 2003).

Sexual selection can take many forms (signaling, grasping, fighting, copulatory courtship, etc), and it would be naive to expect all "sexually selected" traits to be positively allometric (Bonduriansky 2007). Thus, the presence or absence of positive allometry cannot be used simply to infer the presence or absence of sexual selection. Furthermore, some naturally selected traits are positively allometric. What then can be gained from examining the allometry of a trait in the hope of understanding its function? If the trait in question does not depart greatly from isometry, it could have a sexual or a nonsexual function. If, however, the trait departs from isometry, the stronger the departure is, the stronger the selective force favoring that departure must be (Kodric-Brown et al. 2006). The cases where natural selection favors positive allometry arise for thermoregulatory or biomechanical reasons, and fortunately these make explicit scaling predictions derived from physical laws (Schmidt-Nielsen 1984). Thus, while the absence of positive allometry leaves us no closer to understanding the evolutionary forces behind a trait, its presence leaves us with the possibility of testing the allometry against the predictions derived from the physical laws behind the hypothesized function. If the trait has an allometry significantly in excess of the exponent expected from physics, then an alternative explanation is needed. In these cases, sexual selection must be a strong candidate

for the driver of trait elaboration, particularly where the allometry is extreme, since sexual selection can drive "extreme elevation of allometric slopes" (Bonduriansky 2007, p. 844).

Positive interspecific allometry occurs in the sexually selected traits of a range of extant taxa (table A1 in the online edition of the *American Naturalist*; Kodric-Brown et al. 2006). This pattern, where larger species bear relatively larger traits, contrasts with the general pattern of isometry or negative interspecific allometry for nonsecondary sexual traits (Schmidt-Nielsen 1984). Across species, just as within, scaling of biomechanical and thermoregulatory function predicts allometries against which traits of unknown function can be tested. Here we use scaling predictions to ask whether the naturally selected functions proposed to explain the crest of the *P. longiceps* and the sails of the *Dimetrodon* and *Edaphosaurus* predict the allometries observed in these traits.

Allometric Scaling Expected under Biophysical Hypotheses for Crests and Sails

In order to deal with a range of data from different sources, we converted all trait measurements into their linear equivalents. In doing so, we implicitly assume isometry and geometric similarity. Linear equivalents are denoted by L with a subscript indicating whether they are derived from an area ($A \propto L_A^2$) or from body mass ($M \propto L_M^3$). We further assume that metabolic rate (R) scales allometrically with body mass such that $R \propto M^{0.75} \propto L_M^{2.25}$, noting that this makes no assumptions about absolute metabolic rates.

For organs dedicated to the dissipation of metabolic heat generated, for example, through exercise, the expectation is that their surface area should exhibit isometry with respect to metabolic rate and so scale with mass (M) with an exponent of ∼0.75 (Tracey et al. 1986). Given the assumption that the traits are essentially two-dimensional, Tracey et al. (1986) argue that the trait will need to match the increase in metabolic rate associated with increased body size. Metabolic rate scaling in poikilotherms in general, and reptiles in particular, is similar to that in homeotherms, lying between $M^{0.7}$ and $M^{0.9}$ (Peters 1986; Glazier 2006). We calculated the predicted allometry based on Tracey et al.'s expectation and obtained a relationship of $L_A \propto L_M^{1.125}$. This prediction fits the scaling of ear dimensions in jackrabbits (see appendix in the online edition of the *American Naturalist*).

We calculated the predicted allometry of heat-collecting organs based on the hypothesis (Romer 1948; Tracey et al. 1986) that the area of these organs should scale isometrically with mass (i.e., $A \propto M^{1.0}$). The linear equivalent of this relationship is $L_A \propto L_M^{1.5}$ (table 1). The sail of *Dimetrodon* is the only trait we know of that has been thought

Table 1: Allometric predictions for trait size based on physical models

Mechanism	Expectation	Equivalence	Linear equivalent	Colloquial description
Heat dissipation	$A \propto R$	$A \propto M^{.75}$	$L_A \propto L_M^{1.125}$	$L_{trait} \propto L_{body}^{1.125}$
Heat collection	$A \propto M$		$L_i \propto L_M^{1.5}$	$L_{trait} \propto L_{body}^{1.5}$
Rudder torque (1)	$A \propto L^4/L \times U^2$	$A \propto L^2$	$L_A \propto L_M$	$L_{trait} \propto L_{body}^{1.0}$
Rudder torque (2)	$A \propto M \times L^2/L \times U^2$	$A \propto L^3$	$L_A \propto L_M^{1.5}$	$L_{trait} \propto L_{body}^{1.5}$

