

CRANIAL KINESIS IN GECKOES: FUNCTIONAL IMPLICATIONS

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Summary

Although it is generally assumed that cranial kinesis is a plesiomorphic characteristic in squamates, experimental data tend to contradict this hypothesis. In particular, coupled kinesis (i.e. streptostyly and mesokinesis) presumably arose independently in only a limited number of highly specialised groups. In this study, we investigated cranial kinesis in one of the most specialised of these groups: geckoes. On the basis of cineradiographic and electromyographic data, the fast opening and the slow closing/power stroke phases were modelled to elucidate possible functions of the observed kinesis. The results of these analyses show that the retraction of the muzzle unit during crushing is a self-reinforcing system that increases bite force and reduces the joint forces; the active protraction of the kinetic system during jaw opening, in contrast, enhances opening speed through the coupling of

the intracranial units. It can be argued that cranial kinesis in geckoes is probably not an adaptive trait as such but, instead, a consequence of the 'Bauplan' of the cranial system in these animals. Presumably as a result of constructional constraints on the size of the jaw musculature and eyes, the supratemporal and postorbital bars were lost, which resulted in enormous mobility in the skull. To counteract the potential negative factors associated with this (decrease in bite force, skull damage), the kinetic system may have become coupled, and thus functional.

Key words: cranial kinesis, Gekkonidae, modelling, feeding, constructional morphology, *Gekko gecko*, *Phelsuma madagascariensis*.

Introduction

The function of the kinetic skull has intrigued many workers during the last century and a half (for references, see Frazzetta, 1962; Smith, 1982). A kinetic skull was defined by Versluys (1910, 1912) as allowing any intracranial movements (besides those of the lower jaw). Thus, kinetism occurs whenever the upper jaw and palate (the maxillary segment) can move relative to the braincase (axial segment). Generally, cranial kinesis is considered to be ancient feature of the vertebrate skull that is widespread among modern tetrapods (Iordansky, 1990).

Within amniotes, cranial kinesis is most prominent in Archosauria (i.e. birds) and Lepidosauria. In the former group, a kind of streptostyly (antero-posterior quadrate movement) coupled to prokinesis (allowing dorso-ventral movements of the upper bill independent of mouth opening) is generally observed (Bock, 1964; Zusi, 1967, 1993; Zweers, 1982). Within the lepidosaurians, varying degrees of cranial kinesis are observed, with snakes having the most kinetic skulls (Gans, 1961; Frazzetta, 1966; Kardong, 1977; Cundall, 1983; Kardong et al., 1986; Cundall and Shardo, 1995). In lizards, three types of cranial kinesis exist (Versluys, 1910): (i) movement of the quadrate (streptostyly), (ii) movement of the braincase at the paroccipital process (metakinesis), and (iii) movement of the palato-maxillary unit at the frontal-parietal

joint (mesokinesis) (Fig. 1). Amphikinesis is the combination of meso- and metakinesis (Frazzetta, 1962).

The function of the kinetic skull is generally well understood for most of the vertebrate groups discussed above; it is usually involved in the function of the cranial system during feeding (e.g. facilitating food passage in amphibians, improved manipulative abilities of the bill in birds, allowing the ingestion of extremely large food items in snakes). However, no consensus exists concerning the functional significance of this kinetic system in lizards. Consequently, many investigators have attempted to demonstrate kinesis in lizard skulls and speculated on its functional role (Frazzetta, 1962, 1983; Throckmorton, 1976; Rieppel, 1979; Throckmorton and Clarke, 1981; Smith and Hylander, 1985; De Vree and Gans, 1987, 1989; Condon, 1987; Arnold, 1998). However, the techniques used provide contradictory results and are often criticized.

The aim of the present study is to examine the origin and adaptive significance of cranial kinesis within a group of lizards in which the presence of pronounced amphikinesis has been demonstrated (Herrel et al., 1999). On the basis of the movements of the cranial elements and the corresponding muscular activities, the system in geckoes is modelled in an

