

The evolution of cranial design and performance in squamates: Consequences of skull-bone reduction on feeding behavior

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Synopsis The evolution of cranial design in lepidosaurians is characterized by a general trend toward the loss of cranial elements. The evolution of relatively lighter skulls in squamates appears tightly coupled to a reduction in relative mass of the jaw adductor, implying functional consequences for bite force and feeding behavior. Interestingly, among squamates the postorbital bar was reduced or lost at least twice independently and taxa characterized by the loss of these cranial elements (e.g., geckos and varanids) are generally reported as having a mobile skull. In Gekkotans, the loss of the postorbital bar was accompanied by a reduction of the supratemporal bar, resulting in a pronounced cranial kinesis. Our data show that having a kinetic skull has functional consequences and results in a reduction in bite force. The lower bite force may in turn be responsible for the decreased feeding efficiency as reflected in the longer duration of intra-oral transport cycles. Gekkotans, however, appear to exploit their intracranial mobility in ways that increases the velocity of jaw movement during opening and closing, which may allow them to capture more elusive prey. The morphological changes observed in the evolution of the cranial system in squamates appear tightly linked to functional and constructional demands on the skull, making squamate skull evolution a model system to investigate the consequences of morphological changes in a complex integrated system of performance, behavior, and ecology.

Introduction

The vertebrate cranial system is a striking example of a complex, integrated system. The cranial system is composed of a multitude of highly integrated structural units (e.g., hyolingual system, jaws, brain, and sensory organs), each associated with, and shaped by, the different functional and structural demands exerted on the system as a whole. Although various components of the cranial system are of crucial importance in many ecologically and behaviorally relevant contexts, the use of the jaws and tongue for feeding (reviewed by Schwenk 2000), drinking (reviewed by Bels et al. 1994), and fighting behaviors (Lailvaux et al. 2004; Huyghe et al. 2005; Lappin and Husak 2005; Lappin et al. 2006) appears to be of prime importance for fitness. However, another important function of the cranial system is to house and protect the brain and major sensory systems. Thus, competing demands for space (e.g., Barel 1983) and function (Herrel et al. 2001b) will likely shape the evolution of the

system as a whole. Since not all functions can be optimized simultaneously (e.g., large eyes in nocturnal predators take up space which may reduce the space available for jaw muscle), the cranial system is the product of conflicting selective pressures resulting in functional trade-offs. Thus, the vertebrate cranial system would appear at first sight highly constrained through evolution.

Some vertebrate groups such as lepidosaurians (*Sphenodon*, lizards, and snakes) show a remarkable diversity in cranial structure, making the lepidosaurian cranium an ideal test case for exploring the role of functional trade-offs and constructional constraints (*sensu* Barel 1983) in complex, integrated systems. For example, feeding on large, hard or tough prey puts demands on increased bite performance. An increase in bite force can only occur by (1) increasing muscle mass of the jaw adductor, (2) changes in muscle architecture or physiology (e.g., pennate muscles with short fibers; expression of different fiber types) or (3) changes in the mechanics of the lever system (Herrel

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et al. 2002a, 2002b). Unless animals shorten the outlever of the jaw system and bite closer to the fulcrum, the increase in muscle force and bite force will impose greater loads on the cranial elements that need to withstand these larger forces. Thus, increases in bite force and muscle mass are expected to be correlated with an increased robustness of the skull. Yet, mechanical systems optimized for force generation cannot be optimized for speed at the same time due to constraints on lever mechanics and muscle physiology. Because of this, species preying on fast, elusive prey are expected to have long snouts, long parallel fibered muscles and long jaw-opening inlevers.

As mentioned earlier, not only functional demands but also constructional constraints may drive cranial evolution, as has been demonstrated previously for chichlid fish (Barel 1983). For example, space taken up by the jaw adductors cannot be used for sensory organs or the central nervous system if the total volume of the skull is to remain the same. Also, in some groups of lizards, a strong dominance of specific sensory systems may be present, and may put distinct selective pressures on the cranial system. For example, animals relying heavily on chemosensation have elongate, bifurcated tongues with a relatively small tongue surface area and long snouts. Thus the tongue can no longer be used for prey transport and alternative transport modes have to be developed. In snakes, this has resulted in the well-known highly kinetic jaw system that is used to transport prey through the oral cavity (Gans 1961). Similarly, in nocturnal animals such as geckos visual and olfactory senses dominate and eyes are much larger than in other lizards. The increase in size of the eye ball (Werner and Seifan 2006) is likely associated with the loss of the postorbital and supratemporal bar in these animals (Herrel et al. 1999c, 2000). Obviously, the loss of these cranial elements will have functional implications for stability and strength of the skull and will affect the use of the system during feeding.

In other groups, a reduction in cranial elements appears related to crevice-dwelling habits (Arnold 1998). It has been hypothesized that the flat heads and mobile skulls of cordylids (Cooper et al. 1999), xenosaurs (Ballinger et al. 1995; Lemos-Espinal et al. 1996; Herrel et al. 2001c), and some lacertids (Arnold 1998) allow animals to wedge themselves in crevices as an anti-predation tactic. Thus, different selection pressures may lead to similar functional demands and may have similar functional consequences in different groups. Yet, as the ancestral *Bauplan* may differ for these groups,

similar functional demands may potentially also lead to alternative solutions. Functional convergence need not to be associated with similar morphological changes in the underlying components of the system across different groups.