Note: Equivalence denotes further assumptions applied to convert between variables such as mass and metabolic rate (see text for details of assumptions). Colloquial description indicates which terms refer to traits and which to body size/mass.

to function in this manner, putting this hypothesis at odds with current thought on thermoregulation in extant taxa. There are no empirical tests or more sophisticated models relating to this hypothesis (e.g., taking thermal inertia into account) that we are aware of. For both *Pteranodon* and *Dimetrodon*, most of the variation in organ area between specimens is encapsulated in the length measures.

Most remaining hypothesized functions of the *Pteranodon* crest, such as feeding aids, counterbalances, or muscle attachment sites, should exhibit isometry. However, one putative function might be expected to predict a positive allometry: the use of the crest as a rudder. Two arguments arising from aerodynamic considerations can be made for the predicted allometry of a rudder. The first prediction is that the aerodynamic torque (τ_{aero}, the tendency for a force to rotate an object) exerted by an aerial rudder will increase as the product of the length of the animal, the area of the rudder (A_{rudder}), and the square of its speed (U^2). As larger animals must fly faster in order to remain airborne, their "glide speed" increases with the square root of body length ($L^{0.5}$; Vogel 2003), resulting in τ_{aero} increasing with L^4 (see table 1). Aerodynamic torque must in turn be equivalent to the muscular torque applied to the head (τ_{musc}, assuming isometric scaling of muscle mass). Expansion of the relationship $\tau_{musc} = \tau_{aero}$ gives $L_{body} \times (L_{body}^{0.5})^2 \times A_{rudder} \propto L^4$, which can then be rearranged to show that $A_{rudder} \propto L_{body}^2$, leading us to expect isometry between the linear equivalent of rudder area and the linear equivalent of mass ($L_A \propto L_M^{1.0}$; table 1). The second prediction is that positive allometry will arise, because τ_{musc} needs to overcome the mass moment of inertia (I, a measure of an object's resistance to changes in its rotation rate). If this is the case, then (assuming isometry) τ_{musc} must scale equivalently to I ($\tau_{musc} \propto I$), which itself scales as mass times (rudder) area. Rearranging this relationship gives $A_{rudder} \propto M \times L_{body}^2/L_{body} \times U^2$. Expansion and conversion to linear equivalents then leads us to $L_A \propto L_M^{1.5}$ (table 1).

Material and Methods

Pteranodon

We analyzed published data on crest length and orbit (eye socket) diameter for nine *Pteranodon longiceps* skulls col-

lected exclusively from the Smoky Hill Member of the Niobrara Chalk in Kansas (Bennett 1992). For the skulls that are complete enough to be used for crest data, there are no other skeletal remains from which other measures of body size could be taken (Bennett 1992); hence, our analysis was restricted to using the orbit as a measure of body size. We do not know how orbit diameter scales with overall size in *Pteranodon*; if it exhibits negative allometry, our estimate of crest allometry might be inflated. However, orbit diameter scales isometrically with basal length of the skull in *Protoceratops* (allometric exponent $= 1.07$, $n = 24$; Dodson 1976) and with the length of the skull in the Triassic rhyncosaur *Scaphonyx fischeri* (allometric exponent $= 1.04$, $n = 13$; Benton and Kirkpatrick 1989), and with snout-vent length in the (extant) gecko *Hemidactylus turkikus* (allometric exponent $= 0.96$; confidence interval [CI] $= 0.86$, 1.08; $n = 284$; data extracted from Werner and Seifan 2006 using GraphClick [Arizona Software, http://www.arizona-software.ch]). Hence, the available empirical data suggest that orbit diameter scales isometrically with body size in reptiles. Nevertheless, we also took data (using ImageJ; Rasband 2009) from a scale drawing in Bennett (fig. 5 in 1995) of the ontogenetic scaling for the pterosaur *Rhamphorhynchus muensteri*. Reduced major axis (RMA) regression of logged data (orbit width on skull length) gives an allometric exponent of 0.752 (95% CI of 0.646 and 0.875). Hence, we use an allometry of 0.75 to test whether the potential of negative allometry in the orbit might confound our results.