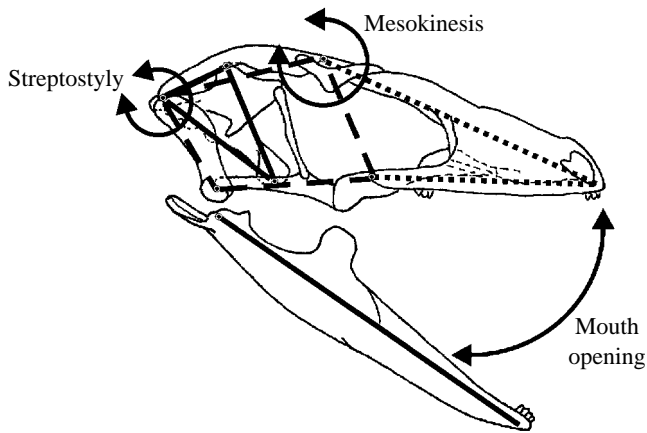


Fig. 1. Graphical representation of cranial kinesis in lizards. Streptostyly involves an antero-posterior rotation of the quadrate at the quadrato-squamosal joint; mesokinesis an elevation or depression of the snout unit relative to the rest of the skull.

attempt to unravel the mechanistic aspects and potential functional advantages of the observed kinesis.

Materials and methods

Anatomy

Fresh and preserved specimens of adult *Gekko gekko* (L.) and *Phelsuma madagascariensis* (Gray) were used for dissection, to describe the skull morphology and to characterize the jaw muscles. Drawings were made using a Wild M3Z dissecting microscope provided with a *camera lucida*. For each species, three additional specimens were dissected, and all distinct jaw muscle bundles of one side were removed individually and weighed (to within 0.001 g). The muscle bundles were immersed in a 30% aqueous solution of HNO_3 for 24 h to separate the muscle fibres and then stored in a 50% aqueous glycerol solution. Twenty muscle fibres per bundle were chosen randomly and drawn using a Wild M5 dissecting microscope with a *camera lucida*. The average fibre length per bundle was then determined. The physiological cross section of each bundle was approximated by the ratio of the mass to the mean fibre length (assuming a muscle density of 1000 kg m^{-3}). Although individuals differed in their absolute jaw muscle mass, the relative mass (muscle mass relative to the entire adductor mass) was similar for individuals within a species. In the models, morphological data for only one individual per species were used.

Dynamic jaw-opening model

Inverse dynamics were applied to a model jaw with the dimensions and inertial properties of the lower jaws of either *Gekko gekko* or *Phelsuma madagascariensis*. This implies that the lower jaw was considered as a free body for which the dynamic equilibrium of external forces and moments is solved (e.g. Winter, 1990). Contrary to what happens in reality (Herrel et al., 1999), it is intentionally assumed that the quadrate does

not rotate during mouth opening. This allowed us to calculate the forces (magnitude and orientation) acting from the jaw onto the quadrate as a result of simple jaw depression. With the quadrate in the position observed at the onset of depression (the resting position; Herrel et al., 1999), it was then judged whether simple jaw depression (through the induced joint forces) would tend to rotate the quadrate forwards or backwards. It is obvious that entering quadrate movements into the inverse modelling will bias this interpretation.

The modelling procedure was as follows. The angular movements of the mathematical model jaw were described by a cosine function in such a way that angular velocities are zero at the onset and end, and maximal half-way through, the depression movement. The maximal depression angle and duration of depression were based on video and cineradiographic recordings of feeding in unrestrained specimens (Herrel et al., 1999). This procedure allowed us to describe the actual angular movement patterns of the jaw in a simple mathematical way. The external moments acting on the jaw during depression were derived from the resistive forces of the jaw apparatus (mainly the passive extension of the massive jaw-closing musculature) and from the contraction of the depressor mandibulae muscles. The resistive forces were entered into the model as a linear spring and an angular-velocity-dependent dashpot (see Fig. 2A). Spring stiffness was deduced from the degree of mouth opening due to gravitational forces observed in anaesthetized specimens. The angular equation of motion (i.e. the sum of all external moments acting on the jaw is equal to the product of the angular acceleration and the moment of inertia of the lower jaw) was then applied in an iterative way. Dashpot characteristics (damping coefficients) were adjusted until the maximal forces required from the jaw depressor muscles to rotate the jaw in the manner described above (i.e. the peak value of the depressor curves shown in Fig. 2) were of similar magnitude to the maximal force output deduced from the physiological cross sections of these muscles (muscle stresses of 25 kPa were used; see also Herrel et al., 1998a,b). In calculating this depressor force, the changing orientation of the line of action of the depressor muscles due to jaw rotation was taken into account. The rationale for using this procedure is that fast opening of the jaws coincides with the most strenuous activity in the jaw depressors (see Herrel et al., 1999). As a result, all linear forces acting on the jaw, except those at the level of the articulation with the quadrate (i.e. depressor, spring and dashpot force), were known at all stages of jaw depression. The forces from the quadrate on the jaw were then obtained by solving the linear equations of motion in the fore-aft and dorso-ventral directions (i.e. the sum of all external forces is equal to the product of mass and linear acceleration). Because of the bilateral symmetry in morphology and activation of the jaw muscles (see Herrel et al., 1999), transverse force components were assumed to cancel each other out and were not considered in the model. The resultant joint force and its orientation were obtained by combining the two force components. An equal but opposite reaction force acts on the quadrate. The