Here we take an integrated approach to the evolution of cranial structure in lizards by investigating the morphological basis as well as the functional and behavioral consequences of changes in morphology. As an initial approach, we explore whether overall skull robusticity is indeed associated with size of the jaw and the adductor muscles as predicted earlier. If so, changes in robusticity of the skull and loss of cranial bones may have strong functional consequences for bite force, feeding performance, and ultimately animal ecology. We use the striking reduction in cranial bones in geckoes and other lizards groups as a test case to examine the functional consequences of changes in morphology on function, behavior, and ecology.

Materials and methods

Animals

Specimens for dissection (Table 1) were animals that had died in transport for the commercial pet trade. They are deposited in the Functional Morphology Laboratory at the University of Antwerp. Specimens used for analyses of the bite force were collected in the field, tested, and released within 24 h of capture. Specimens filmed to quantify feeding behavior were all obtained through the commercial pet trade.

Morphology

All specimens used for the analysis of muscle mass were preserved in a 10% aqueous formaldehyde solution for 24–48 h, depending on the size of the specimen. After fixation, specimens were rinsed in water and transferred to a 70% aqueous ethanol solution. All specimens were kept in ethanol for at least two months before dissection, thereby assuring a similar degree of dehydration of tissue. All cranial muscles were removed from specimens and stored in 70% ethanol until weighed. Muscles were blotted dry and weighed on a Mettler MT5 electronic balance (accuracy: ± 0.01 mg). As alcohol was evaporating continuously from the muscles even after being blotted dry, masses were recorded after 10 s for all muscles. Skulls and mandibles were manually cleaned from remaining soft tissue after removal of cranial muscles and were weighed separately on an electronic balance. Data on muscle mass for some species were taken from previously published papers

Table 1 Muscle masses of the cranium and jaw

Family	Genus	Species	Skull length (mm)	Skull mass (g)	Adductor mass (mg)	MPPt (mg)
Agamidae	<i>Agama</i>	<i>stellio</i>	24.00	0.53	1250.00	10.00
Agamidae	<i>Pogona</i>	<i>vitticeps</i>	35.21	1.30	3565.25	17.13
Leiolepididae	<i>Uromastix</i>	<i>acanthinurus</i>	32.44	2.06	838.28	8.45
Amphisbaenia	<i>Blanus</i>	<i>cinereus</i>	8.08	0.02	16.59	
Anguidae	<i>Gherronotus</i>	<i>infernalis</i>	28.77	0.39	375.31	5.44
Chameleontidae	<i>Chameleo</i>	<i>calyptratus</i>	36.50	2.00	1864.64	
Cordylidae	<i>Cordylus</i>	<i>tropidosternon</i>	23.55	0.26	155.38	2.39
Corytophanidae	<i>Basiliscus</i>	<i>basiliscus</i>	28.31	0.36	438.37	4.21
Crotaphytidae	<i>Crotaphytus</i>	<i>collaris</i>	26.63	0.89	444.29	6.14
Eublepharidae	<i>Eublepharis</i>	<i>macularius</i>	29.85	0.74	695.91	23.97
Gekkonidae	<i>Gekko</i>	<i>gecko</i>	36.71	1.01	2142.90	66.90
Gekkonidae	<i>Phelsuma</i>	<i>madagascariensis</i>	25.68	0.39	354.60	12.90
Gherrosauridae	<i>Gherrosaurus</i>	<i>major</i>	36.00	1.64	379.30	3.64
Helodermatidae	<i>Heloderma</i>	<i>suspectum</i>	45.00	7.11 ^a	3930.00	34.00
Iguanidae	<i>Iguana</i>	<i>iguana</i>	37.23	0.83	349.41	5.15
Lacertidae	<i>Gallotia</i>	<i>galloti</i>	30.47	0.76	724.03	4.48
Lacertidae	<i>Podarcis</i>	<i>atrata</i>	15.55	0.09	104.60	2.00
Opluridae	<i>Oplurus</i>	<i>cuvieri</i>	29.46	0.60	332.89	4.50
Phrynosomatidae	<i>Phrynosoma</i>	<i>douglassi</i>	17.42	0.29	216.31	1.42
Phrynosomatidae	<i>Phrynosoma</i>	<i>platyrhinus</i>	15.86	0.24	70.18	1.06
Polychrotidae	<i>Anolis</i>	<i>garmani</i>	34.32	0.62	415.98	7.27
Scincidae	<i>Corucia</i>	<i>zebrata</i>	51.10	3.57	4650.00	30.00
Scincidae	<i>Novoeumeces</i>	<i>schneideri</i>	28.14	0.56	259.54	3.51
Scincidae	<i>Riopa</i>	<i>fernandi</i>	25.22	0.33	290.69	7.83
Scincidae	<i>Tiliqua</i>	<i>scincoides</i>	65.80	7.38	10170.00	90.00
Serpentes	<i>Nerodia</i>	<i>fasciata</i>	22.09	0.42	264.60	67.03
Teiidae	<i>Ameiva</i>	<i>ameiva</i>	40.46	1.59	1511.44	3.59
Tropiduridae	<i>Leiocephalus</i>	<i>carinatus</i>	21.43	0.25	134.88	2.87
Varanidae	<i>Varanus</i>	<i>niloticus</i>	38.94	0.44	262.01	12.89
Xantusiidae	<i>Lepidophyma</i>	<i>flavimaculata</i>	19.76	0.19	68.02	0.73

^aBased on a museum specimen of similar cranial length. MPPt, m. protractor pterygoidei. This muscle was not observed in the specimens of *Chameleo calyptratus* and *Blanus cinereus* specimens dissected for this study.

(Herrel et al. 1996b, 1998, 1999a, 2000) and additional data were collected when needed.