Dimetrodon *and* Edaphosaurus

In the analysis of *Dimetrodon*, we combined data on neural spine (sail) height and mass presented in Romer and Price (1940) with those of two species recently described by Berman et al. (Berman 1977; Berman et al. 2001, 2004). The averages of the male and female specimens of *Dimetrodon limbatus* were used for calculating the evolutionary allometry. The method for estimating body weight in *Dimetrodon* is detailed in the appendix.

For the comparative analysis of *Dimetrodon*, we generated a hypothetical phylogeny based on geological evidence of an evolutionary progression in body size from
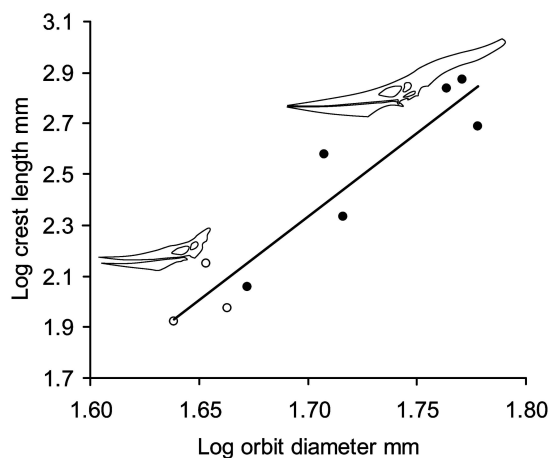
Figure 1: Positive allometry in the head crest of *Pteranodon longiceps*. Filled circles are putative males, and open circles are putative females. Long-crested and short-crested forms are illustrated.

small to large (Romer and Price 1940; Romer 1948; Tracey et al. 1986; Berman et al. 2001, 2004). We used this phylogeny and the program CAIC 2.0 (Purvis 1991) to generate six phylogenetically independent contrasts in the log-transformed linear equivalent of body mass and log-transformed spine height. To make certain that our results were not dependent on this phylogeny, we also created 1,000 randomly generated phylogenies (without constraint) using COMPARE 4.6 (Martins 1996). Each phylogeny was used to generate phylogenetically independent contrasts in log-transformed size and spine height data. We extracted the independent contrasts from COMPARE 4.6 and calculated the mean RMA regression slope and the prediction interval (PI) about this mean. The PI tells us between what range of values we can expect the allometry derived from the true phylogeny to fall with probability of 95% (Walpole and Meyers 1993). Allometric exponents were calculated by RMA regression, using SMATR (Falster et al. 2006).

Results

The Head Crest of Pteranodon longiceps

Across the nine individuals of *Pteranodon longiceps* there was a significant, positively allometric relationship between orbit diameter and crest height (RMA slope = 6.94, 95% CI = 5.18, 9.31: slope > 1; $L^{6.94}$ vs. $L^{1.0}$, $F_{(1,7)} = 732.9$, $P < .001$; fig. 1), indicating that larger individuals had disproportionately large crests. Furthermore, the allometric exponent among putative males alone is 7.40 (95% CI = 4.1, 13.2), so positive allometry is not driven by the differential between the size classes. For thermoregulation,

the area of the organ is important; the area of the crest is mainly a function of its length, and crest allometry is well in excess of the exponents expected (table 1) for thermoregulatory functions ($L^{6.94}$ vs. $L^{1.125}$, $F_{(1,7)} = 572$, $P < .001$; $L^{6.94}$ vs. $L^{1.5}$, $F_{(1,7)} = 308$, $P < .001$). The allometry of crest length in *Pteranodon* is also significantly in excess of either prediction based on it functioning as a rudder ($L^{6.94}$ vs. $L^{1.5}$ and $L^{6.94}$ vs. $L^{1.0}$; table 1; statistical significance as above). Moreover, the allometry of crest height remains significantly (demonstrated by the nonoverlapping CIs) greater than those predicted under any of the naturally selected hypotheses even when we assume negative allometry in orbit diameter of $L^{0.75}$ (6.94 × 0.75 = 5.20, CI = 3.88–6.98) or when we use the interspecific allometry for reptile eyes of $L^{0.77}$ (6.9 × 0.77 = 5.31, CI = 4.0, 7.2; Hall 2008).