orientation of this reaction force relative to the long axis of the quadrate determines the direction in which the quadrate will tend to rotate as a result of jaw depression.

Static bite modelling

The analysis of biting in the geckoes studied here relied on the computation of the static force equilibrium. For an extensive description of the model, we refer to Herrel et al. (1998a,b) and Cleuren et al. (1995). Briefly, the muscle contractile forces were scaled to the physiological cross sections of the muscles or muscle bundles considered. To fulfil the static condition, muscle forces were balanced by the reaction forces of the food on the jaw and the reaction forces in the jaw. Experimental data indicate that forceful biting is characterized by a bilaterally simultaneous activation of the jaw adductor complex (Herrel et al., 1999). Therefore, transverse force components are assumed to cancel each other out and were not taken into account in the model. The lines of action of the jaw-closing muscles were based on the orientation of the muscles observed during dissections. Because the orientation of the food reaction forces is unpredictable (it will depend on tooth shape and on the orientation and structure of the food; see Cleuren et al., 1995; Herrel et al., 1998a,b), this orientation was varied between -130° and -40° in the model.

First, the jaw was considered as a free body and, by solving the static angular equilibrium, the magnitude of the food reaction forces (for the prescribed orientations) was calculated. Logically, these forces are equal but opposite to the bite forces (see Fig. 3D). Using these forces, and by solving the linear equilibrium equations, joint reaction forces were deduced. Next, the jaw and quadrate were considered as the free body for which the static equilibrium conditions must be fulfilled. All external forces (jaw-closing muscles crossing both the quadrato-mandibular and quadrato-squamosal joint and the food reaction forces) acting on this free body were known from the previous modelling step (note that the joint reaction forces are internal forces in this case). Solving the angular equilibrium about the quadrato-squamosal joint allowed us to evaluate the moments required to keep the free body in its static equilibrium. For animals with highly mobile quadrates, these 'remaining moments' will tend to rotate the quadrate/jaw system about its squamosal suspension. In the present paper, the changes in skull configuration observed during biting were taken into account by introducing three different states into the model (see Herrel et al., 1999): the rest position, complete protraction (as observed just after fast closing of the jaws) and complete retraction (as observed at the end of the slow closing/power stroke phase). These three skull configurations were deduced from cineradiographic data gathered for both species (Herrel et al., 1999). Simulations were standardized by using a fixed gape angle (10°) and biting point (=point of application of the bite forces, based upon video recordings of unrestrained feeding sequences). The moments calculated about the quadrato-squamosal joint in the different

configurations allow one to determine the effects of jaw closing on the direction of quadrate rotation. Bite and joint forces were calculated for each configuration (see Fig. 3).

Results

Morphology

The external adductor musculature in geckoes is characterized by a reduction of the basal aponeurotic complex (bodenaponeurosis), so the traditional terminology, which is based on the positions of muscles relative to this complex (e.g. Lakjer, 1926; Haas, 1973; Gomes, 1974), is generally inadequate. Nevertheless, functional units (i.e. muscle bundles with similar origins and insertions) can be discerned and have been described previously for both the species discussed here (Herrel et al., 1999). All jaw closer muscle units described by Herrel et al. (1999) were used as input in the static bite model here; the jaw opener (=m. depressor mandibulae) was used in the jaw opening model.

