Functional Consequences of Extreme Morphologies in the Craniate Trophic System

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ABSTRACT

Extreme morphologies are often associated with extreme demands on performance in a given ecological setting. Even though such extreme morphologies are relatively rare, the craniate trophic system provides many examples of this evolutionary trend despite its highly integrated nature and intrinsic complexity. In this article, as an introduction to the special issue on functional consequences of extreme adaptations of the trophic apparatus in craniates, we survey case studies highlighting the occurrence of extreme morphologies in the trophic system in craniates and briefly review a number of associated conceptual issues: (1) Are extreme morphologies associated with constrained functional versatility? (2) Do high-performance systems necessarily involve extreme morphological adaptations? and (3) Do extreme morphologies limit functional and ecological capacities? An overview of the case studies presented here shows that the craniate trophic system is a suitable model system to explore the evolution of extreme morphologies but currently provides no clear-cut answers to conceptual issues addressed.

Introduction

This article provides the introduction to a compilation of papers on extreme morphologies and the functional consequences thereof in the feeding system of craniates. However, one may ask, Why study such extreme morphologies, such aberrant creatures and freaks of nature as chameleons, mole-rats, or seahorses? Although part of the answer of this question can be provided by man's basic fascination with the bizarre, from a scientific point of view, the study of extreme morphologies is readily justified by the Krogh principle: "there will be some animal of choice or a few such animals on which it [a physiological question] can be most conveniently studied" (Krogh 1929, p. 247). Even more so than understanding specialization as a process of fundamental importance to functional morphologists and ecologists (Ferry-Graham et al. 2002) is understanding the evolution toward extreme specializations. Indeed, insights into many basic scientific problems can be gained by studying extreme morphologies, as they exemplify the limits to which organismal design can be driven and often best and most clearly illustrate the basic design principles at work (Krebs 1975).

However, despite the fact that extreme morphologies are often rare, they can be selected for in certain cases. Indeed, although more often than not selection favors average phenotypes in most environments because of the variable nature thereof (Ridley 2003), both disruptive selection and directional selection can lead toward extremes in the range of possible phenotypes (not excluding other hypothetical indirect scenarios of selection; Barker and Cummins 1969; Ricker 1981; Gross 1985; Santos 1996; Benkman 2003; Bolnick 2004). Obviously, extreme phenotypes will only be selected for if they are associated (directly or indirectly) with a fitness advantage in their current ecological setting (Ridley 2003). Extreme morphologies are thus, by definition, expected to be associated with exceptional functional capacities in specific ecological settings. It could be argued, however, at what point a morphology can be considered extreme. Because there is clearly no objective threshold that could be assigned to demarcate whether something is extreme or not, no clear-cut definition can be given that covers all potentially extreme morphologies (and hence extreme functionalities). Within the context of this paper, we refer to "extreme" when morphologies and functionalities can be considered extraordinary, thus at the tails of normally distributed phenotypic variation around a mean (with the "mean reference" being an individual or a species, depending on the level of comparison). Consequently, extreme morphologies can be identified and interpreted only in the light of morphologies typically observed within a group, making the study of extreme morphologies a comparative endeavor by definition.

The evolution toward extreme phenotypes appears at first sight paradoxical; the more specialized the organism becomes, the less versatile the system, and the higher the probability of extinction when faced with variable and changing environments (but see below; Ralston and Wainwright 1997; Ferry-Graham et al. 2002; Bellwood et al. 2006). Even defining what is a "specialization" can be a subject of discussion, as it is difficult to formulate an unambiguous definition that covers the term

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(and process behind it) as interpretable under different discipline-bound criteria (Ferry-Graham et al. 2002). A well-known example is that of the egg-eating snakes of the genus *Dasypeltis*. In their specialization toward the ingestion of eggs, these snakes have lost most of their teeth. Consequently, they cannot capture and transport other prey types and are stuck in an ecological and evolutionary dead end in being obligate egg eaters (Gans 1952, 1974; de Queiroz and Rodríguez-Robles 2006; Gartner and Greene 2008). A decrease in the resource base (which is narrow by definition), potentially leading to a decline or even extinction of a population or species, may then be more extensive in the case of extreme specialists. This may explain the rarity of obligate egg-eating snakes and their absence in North America (Gartner and Greene 2008).