The Dorsal Sails of Dimetrodon *and* Edaphosaurus

Across seven species in the genus *Dimetrodon*, neural spine height exhibits an RMA exponent of 1.73, (CI = 1.46, 2.04; fig. 2) with respect to the linear equivalent of body mass (L_M). This positive evolutionary allometry ($L^{1.73}$ vs. $L^{1.0}$, $F_{(1,5)} = 76.3$, $P < .001$) is robust to phylogenetic control since the allometry of spine height after controlling for phylogeny using CAIC was significantly greater than 1 (RMA = 1.69, 95% CI = 1.48, 1.94, $F_{(1,4)} = 236$, $P <$
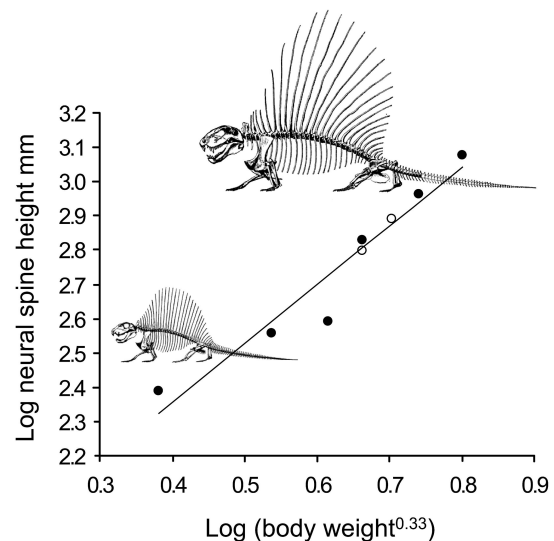

Figure 2: Positive allometry in the dorsal sails of *Dimetrodon*. Filled circles are of unknown sex, and open circles are *Dimetrodon limbatus*, male (*above the line*) and female (*below the line*). Illustrations *Dimetrodon grandis* (*top*, approximate length 3.2 m) and *Dimetrodon milleri* (*bottom*, approximate length 1.9 m) drawn to scale with one another (from Romer and Price 1940).

.001). Furthermore, the mean RMA regression slope calculated from the 1,000 phylogenies we generated (mean = 1.71, 95% CI = 1.45, 1.94) was also significantly greater than 1 (based on nonoverlapping CIs). The prediction interval calculated from the mean RMA indicates that the slope derived from the true phylogeny would fall between 1.42 and 2.00 with a 95% probability. Hence, the positive evolutionary allometry is robust to the phylogeny used and is not driven by the hypothesis that species increased in size over time.

We found that sail height scales with an exponent significantly greater than expected for an organ dedicated to the dissipation of heat ($L^{1.69}$ vs. $L^{1.125}$, $F_{(1,4)} = 45.3$, $P < .001$; table 1). However, the interspecific allometry of sail height was not significantly different from that expected for a heat-collecting organ ($L^{1.69}$ vs. $L^{1.5}$, $F_{(1,4)} = 6.325$, $P = .07$).

Discussion

Although it is not possible to make a simple prediction for the allometry of a sexually selected trait, it is nevertheless clear that sexual signals can show extreme positive allometry, while the allometries of naturally selected traits are delimited strictly by function. We can therefore narrow down the range of possible functions for the extraordinary traits of *Pteranodon*, *Dimetrodon*, and *Edaphosaurus*.

The Head Crest of Pteranodon longiceps

The crest allometry of *Pteranodon* exceeds those expected for thermoregulation, forward ruddering, and all alternative natural-selection hypotheses. A survey of intraspecific positive allometries in the sexually selected traits of extant animals reveals that the allometry we report for *Pteranodon* exceeds that of all but one of the traits gathered by us or others (table A2; Kodric-Brown et al. 2006; Bonduriansky 2007). Hence, the head crest can be argued to represent an extreme example of positive allometry, and neither we nor Bonduriansky (2006) are aware of a naturally selected trait with an allometry to rival this. This is a pattern consistent with a trait that has a history of sexual selection.

Venous canals in the crest bones of pterosaurs have been cited as evidence for a thermoregulatory function (Kellner 1989; Kellner and Campos 2002a, 2002b). However, these canals also occur beneath bird bills and casques, and the horns of ungulates and these structures appear to have a largely coincidental role in thermoregulation (Ward et al. 1999; Bro-Jørgensen 2007). Nevertheless, in the toucan *Rhamphastos toco*, the positively allometric bill has facilitated its use as a "thermal window," increasing blood flow for cooling or reducing it to conserve heat (Tattersall et al. 2009). Clearly there is potential for *Pteranodon* to have used its crest for both thermoregulation and sexual signaling; nevertheless, the extraordinary allometry of the crest rules out thermoregulation as its dedicated function.