Bite forces

Bite forces were obtained for lizards from a single desert community in South Australia. Lizards were caught by hand and induced to bite a custom-made bite-force recorder constructed from a Kistler 9203 force transducer attached to a hand-held Kistler 5058A charge amplifier (see Herrel et al. 1999a, 2001a, 2001c for a description of the apparatus). After data on bite force were collected, lizards were measured (snout-vent length; head dimensions) and returned to their exact site of capture within 24 h.

Kinematics and feeding behavior

Lizards used for feeding-behavior trials (see Table 2 for a list of species) were obtained through the commercial pet trade and kept at the laboratory for Functional morphology at the University of Antwerp. They were provided with water and food *ad libitum* and kept on a 12 h light/dark cycle. A basking spot at higher temperature (45–50°C) was provided for all lizards and allowed them to attain preferred temperatures. Before filming, lizards were transferred to an acrylic cage with narrow projecting corridor and presented with a range of food items. For all insectivorous and omnivorous species data were gathered with crickets, grasshoppers and mealworms

Table 2 Kinematic and feeding behavior of various lizards and snakes

Family	Genus	Species	N	CL (mm)	FO (ms)	FC (ms)	TCD (s)
Agamidae	<i>Agama</i>	<i>stellio</i>	5	23.53	67.24	73.82	0.59
Agamidae	<i>Pogona</i>	<i>vitticeps</i>	5	38.29	65.75	65.05	0.36
Leiolepididae	<i>Uromastix</i>	<i>acanthinurus</i>	2	31.18	64.00	73.50	0.66
Anguidae	<i>Ophisaurus</i>	<i>apoda</i>	2	32.43			1.25
Chameleonidae	<i>Bradypodion</i>	<i>fischeri</i>	2	25.90			0.50
Chameleonidae	<i>Furcifer</i>	<i>oustaleti</i>	3	43.30			1.30
Chameleonidae	<i>Rhampholeon</i>	<i>brevicaudatus</i>	3	15.84			1.43
Cordylidae	<i>Cordylus</i>	<i>tropidosternon</i>	2	23.55	76.15	56.15	1.20
Crotaphytidea	<i>Crotaphytus</i>	<i>collaris</i>	2	31.52			0.69
Eublepharidae	<i>Eublepharis</i>	<i>macularius</i>	2	29.85	41.2	17.60	1.43
Gekkonidae	<i>Gekko</i>	<i>gecko</i>	4	30.80			1.00
Gekkonidae	<i>Phelsuma</i>	<i>madagascariensis</i>	2	25.68	18.00	29.11	3.30
Opluridae	<i>Oplurus</i>	<i>cuvieri</i> ^a	5	29.46	60.00	70.00	0.31
Phrynosomatidae	<i>Sceloporus</i>	<i>magister</i>	2	23.61			0.42
Pygopodinae	<i>Lialis</i>	<i>jicari</i>	2	18.06			9.59
Scincidae	<i>Corucia</i>	<i>zebrata</i>	2	56.00	51.53	50.15	0.31
Scincidae	<i>Tiliqua</i>	<i>scincoides</i>	4	57.61	93.05	73.15	0.63
Serpentes	<i>Nerodia</i>	<i>fasciata</i>	7	22.09			4.13
Teiidae	<i>Tupinambis</i>	<i>merrianae</i>	3	66.51	55.13	51.97	0.49
Varanidae	<i>Varanus</i>	<i>ornatus</i>	3	70.02	53.4	83.6	0.50

Table entries are species averages based on multiple feeding sequences with different prey. ^aData from Delheusy and Bels 1992. CL, cranial length; F, fast opening duration; FC, fast-closing duration; TCD, transport cycle duration. N, number of individuals upon which data are based.

as prey items. For herbivorous and omnivorous lizards, banana, tomato, and endive were included as additional food items (Herrel et al. 1996a, 1999b, 1999c; Herrel and De Vree, 1999).

Images were recorded using high-speed cameras (Redlake Motion Scope 500, Redlake MotionPro 500, and NAC-1000 systems) set at 100–500 frames per second depending on the species (Herrel et al. 2000; Meyers and Herrel 2005). Additionally, for larger species, kinematic data were gathered using a 6 camera VICON infrared tracking system at 250 Hz. Videofluoroscopic images were recorded using a Phillips Optimus M200 X-ray system coupled to a RedLake MotionPro 2000 high resolution digital camera at 100–500 Hz (Vincent et al. 2006). Cineradiographic images were recorded using a Siemens Tridoros-Optimatic 880 X-ray apparatus equipped with a Sirecon-2 image intensifier. Feeding bouts were recorded laterally using an Arriflex 16 mm ST camera equipped with a 70 mm lens at a film speed of 50 frames s⁻¹ (Herrel and De Vree 1999; Herrel et al. 1996a, 1999b, 1999c).