The constrained distribution of phenotypes in morphospace may simply be a consequence of many developmental, physical, and functional constraints (Arnold 1992; Schluter 1996; Klingenberg 2005). Because most phenotypic traits are part of complex integrated functional systems, changing the morphology of one part of such an integrated system is likely to have a profound impact on the functional performance of that system as a whole and on all its functions (Herrel et al. 2001; Russell and Bauer 2005). Specialization of the tongue for chemoreceptive purposes in snakes, for example, prevents its use in prey transport and could explain the coevolution of an alternative prey-transport mechanism: the pterygoid walk (Schwenk 1993, 1994; Cundall and Greene 2000). Even though the polarity of cause and effect between structural modifications and functional implications is difficult to unravel, a proper design of comparative and experimental work may provide some insights into the close match between structure and function (Russel and Bauer 2005).

In many organisms, the evolution toward extreme morphologies may also be constrained by modularity (constraining interindependency of module component morphologies) or selection for developmental homeostasis (overruling selection for function on morphology; Badyaev and Foresman 2004; Klingenberg 2005; Young and Badyaev 2006, 2007). Consequently, selective pressures acting on one component of a module may constrain the degree of specialization of the remainder of components in the module (Badyaev and Foresman 2004). Duplication and/or functional decoupling, allowing an organism to overcome constraints imposed by modularity, have been proposed as a major evolutionary pathway toward extreme specialization (Schaefer and Lauder 1986, 1996). If structural or functional duplication occurs, then one of the two functional units is free to specialize without compromising the functional integrity of the system as a whole. In osteoglossomorph fish, for example, the modified hyoid system has become decoupled from its primitive function of buccal expansion during suction feeding, prey manipulation, and lower jaw depression to provide a novel way of immobilizing and macerating prey (Sanford and Lauder 1989, 1990). Similarly, the decoupling of the hyoid from its function during respiration has allowed the evolution of the extremely specialized tongue-projection system observed in plethodontid salamanders (Deban et al. 1997; Wake and Deban 2000).

Even though the constraining effect of extreme morphologies seems very plausible, with empirical evidence supporting it, other studies have also shown that it is not inherent. First, there is the conceptual issue of defining what is an extreme specialization and what is not (following the problems when trying to define what a "specialization" is; Ferry-Graham et al. 2002). Second, it seems evenly plausible that morphological specializations by themselves may actually involve an increase in diet versatility because they allow an addition of prey types to the diet (compared to the generalist condition). This has, for example, been suggested for algae-scraping cichlids and scale-eating piranhas (Liem 1980; Janovetz 2005).

Interestingly, the evolution of the trophic system in craniates, despite being a structurally and functionally complex and integrated system, is often characterized by the appearance of extreme morphologies. The goal of this introduction is to highlight cases of apparent extreme trophic specialization and function in different groups of vertebrates (mainly at the interspecific level) discussed in detail in this special issue. Additionally, we investigate, in the case studies reviewed in this special issue, whether we see any evidence of extreme morphologies constraining functional versatility and whether all high-performance systems are associated with extreme morphologies, and we explore potential ecological consequences of extreme trophic morphologies.

Extreme Morphologies and Functional Versatility

One obvious example of extreme morphologies coupled to extreme functional performance is provided in the study on the cranial movements in seahorses. This study shows that these fishes are performing at extreme speeds (Roos et al. 2009, in this issue) and exhibit highly specialized and unique cranial morphologies, such as narrow and elongated snouts, relative to basal gasterosteiforms. The study on shark biting forces by Huber et al. and the paper on chisel digging using incisors in African mole-rats by Van Daele et al. provide nice examples of systems where demands for extreme forces are apparent in the cranial morphology (Huber et al. 2009, in this issue; Van Daele et al. 2009, in this issue).

Especially morphologies forming the basis for extreme performance in relation to force and velocity may be expected to show a constrained functional versatility. Extreme velocities require that moving structures deviate as little as possible from their normal path, thus minimizing the distance traveled over time. Extreme forces require structural and/or material reinforcements of the components of an articulated system, to resist high muscle forces, food reaction forces, and joint reaction forces and to avoid damage or disarticulation. Natural selection could thus especially favor those phenotypes that show little deviation from these criteria of optimality. However, whether or not the variation in the moving components is lower than that of more generalized performers still needs to be tested. Ferry-Graham et al. (2002) did show that, at least for some kinematic parameters, variation is indeed narrower in specialists.