Apart from allometric arguments, there are other reasons to reject the forward rudder hypothesis for the crest of *Pteranodon*. Rudderless flight is the norm in extant fliers, and the loss of the tail in later forms suggests its adoption in pterosaurs (Pennycuick 1972); the subsequent evolution of a head-based rudder appears to be an unlikely scenario. Furthermore, many *Pteranodon* species completely lack a crest (Martill and Naish 2006). This suggests that crests did not evolve extreme allometry from traits that already existed for a naturally selected function.

Until now the interpretation of a sexually selected function for the crest of *Pteranodon longiceps* has been based on the hypothesis that there were two classes of individuals in the sample, small-bodied females and larger-bodied males. Under sexual dimorphism, we would expect sex differences in the intercept or the slope of the scaling relationship of the crest. The paucity of data for putative females makes such tests ineffectual. If we relax the assumption of sexual dimorphism and assume either that all the individuals are male or that there is a random mixture of males and females—perhaps subject to mutual or even role-reversed sexual selection (where the females might be larger)—then the allometry across the entire sample remains consistent with the idea of crests as a secondary sexual trait. Alternatively, if the hypothesis that *Pteranodon* was sexually dimorphic is correct, the allometry of the large size-class alone is as expected if these specimens were males expressing larger crests through elevated condition dependence. If the large and small individuals represented different species instead of sexes, allometry in the large class remains indicative of condition-dependent sexual selection. Bennett (1992) reports that the material was of adult specimens, suggesting the allometry is not an ontogenetic one. Even so, indeterminate growth in reptiles can lead to steeper positive allometries in secondary sexual traits than in species with determinate growth, and this might be one such example (Bonduriansky 2006). Finally there is the possibility that each individual represented a different species. However, the steep positive allometry of the crest argues against the sample being either an evolutionary or interspecific pattern, which tend to be lower (tables A1, A2; Kodric-Brown et al. 2006). Our analysis of *Pteranodon longiceps* suggests that no matter whether variation between specimens originates due simply to size, sex, species, or time, head crests had a history of intense condition-dependent sexual selection as a signal.

The Dorsal Sails of Dimetrodon *and* Edaphosaurus

We found no evidence that the sails of *Dimetrodon* and their positive evolutionary allometry were an adaptation for dumping metabolic heat. As in *Pteranodon*, the sail might have had a role in thermoregulation if it was used as a thermal window, but the allometry is too steep for heat dissipation to be the primary adaptation favoring sail evolution.

In terms of the unique hypothesis that sails enabled *Dimetrodon* species to warm up faster than their prey, the interspecific allometry of sail height was not significantly different from that expected for a heat-collecting organ. However, there appears to be an overlooked allometric reason why thermoregulation cannot have driven the evolution of eupelycosaur sails. This is simply that sails evolved in very small species, reaching 0.24 m high in *D. teutonis*, a species ca. 1.5 m in total length and 14 kg in weight (Berman et al. 2001), and according to recent models (O'Connor and Dodson 1999), reptiles of this size could not have derived significant benefit from sails for either heating or cooling. This is a fundamental flaw in the thermoregulation argument and can be seen in biophysical models that show a declining efficacy of sails as body size decreases from *D. gigashomogenese* (166 kg) and *D. grandis* (254 kg) to *D. milleri* (47 kg; Haack 1986; Tracey et al. 1986) and the limited effect of sails on the warming rates of *D. limbatus* (110 kg; Florides et al. 1999). Furthermore, were sails to have been well supplied with blood, *D. milleri* and *D. limbatus* would have been at an almost daily risk of hyperthermia due to their low thermal inertia (Haack 1986; Florides et al. 1999), and the encumbrance of the sail in seeking shade or entering crevices or burrows would have exacerbated the problem. In our view it is the small size of the sail-bearing ancestral species that excludes thermoregulation as the driver of sail evolution.

Edaphosaurus (fig. A1 in the online edition of the *American Naturalist*) had sails similar to those of *Dimetrodon*, and although these were relatively shorter, they were elaborated with tubercles and crossbars (Romer and Price 1940; Bennett 1996). The advantage of warming more rapidly than other species seems not to apply to *Edaphosaurus* since they are thought to have been herbivorous (Haack 1986). Furthermore, like *Dimetrodon*, early *Edaphosaurus* bearing elongated neural spines were too small to require morphological adaptations to thermoregulation (O'Connor and Dodson 1999). The inconsistency between small size and the thermoregulatory function of the sail applies equally to other sailed eupelycosaurs that were even smaller than the known *Edaphosaurus* specimens, such as *Xyrospondylus ecordi*, ∼10 kg (Peabody 1957; Reisz et al. 1982) and the even smaller (head and body ∼0.5 m) ancestral edaphosaurid *Ianthasaurus hardestii*

(Reisz and Berman 1985), both of which carried sails ∼0.1 m high.