Analyses

All data were log₁₀ transformed before analysis. Regressions were run to explore relationships

between cranial size and muscle mass or bite force. Head size was chosen as the independent variable, instead of snout-vent length (the traditional measure of body size in lepidosaurians) due to large differences in body shape among taxa (e.g., snakes and legless lizards have extremely elongated bodies) and because of its relevance to feeding behavior. As species or species groups are not independent data points, the historical nature of the data was taken into account when exploring relationships among variables by calculating independent contrasts (Felsenstein 1985). Two radically divergent hypotheses for the interrelationships among major lizard groups were used in the analyses. The first is a consensus tree largely based on morphological data that places iguanians (acrodonts + Iguanidae s.l.) basal to all other lizards and xantusid lizards as a sister taxon to lacertiforms (Estes et al. 1988) (Fig. 1A). The placement of snakes as a sister taxon to varanids is based on Lee (1998). The second tree is again a consensus tree, but based on molecular data. This analysis places gekkos basal to all other lizards and places xantusids and cordylids as sister taxa to scincids (Vidal and Hedges 2004; Townsend et al. 2004; Fry et al. 2005; Fig. 1B). Given the strong evidence for sister relationships between

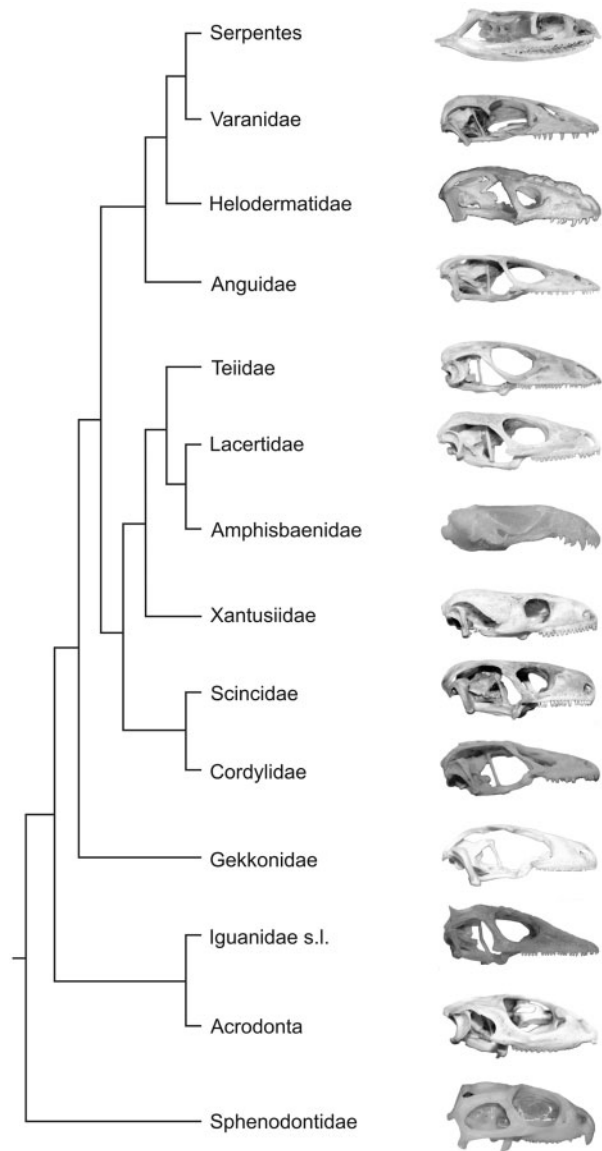


Fig. 1 Phylogenetic tree depicting relationships between the major clades of lepidosaurs based on morphological data (see "methods"). To the right of the morphological consensus tree pictures of the skulls of a representative species of each group is shown. Serpentes, *Nerodia fasciata*; Varanidae, *Varanus bengalensis*; Anguillidae, *Gerrhonotus infernalis*; Teiidae, *Ameiva ameiva*; Lacertidae, *Gallotia galloti*; Amphisbaenidae, *Blanus cinereus*; Xantusiidae, *Lepidophyma flavimaculata*; Scincidae, *Corucia zebrata*; Cordylidae, *Cordylus tropidosternon*; Gekkonidae, *Eublepharis macularius*; Iguanidae *sensu lato*, *Anolis garmani*; Acrodonta, *Placidoderma stellio*; Sphenodontidae, *Sphenodon punctatus*.

lacertids and amphisbaenids (Harris et al. 2001; Vidal and Hedges 2004; Townsend et al. 2004; Fry et al. 2005) these were considered sister taxa in all analyses. Within-group relationships were established as per Metzger and Herrel (2005). As we were unable to establish divergence times for all species

in the analysis, all branch lengths were set to unity (Martins and Garland 1991; Diaz-Uriarte and Garland 1998). We used the PDAP package (Garland et al. 1999) for our analysis. We inspected the diagnostic graphs and statistics in the PDTREE program to verify that our constant branch lengths were adequate for all traits (Garland et al. 1999).

To test whether species with distinctly kinetic skulls (as shown by our cineradiographic data, i.e., geckos, *Cordylus*, and snakes) have larger *constrictor dorsalis* muscles than do other lizards (Table 1), simulation analyses were performed using the PDSIMUL and PDANOVA programs (Garland et al. 1993). In the PDSIMUL program, we used Brownian motion as our model for evolutionary change and ran 1000 unbounded simulations to create an empirical null-distribution against which the *F*-value from the original data could be compared. In the PDANOVA program, skull kineticism was entered as a factor, the mass of the *m. protractor pterygoidei* (MPPt) was used as the independent variable and cranial length as co-variate. We considered differences among categories significant if the original *F*-value was higher than the F_{95} -value derived from the empirical distribution based on the simulations. Again, analyses were run for two sets of phylogenetic relationships among taxa (see above).

To test for differences among groups in kinematics and feeding behavior (Table 2), traditional ANCOVA's were used. No phylogenetically informed analyses were carried out on these data as only a few groups with radically divergent skull morphology were being contrasted (e.g., geckoes versus all other lizards). No herbivorous species were included in this comparison. To avoid a bias in the results due to the effect of type of prey, only data for lizards feeding on similar prey (crickets, grasshoppers, and mealworms) were used. Note, however, that snakes were fed goldfish during the feeding trials.