The study of morphological variation in oral and pharyngeal jaws and their relationship to trophic specialization in moray eels (Mehta and Wainwright 2007, 2008; Mehta 2009, in this issue) suggests that the oral jaws are morphologically more constrained in durophagous moray eels, compared to the wider range of morphologies found in piscivorous anguilliforms. It is suggested that durophagy is derived for anguilliforms and thus could be an example of reduced structural (and functional) variation of extreme trophic types (durophagous eels do show limited extreme specializations, including jaw muscle hypertrophy). On the other hand, gape constraints of the oral system are suggested to be linked to the origin of a highly specialized pharyngeal jaw apparatus, with an extreme case of jaw protraction (Mehta and Wainwright 2008).

Extreme Morphology and Extreme Performance

Interestingly, morphological specializations need not always lead to increases in performance traits associated with the ancestral function of the system. For example, even though jaw protrusion has frequently been linked to an improved suction-feeding performance, some New World cichlids exhibiting extreme protrusion (up to 55% of head length) actually show a reduced suction-feeding performance (Waltzek and Wainwright 2003). The study by Cundall (2009, in this issue) suggests that neuromuscular control may also be the subject of selection, where speed (in this case the speed of fang placement in vipers) is combined with kinematic versatility (i.e., correcting fang placement after a miss). The venom-spitting performance exhibited by cobras also does not seem to rely on structural specializations but rather depends on a precise control of head position coupled to a rather typical fang morphology (Young et al. 2009, in this issue).

However, in some cases extreme performances are strongly dependent on extreme morphologies. In this volume, several cases are given that suggest such a relation. Suction-feeding performance in syngnathid fishes (seahorses and pipefishes) is extremely fast and powerful and has been linked to the presence of a narrow and elongated snout (Bergert and Wainwright 1997). The associated four-bar mechanism, which has been suggested to be a lock-and-trigger system, allows for the storage of strain energy that is released and acts as a power amplifier during suction feeding (Muller 1987; Van Wassenbergh et al. 2008; Roos et al. 2009, in this issue). Structural modifications of both the snout and the hyoid apparatus make this group of teleosts quite unique. Moreover, the velocities of neurocranial elevation and hyoid depression are at the extreme range of what has been recorded for teleosts in general. Interestingly, in some cases extreme performance may be dependent on specialization at the physiological or ultrastructural level. For example, storing and then releasing strain energy, possible because of the elastic properties of tendons, is known to act as a power amplifier and may enhance performance considerably (see, e.g., Alexander and Bennet-Clark 1977; Van Wassenbergh et al. 2008). Similarly, specializations of the Z-disks in chameleons and helically arranged muscle fibers in the tongue protractors of chameleons and plethodontid salamanders allow for extreme muscle shortening and power amplification, respectively (for an overview, see Herrel et al. 2009, in this issue).

Although relations between structural and functional modifications clearly exist in some groups, this is no universal pattern. Indeed, small changes in morphology may have major functional implications in some cases, whereas in other cases substantial structural changes seem to have no apparent effect on functional performance (Russell and Bauer 2005). Because nonadaptive structural changes may arise as morphological side effects of true adaptive modifications (e.g., “spandrels” or other forms of neutral evolution), the lack of effects on performance may be more frequent than sometimes assumed. For example, bipedal running in lizards was initially assumed to be beneficial for improving running speed and energy consumption during locomotion (Snyder 1949). Later, it was experimentally proven that this was not the case (Irschick and Jayne 1999; see also Clemente et al. 2008). Moreover, Aerts et al. (2003) showed that bipedal running may even be a mechanical consequence of being adapted to intermittent running with high accelerations.

Ecological Consequences of Extreme Morphologies

If extreme morphologies are indeed associated with unique performance capacities that may limit the overall functional versatility of an organism, a decreased response capacity to changing environmental conditions may be the result. Sticklebacks, being at the base of the gasterosteiform clade (Nelson 2006), and having a generalized teleostean trophic morphology, can be considered good representatives of the ancestral syngnathid morphology. As such, one would expect phenotypic variation and functional versatility to be greater than in syngnathids, thus allowing them to occupy a wider range of ecological niches. Interestingly, large phenotypic variation has been noted in three-spine stickleback (*Gasterosteus aculeatus*) and has been considered to be the result of selection for divergent habitat use and diet (Caldecutt and Adams 1998). This suggests that the less specialized sticklebacks are indeed functionally and ecologically less constrained than syngnathids. Indeed, the reduced functional versatility as a consequence of the extreme morphological specialization in many syngnathids could explain (at least partially, next to fisheries pressure for the pet trade, etc.) the current vulnerable status of many syngnathids, especially the most specialized seahorses (Lourie et al. 2005).