If we reject a dedicated thermoregulatory function for sails, what alternative hypotheses might explain these structures? Defense against predators is one possibility. However, larger and less vulnerable species invested relatively more in the potentially defensive trait than smaller, more vulnerable ones. Furthermore, *Dimetrodon*, at least, were the dominant carnivores of their day (Romer and Price 1940).

In the absence of other hypotheses, there remains sexual selection. The allometric exponent for sail height is similar in magnitude to the scaling of interspecific antler length to shoulder height in cervids (table A1). Furthermore, as Bakker (1970) observed in the context of *Dimetrodon*, many lizard species raise a dorsal ridge of skin during threat and courtship displays, and positively allometric, sexually dimorphic frills and dewlaps are present in extant lizards (Echelle et al. 1978; Christian et al. 1995). There is also evidence of sexual dimorphism both in the robustness of the skeleton and in the relative height of the spines of *D. limbatus* (Romer and Price 1940). Although there are too few *Edaphosaurus* to calculate an evolutionary allometry with confidence, there is a progression of increasing complexity of the spines in the evolutionary trend toward larger body size (Romer and Price 1940; Peabody 1957; Reisz and Berman 1985). This pattern is similar to the increasing number of antler tines with size and polygyny in deer (Caro et al. 2003) and also supports a sexually selected function for the sail.

There are few secondary sexual traits, particularly among terrestrial vertebrates, that can compare with the sails of *Dimetrodon* and *Edaphosaurus* in terms of somatic investment relative to size. The fitness advantage of producing and bearing such costly traits in the small species where they first evolved could, it seems to us, have been realized only through sexual selection. Indeed the sail's cost would have made it an ideal signal of condition (Kotiaho 2001; Tomkins et al. 2004). Hence we suggest that it is more parsimonious to view the sails of *Dimetrodon* and *Edaphosaurus* as among the earliest and most extreme examples of secondary sexual traits in terrestrial vertebrates.

Conclusions

Recent advances in the understanding of patterns of allometry in sexually selected traits (Bonduriansky and Day 2003; Kodric-Brown et al. 2006; Bonduriansky 2007) combined with the predictions from biomechanics and thermoregulation make the cautious use of allometry to understand the function of exaggerated traits in fossil taxa a productive area of research. Our analysis reveals patterns

of allometry contradicting the arguments underlying the widely held notion that crests and sails evolved as organs dedicated to thermoregulation. Instead the patterns of allometry, sexual dimorphism and ornamentation are consistent with condition-dependent sexual signaling driving the evolution of elaborate crests and sails in long-extinct reptiles.

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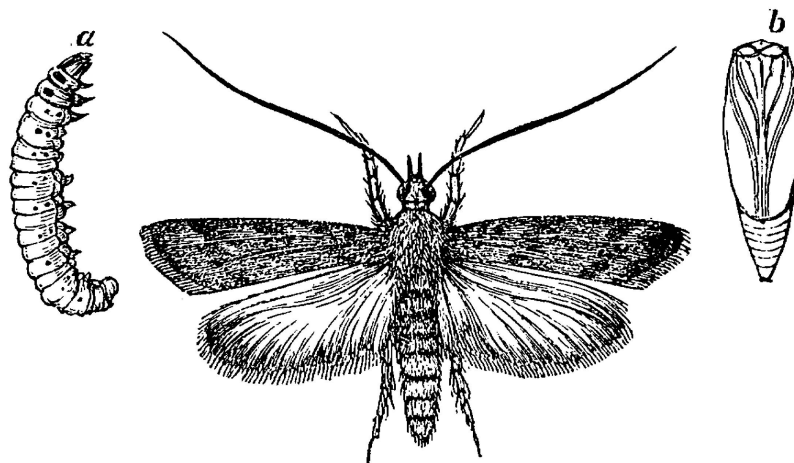
Center, *Nephopteryx edmandsii*; *a*, larva; *b*, chrysalis or pupa. From "The Parasites of the Honey-Bee" by A. S. Packard Jr. (*American Naturalist*, 1868, 2:195–205).