Results and discussion

The cranial morphology of lizards is remarkably diverse and appears characterized by the repeated, independent loss of cranial elements in some lineages (Figs 1 and 2; Table 1). Compared to the basal diapsid condition as represented by *Sphenodon*, squamates are characterized by the absence of a quadratojugal and the loss of the lower temporal bar (Rieppel and Gronowski 1981). The reduction of the lower temporal bar and the opening of the lower temporal fenestra likely happened before the split

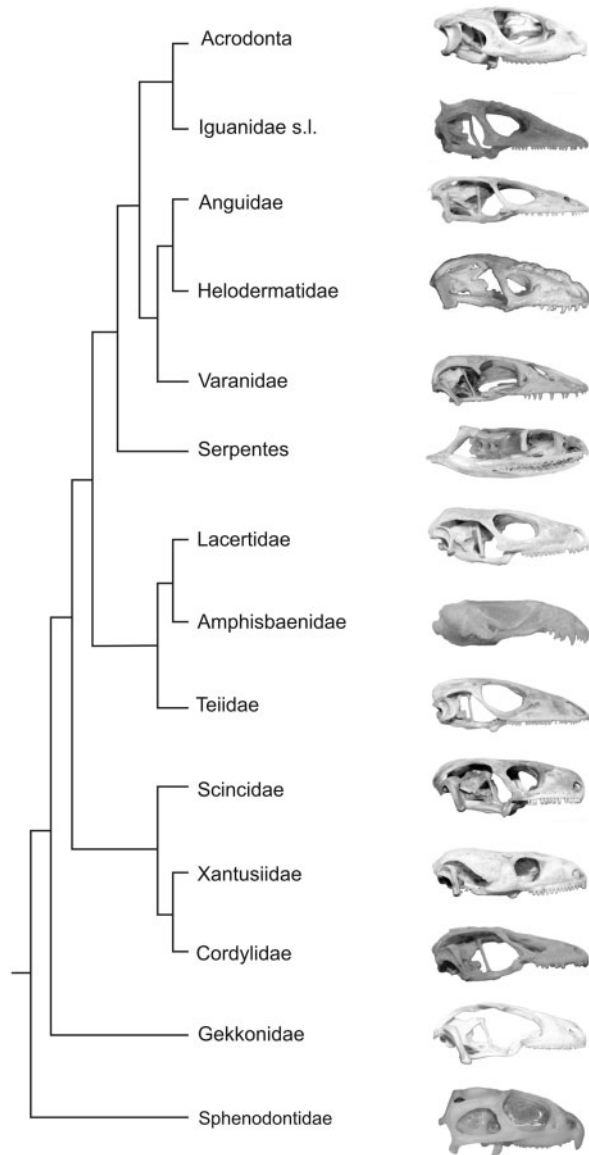


Fig. 2 Phylogenetic tree based on molecular data (see “methods”). Note the major differences in the position of gekkotans and iguanians in the two trees. To the right the evolution of morphological diversity in cranial form is represented.

between squamates and rhynchocephalians (Muller 2003), and appears to be associated with an expansion of the external adductor to the lateral aspect of the lower jaw (Rieppel and Gronowski 1981).

Among squamates, the upper temporal bar has been lost only in geckos, snakes, and amphisbaenians. Despite the putatively basal position of geckos among squamates (based on molecular phylogenies) (Fig. 2), this appears to be a unique and derived trait for the group. The radically divergent cranial morphology in snakes and amphisbaenians also

appears to be unique and derived for both groups and may be related to fossorial habits in extant or ancestral forms. In other squamates such as most varanids, some anguids (e.g., *Gherronotus*) and some teiids (e.g., *Aspidoscelis*), the upper temporal bar has become much thinner and provides attachment for the superficial adductor aponeurosis only. In other squamates, the upper temporal bar also functions as an attachment site for the fibers of the superficial portion of the external adductor. Among non-burrowing forms, both varanids and geckos are further characterized by the reduction of the postorbital bar.

Thus, despite the hypothesis that the cranial system should be highly constrained in evolution, a lot of variation appears to be present. This raises the question of which functional constraints may act on cranial design, and whether these are different in different lizard clades. One of the hypotheses put forward in the introduction is that the cranial system is likely constrained by its function during feeding and the generation of bite force in general (e.g., during feeding, fighting and defensive behaviors). Mechanically, it can be expected that the skull should be constructed in ways that minimally withstand reaction forces to food and direct muscular forces applied at sites of origin and insertion. Thus a correlation between skull strength and the operating loading regime during different behaviors is expected and may impose a ‘minimal design’ constraint on skull design.

To gain insights into this question, muscle masses and cranial size were compared for most lineages of lizards. If minimal design criteria are operating on the evolution of the skull in lizards, then associations between skull size and forces should be present. As it is nearly impossible to assess the *in vivo* loading regime for a wide range of representatives of different sizes, we used the mass of the jaw closing musculature as an indicator of the maximal force that may be exerted on the cranium. Our analyses indicate that both cranial mass and jaw adductor mass are highly correlated with length of the cranium (regressions of standardized independent contrasts using a morphological tree: $R^2 = 0.83$; $P < 0.001$; using a molecular tree: $R^2 = 0.84$; $P < 0.01$). Thus, the evolution of a larger head is, not surprisingly, associated with an evolutionary increase in mass of the jaw adductor muscle. More interestingly, however, is that skull robustness (i.e., the residuals of the independent contrasts of skull mass over the independent contrasts of skull length) is significantly associated with the residual contrasts of jaw-adductor mass (morphological tree: $r = 0.52$,

$P=0.004$, Fig. 3A; molecular tree: $r=0.53$, $P=0.003$, Fig. 3B). Thus species with more massive and more robust skulls have relatively larger jaw adductors. Thus, our minimal—design—constraint hypotheses appears confirmed by the data and suggests that biting does indeed shape the evolution of the design of the skull and the entire cranial system.