However, even though extreme specializations of a certain functional component within a bauplan may imply a narrowing down of the ecological capacities of an organism, this should not necessarily result in reduced fitness. Specializations of other components of the same bauplan may well compensate for this, so that the performance of the total design, and thus the fitness of the organism, may be maintained. For example, the cryptic coloration and behavior in chameleons may well compensate for being more exposed to predation during extended phases of prey transport (Herrel et al. 2009, in this issue). Similarly, in cave-dwelling populations of a characiform fish (*Astyanax mexicanus*), the loss of the eye is on a sensory level compensated for by a more developed lateral line system (compared to that of surface-dwelling populations; Montgomery et al. 2001).

Extreme morphological specializations may, on the other hand, also provide unique ecological opportunities. The South American suckermouth catfishes of the Loricariidae are known to be extremely diverse (716+ species; Ferraris 2007) and to have colonized new and variable ecological niches (Montoya-Burgos 2003). Their extreme historical divergence has been linked to paleohydrological events in South America, but the success of their adaptation to the different habitats may in part be due to some unique specializations, including the large dermal plates and highly mobile jaws supporting a sucker mouth (Schaefer and Lauder 1986; Adriaens et al. 2009, in this issue). The increased mobility of the jaws, which has resulted in their unique ability to simultaneously suck and scrape, has been suggested to be the result of decoupling events (Schaefer and Lauder 1996). Whether these decoupling events have resulted in increased functional versatility remains to be tested, but first indications at least show that within loricarioid catfishes, the clade having experienced the most extensive level of decoupling events (i.e., loricariid suckermouth catfishes) does show a high level of jaw mobility (Adriaens et al. 2009, in this issue) and consequently may explain the ecological success of the group.

Conclusions

Despite the integrated nature of the craniate trophic system, it does seem to be susceptible to extreme specializations, making it a model system for the study of the evolution of extreme morphologies and functions. Comparative studies quantifying phenotypic variation (at both the intra- and interspecific levels) and estimates of performance may provide a better understanding of the extraordinary results of evolutionary processes that have fascinated mankind for many centuries.

Special attention should be paid to elucidating developmental and evolutionary causative relations between components constituting extreme morphological designs, as well as between structural and functional modifications. Combining this with a robust phylogenetic framework, with a crisp understanding of behavioral and ecological preferences and versatilities of individuals, populations, and species, will provide the big picture on the evolution of extreme designs. Isn't this what we all strive for?

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Literature Cited

Adriaens D., T. Geerinckx, J. Vlassenbroeck, L. Van Hoorebeke, and A. Herrel. 2009. Extensive jaw mobility in suckermouth armored catfishes (Loricariidae): a morphological and kinematic analysis of substrate scraping mode of feeding. Physiol Biochem Zool 82:51–62.

Aerts P., R. Van Damme, K. D'Août, and B. Van Hooydonck. 2003. Bipedalism in lizards: whole-body modelling reveals a possible spandrel. Philos Trans R Soc B 358:1525–1533.

Alexander R.M. and H.C. Bennet-Clark. 1977. Storage of elastic strain energy in muscle and other tissues. Nature 265:114–117.

Arnold S.J. 1992. Constraints on phenotypic evolution. Am Nat 140:85–107.

Badyaev A.V. and K.R. Foresman. 2004. Evolution of morphological integration. I. Functional units channel stress-induced variation. Am Nat 163:868–879.

Barker J.S.F. and L.J. Cummins. 1969. Disruptive selection for sternopleural bristle number in *Drosophila melanogaster*. Genetics 61:697–712.

Bellwood D.R., P.C. Wainwright, C.J. Fulton, and A.S. Hoey. 2006. Functional versatility supports coral reef biodiversity. Proc R Soc B 273:101–107.

Benkman C.W. 2003. Divergent selection drives the adaptive radiation of crossbills. Evolution 57:1176–1181.