Previous analyses of cranial mass in lizards (Metzger and Herrel 2005) suggested that herbivorous lizards have relatively light skulls. Analyses of bite force in herbivores and omnivores, on the other hand, suggest that they bite harder than other lizards (Herrel et al. 2004). Although this might suggest that these species have circumvented the demands on skull design imposed by the loading regime, this appears unlikely given the generality of our results based on a dataset that included several herbivorous and omnivorous species (e.g., *Iguana iguana*, *Pogona vitticeps*, *Uromastix acanthinurus*, *Gallotia galloti*, *Podarcis atrata*, and *Corucia zeb-rata*). Interestingly, analyses of cranial form also suggest that species that include plant matter in their diets have relatively short snouts (Metzger and Herrel 2005). By reducing snout length, the jaw outlever length is minimized relative to the closing inlever, thus increasing the mechanical advantage of the system without increasing muscle forces. Yet, in some dedicated herbivores, muscular adaptations including increases in muscle mass have been demonstrated as well (Herrel et al. 1998). A close examination of the skulls of some of these species (i.e., *Corucia zeb-rata*, and *Gallotia galloti*) suggests that the skulls are reinforced by dermal osteoderms, which are not included in estimates of cranial mass. In other species, a greater jaw-closing moment around the jaw joint is achieved without an increase in muscular force primarily through a shift in the orientation of the jaw muscles (Herrel et al. 1998). Thus herbivorous and omnivorous lizards also appear to meet the minimal design criteria put forward and have skulls built to withstand the loading regime imposed by the muscular forces of the jaw adductors.

Clearly, muscle forces are not the only constraint on the design of the cranial system and in some lizards (e.g., geckos) skull design has been linked to the presence of well-developed sensory systems. It has been suggested previously that the nocturnal lifestyle of the common ancestor of geckos led to an increase in eye size as is observed in recent geckos (Werner and Seifan 2006). Due to constraints of physical space, an increase in eye size resulted in a loss of the postorbital and supratemporal cranial

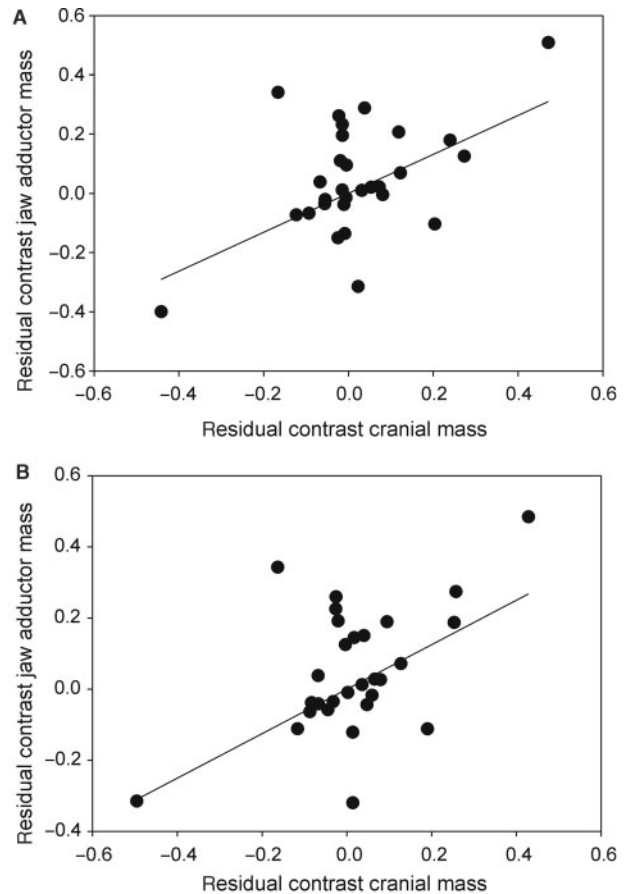


Fig. 3 Relationships between skull robustness and size of the jaw adductor in lizards. Lizards with relatively heavier skulls (relative to skull length) have relatively larger jaw-adductor muscles. **(A)** Analysis based on the morphological tree depicted in Fig. 1. **(B)** Analysis based on the molecular tree depicted in Fig. 2.

elements which likely gave rise to a pronounced intracranial mobility in these animals (Herrel et al. 2000). Thus spatial constraints may potentially drive cranial design in lizards. However, minimal design criteria must be met and the spatial constraints operating on the skulls of geckos may have serious consequences on the maximal allowable loading regime and thus also bite-force capacity in these animals. To explore this issue we analyzed bite force data for lizards from a single community of desert lizards in Australia. Our data indicate that geckos do indeed have significantly lower bite forces for their head size (head length) than do agamid or scincid lizards from the same community (ANCOVA: $F_{2,129}=39.9$; $P<0.001$; Fig. 4). Given that this analysis is based on the community level we can evaluate the implications of skull design on resource partitioning in the community. Because of their lower bite forces, geckos could potentially be

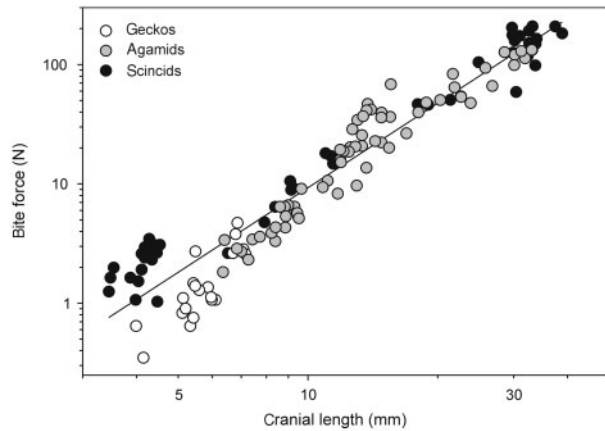


Fig. 4 Graph depicting relationships between head length and bite force ($R^2=0.92$; $P<0.001$; slope = 2,35; intercept = -1,39) for lizards of a single community of desert lizards from Australia. Note how geckos bite significantly less hard for their head size than do agamids or scincids based on an analysis of covariance.

restricted in their dietary scope as bite forces have been demonstrated to be related to feeding efficiency and dietary breadth along functional axes (i.e., prey size, hardness, and evasiveness) (Verwaijen et al. 2002; Herrel et al. 2006). Yet, because of their nocturnal habits, geckos likely have little or no competition from diurnal lizards and can specialize on the softer prey available.

Yet, geckoes are not the only lizards that are thought to have kinetic skulls and may thus be faced by the same constraints on bite force (see Metzger 2002 for a review). Surprisingly, however, a survey of feeding behavior in lizards using cineradiography (Herrel et al. 1996a, 1997, 1999b; Herrel and De Vree 1999) suggests that only geckos and *Cordylus* have true coupled kinesis where streptostyly (i.e., rotation of the quadrate at the quadrato-squamosal joint) is associated with mesokinesis during feeding. Among the species included in the present study, snakes are the only other group that displays a striking degree of intracranial mobility. Representatives of other groups such as anguids (*Gherronotus liocephalus*, *Ophisaurus apoda*) and varanids (*Varanus ornatus*, *Varanus niloticus*) that have been reported in the literature to have kinetic skulls showed no movement in X-ray movies at the mesokinetic axis during feeding.

To test for a potential effect of the decreased bite force on the efficiency of feeding behavior in lizards with kinetic skulls, we quantified the duration of intraoral transport cycles in a range of lizards (Table 2). An analysis of covariance on the duration of transport cycles (cranial length as covariate) and testing for differences among animals with kinetic

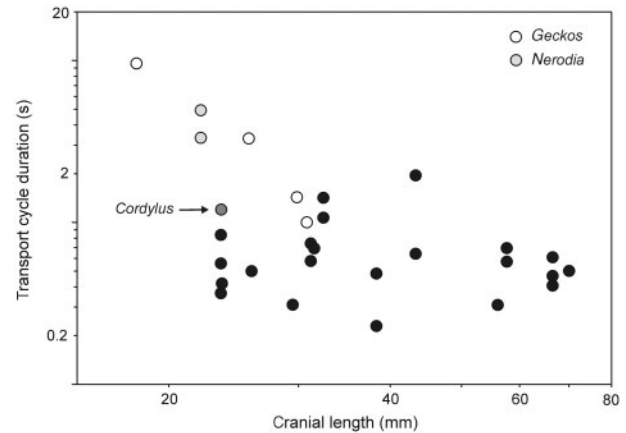


Fig. 5 Duration of prey transport cycles in squamates. Note how the duration of intraoral transport cycles is greater in squamates with kinetic skulls (geckos, snakes, and *Cordylus*). White circles, geckos; light grey circle, snakes; dark grey, cordylus; black, other lizards.

skulls (geckos, *Cordylus*, and *Nerodia*) and all others shows that transport is significantly longer in squamates with kinetic skulls (akinetic: 0.67 ± 0.37 s; kinetic: 3.44 ± 3.27 ; $F_{2,17} = 13.77$; $P<0.01$; Table 2, Fig. 5). Thus the consequence of having a kinetic skull appears to be an increase in the duration of transport cycles. The number of cycles needed to reduce a prey item is also greater (10.91 ± 5.44 versus 31.92 ± 9.43 ; $F_{1,10} = 11.78$; $P<0.01$) in lizards with kinetic skulls, and this implies that these squamates take significantly (almost 10-fold) longer to transport prey. This may again have serious ecological implications as this would increase exposure to potential predators. Yet behavioral changes, including crypsis (e.g., *Cordylus*), nocturnality (geckos) or infrequent feeding (snakes) may ameliorate these potential drawbacks.

Although it appears that cranial kinesis is a disadvantageous side product of a loosely constructed skull, some benefits of cranial kinesis have been suggested in the literature. For example, it has been suggested that the kinetic mechanism of an extra joint would allow for faster jaw opening and closing in geckos (Herrel et al. 2000). However, this has never been tested quantitatively. We tested this hypothesis using a restricted dataset on kinematic phases of the gape cycle. An ANCOVA with cranial length as co-variate and testing for differences in fast opening (FO) duration between animals with kinetic skulls (i.e., geckos and *Cordylus*; snakes clearly have an extremely different kinetic mechanism and are not expected to be faster) and those with akinetic skulls is, however, not significant ($F_{1,8} = 2.92$; $P = 0.13$; Table 2). Yet, if only geckoes are coded as kinetic,

differences in FO duration are highly significant ($F_{1,8} = 14.89$; $P < 0.01$). Thus, the geckos tested here differ from cordylids in having a much faster FO phase (Table 2, Fig. 6A). Although this is rather surprising at first, our morphological data suggest why this may be the case. Although squamates with kinetic skulls (geckos, *Cordylus*, and snakes) have a significantly larger MPpT for a given cranial length than do squamates with akinetic skulls (simulation analysis based on morphological tree: $F_{\text{physi}} = 7.74$; molecular tree: $F_{\text{physi}} = 10.45$; $F_{\text{trad}} = 11.68$, $P < 0.05$; Table 1, Fig. 7), this pattern is largely driven by the disproportionately large MPpT in snakes and geckos (Fig. 7). The MPpT has been implicated in the protraction of the cranial unit in geckos and may help rotate the jaws open more rapidly in these animals. *Cordylus* on the other hand has a relatively smaller MPpT and thus cannot rotate its upper jaw as