Bergert B.A. and P.C. Wainwright. 1997. Morphology and kinematics of prey capture in the syngnathid fishes *Hippocampus erectus* and *Syngnathus floridae*. Mar Biol 127:563–570.

Bolnick D.I. 2004. Can intraspecific competition drive disruptive selection? an experimental test in natural populations of sticklebacks. Evolution 58:608–618.

Caldecutt W.J. and D.C. Adams. 1998. Morphometrics of trophic osteology in the threespine stickleback, *Gasterosteus aculeatus*. Copeia 1998:827–838.

Clemente C.J., P.C. Withers, G. Thompson, and D. Lloyd. 2008. Why go bipedal? locomotion and morphology in Australian agamid lizards. J Exp Biol 211:2058–2065.

Cundall D. 2009. Viper fangs: functional limitations of extreme teeth. Physiol Biochem Zool 82:63–79.

Cundall D. and H.W. Greene. 2000. Feeding in snakes. Pp. 293–333 in K. Schwenk, ed. Feeding: Form, Function and Evolution in Tetrapod Vertebrates. Academic Press, San Diego, CA.

Deban S.M., D.B. Wake, and G. Roth. 1997. Salamander with a ballistic tongue. Nature 389:27–28.

de Queiroz A. and J.A. Rodríguez-Robles. 2006. Historical contingency and animal diets: the origins of egg eating in snakes. Am Nat 167:684–694.

Ferraris C.J., Jr. 2007. Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes), and catalogue of siluriform primary types. Zootaxa 1418:1–628.

Ferry-Graham L.A., D.I. Bolnick, and P.C. Wainwright. 2002.

Using functional morphology to examine the ecology and evolution of specializaion. Integr Comp Biol 42:265–277.

Gans C. 1952. The functional morphology of the egg-eating adaptations in the snake genus *Dasypeltis*. Zoologica 37:209–244.

———. 1974. Biomechanics: An Approach to Vertebrate Biology. Lippincott, Philadelphia.

Gartner G.E.A. and H.W. Greene. 2008. Adaptation in the African egg-eating snake: a comparative approach to a classical study in evolutionary functional morphology. Zoology 4: 368–374.

Gross M.R. 1985. Disruptive selection for alternative life histories in salmon. Nature 313:47–48.

Herrel A., S.M. Deban, V. Schaerlaeken, J.-P. Timmermans, and D. Adriaens. 2009. Are morphological specializations of the hyolingual system in chameleons and salamanders tuned to demands on performance? Physiol Biochem Zool 82:29–39.

Herrel A., J.J. Meyers, K.C. Nishikawa, and F. De Vree. 2001. The evolution of feeding motor patterns in lizards: modulatory complexity and constraints. Am Zool 41:1311–1320.

Huber D.R., J.M. Claes, J. Mallefet, and A. Herrel. 2009. Is extreme bite performance associated with extreme morphologies in sharks? Physiol Biochem Zool 82:20–28.

Irschick D.J. and B.C. Jayne. 1999. Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. J Exp Biol 202: 1047–1065.

Janovetz J. 2005. Functional morphology of feeding in the scale-eating specialist *Catoprion mento*. J Exp Biol 208:4757–4768.

Klingenberg C.P. 2005. Developmental constraints, modules and evolvability. Pp. 219–247 in B. Hallmgrímson and B.K. Hall, eds. Variation: A Central Concept in Biology. Elsevier Academic, Amsterdam.

Krebs A.H. 1975. The August Krogh principle: “for many problems there is an animal on which it can be most conveniently studied.” J Exp Zool 194:221–226.

Krogh A. 1929. Progress in physiology. Am J Physiol 90:243–251.

Liem K.F. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. Am Zool 20:295–314.

Lourie S.A., D.M. Green, and A.C. Vincent. 2005. Dispersal, habitat differences, and comparative phylogeography of Southeast Asian seahorses (Syngnathidae: *Hippocampus*). Mol Ecol 14:1073–1094.

Mehta R.S. 2009. Ecomorphology of the moray bite: relationship between dietary extremes and morphological diversity. Physiol Biochem Zool 82:90–103.

Mehta R.S. and P.C. Wainwright. 2007. Raptorial jaws in the throat help moray eels swallow large prey. Nature 449:79–82.

———. 2008. Functional morphology of the pharyngeal jaw apparatus in moray eels. J Morphol 269:604–619.

Montgomery J.C., S. Coombs, and C.F. Baker. 2001. The mechanosensory lateral line system of the hypogean form of *Astyanax fasciatus*. Environ Biol Fishes 62:87–96.

Montoya-Burgos J.I. 2003. Historical biogeography of the catfish genus *Hypostomus* (Siluriformes: Loricariidae), with implications on the diversification of Neotropical ichthyofauna. Mol Ecol 12:1855–1867.

Muller M. 1987. Optimization principles applied to the mechanism of neurocranium elevation and mouth bottom depression in bony fishes (Halecostomi). J Theor Biol 126:343–368.

Nelson J.S. 2006. Fishes of the World. 4th ed. Wiley, Hoboken, NJ.

Ralston K.R. and P.C. Wainwright. 1997. Functional consequences of trophic specialisation in pufferfishes. Funct Ecol 11:43–52.

Ricker W.E. 1981. Changes in the average size and average age of Pacific salmon. Can J Fish Aquat Sci 38:1636–1656.

Ridley M. 2003. Evolution. Oxford University Press, Oxford. 472 pp.

Roos G., H. Leysen, S. Van Wassenbergh, A. Herrel, P. Jacobs, M. Dierick, P. Aerts, and D. Adriaens. 2009. Linking morphology and motion: a test of a four-bar mechanism in seahorses. Physiol Biochem Zool 82:7–19.

Russell A.P. and A.M. Bauer. 2005. Variation in structure and its relationship to function: correlation, explanation and extrapolation. Pp. 399–434 in B. Hallmgrímson and B.K. Hall, eds. Variation: A Central Concept in Biology. Elsevier Academic, Amsterdam.

Sanford C.P.J. and G.V. Lauder. 1989. The functional morphology of the “tongue-bite” in the osteoglossomorph fish *Notopterus*. J Morphol 202:379–408.

———. 1990. Kinematics of the tongue-bite apparatus in osteoglossomorph fishes. J Exp Biol 154:137–162.

Santos M. 1996. Apparent directional selection of body size in *Drosophila buzzatii*: larval crowding and male mating success. Evolution 50:2530–2535.

Schaefer S.A. and G.V. Lauder. 1986. Historical transformation of functional design: evolutionary morphology of feeding mechanisms in loricarioid catfishes. Syst Zool 35: 489–508.

———. 1996. Testing historical hypotheses of morphological change: biomechanical decoupling in loricarioid catfishes. Evolution 50:1661–1675.

Schluter D. 1996. Adaptive radiation along genetic lines of least resistance. Evolution 50:1766–1774.

Schwenk K. 1993. The evolution of chemoreception in squamate reptiles: a phylogenetic approach. Brain Behav Evol 41: 124–137.

———. 1994. Why snakes have forked tongues. Science 263: 1573–1577.

Snyder R.C. 1949. Bipedal locomotion of the lizard *Basiliscus basiliscus*. Copeia 1949:129–137.

Van Daele P.A.A.G., A. Herrel, and D. Adriaens. 2009. Biting performance in teeth-digging African mole-rats (*Fukomys*, Bathyergidae, Rodentia). Physiol Biochem Zool 82:40–50.

Van Wassenbergh S., J.A. Strother, B.E. Flammang, L.A. Ferry-Graham, and P. Aerts. 2008. Extremely fast prey capture is powered by elastic recoil. J R Soc Interface 5:285–296.

Wake D.B. and S.M. Deban. 2000. Terrestrial feeding in salamanders. Pp. 95–116 in K. Schwenk, ed. Feeding: Form, Function and Evolution in Tetrapod Vertebrates. Academic Press, San Diego, CA.

Waltzek T.B. and P.C. Wainwright. 2003. Functional morphology of extreme jaw protrusion in Neotropical cichlids. J Morphol 257:96–106.

Young B.A., M. Boetig, and G. Westhoff. 2009. Functional bases of the spatial dispersal of venom during cobra "spitting." Physiol Biochem Zool 82:80–89.

Young R.L. and A.V. Badyaev. 2006. Evolutionary persistence of phenotypic integration: influence of developmental and functional relationships on evolution of complex trait. Evolution 60:1291–1299.

———. 2007. Evolution of ontogeny: linking epigenetic remodeling and genetic adaptation in skeletal structures. Integr Comp Biol 47:234–244.