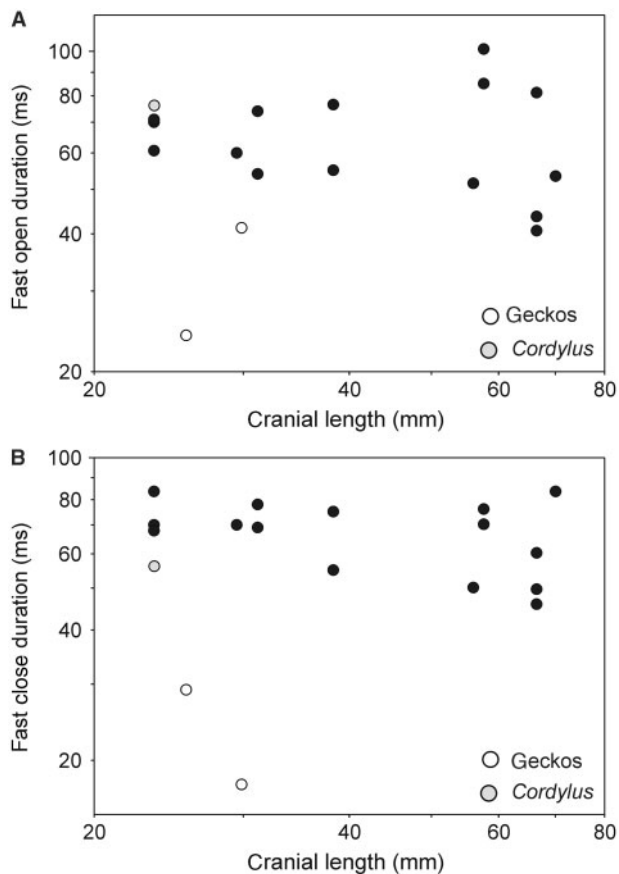


Fig. 6 (A) Duration of the fast-opening phase of the jaws during prey transport. Note how geckos are extremely fast. *Cordylus* on the other hand, despite having a kinetic skull is not faster than lizards with akinetic skulls. (B) duration of the fast-closing phase of the jaws during prey transport. Note how geckos (white circles) are again extremely fast. *Cordylus* (grey circle) is also faster than lizards with akinetic skulls (black circle).

quickly as do geckos. Clearly more data are needed to provide conclusive tests of the patterns suggested by these data.

During jaw closing, however, the jaw adductors are responsible for both the ventrad rotation of the snout and the elevation of the lower jaw and thus both geckos and *Cordylus* are expected to be faster than lizards with akinetic skulls. Indeed, differences in FC duration are significantly different between species with kinetic and those with akinetic skulls ($F_{1,8} = 11.66$; $P < 0.01$). Thus the geckos and cordylid included in the present analysis are similar in having short FC durations (Table 2, Fig. 6B). The rapid jaw-closing movements in lizards with kinetic skulls may be important as it can bestow a potential advantage when feeding on elusive, mobile prey. Although this has never been quantified previously, this should provide an interesting avenue for further research.

In conclusion, our data suggest that cranial design in lizards is driven by minimal-design constraints related to biting. The constructional demands imposed by other selective pressures (e.g., nocturnality) may compete with functional demands for cranial strength, with potentially far reaching implications for the use of the feeding system and ultimately the ecology of the animals. Thus, the lizard cranial system does indeed appear to be an ideal system to explore how different selective pressures and potential constraints may act to shape the evolution of a complex integrated system.

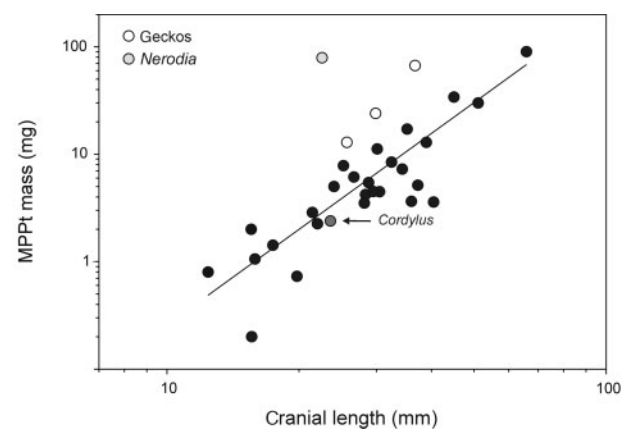


Fig. 7 Graph depicting the relationship between skull length and the mass of the MPpT involved in protraction of the snout during jaw opening in geckos. Note how geckos have large MPpT muscles which may explain the extremely rapid fast-opening phase. *Cordylus*, despite having a kinetic skull does not have a MPpT which is larger than that of lizards with akinetic skulls.

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