Modelling

Jaw opening

The results for the two species were very similar (Fig. 2B,C), indicating a general pattern for the group as a whole. The calculated joint forces were of approximately the same magnitude as the contraction forces of the jaw openers (Fig. 2B,C). In its resting position, the quadrate inclines at an angle of approximately 115° relative to the long axis of the skull in both species. At least during the first part of the depression cycle, joint forces act in front of the quadrate. Therefore, jaw depression can be expected to protract the quadrate (and thus lift the snout). Moreover, protraction will increase the inclination of the quadrate, thus shifting the protraction–retraction boundary (the horizontal line in Fig. 2B,C) upwards. The active degree of protraction due to simple jaw depression cannot be predicted because we have no information about the inertial and visco-elastic properties countering this movement. Nevertheless, given the size of the joint forces (maximal joint forces during opening: *G. gecko*, 6.00 N; *P. madagascariensis*, 2.87 N), considerable protraction of the system is likely to occur.

During the entire opening phase, joint forces tend to rotate the quadrate anteriorly, indicating that protraction of the kinetic system will occur even without activation of the m. protractor pterygoidei. The implication of this finding is that, for a given lower jaw depression, the actual gape angle will be much larger in lizards with kinetic skulls because of the mechanical links in the system (jaw depression results in a forward displacement of the quadrate, which causes snout lifting, see Fig. 1).

Jaw closing

Although the absolute values of the forces calculated differ for the two geckoes studied here, the observed trends are similar for both species. As in other lizards (see Herrel et al., 1998a,b), bite forces are highest for food reaction forces

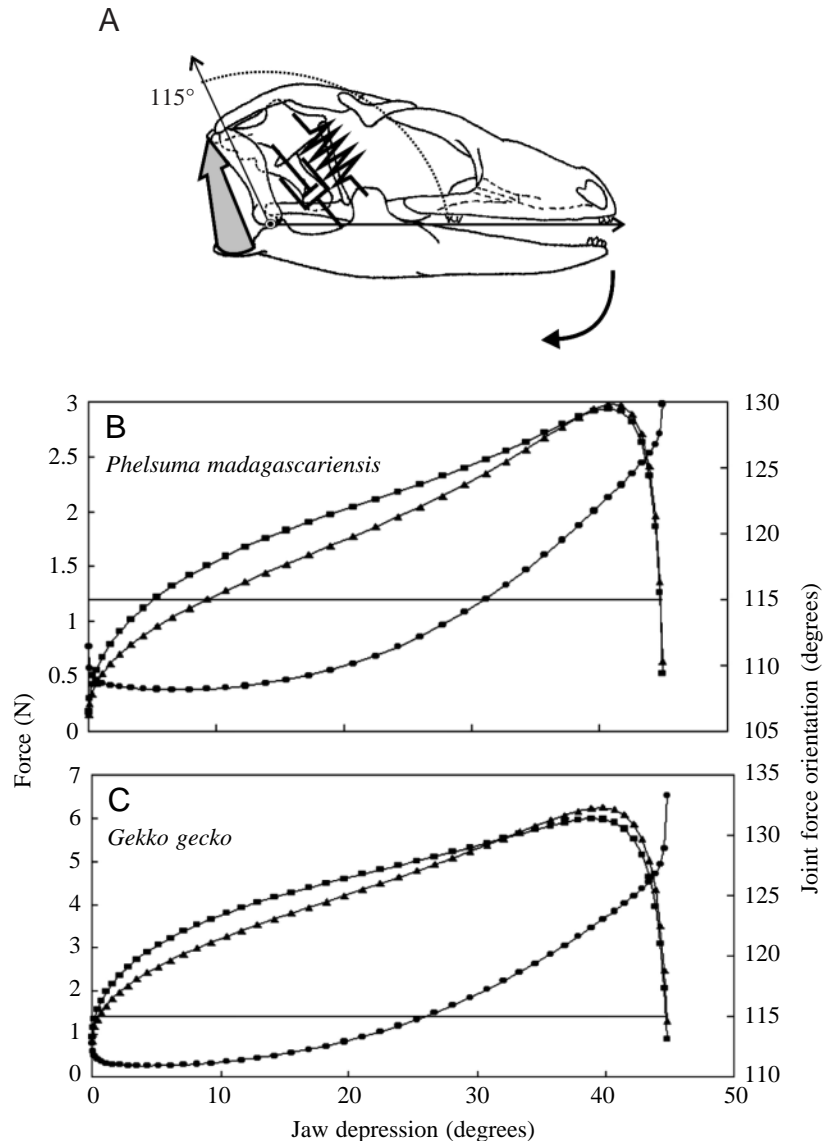


Fig. 2. Results of the dynamic model used to simulate jaw opening. (A) A pictorial representation of the model. In the model, jaw opening (curved arrow) is caused by depressor activity only and occurs according to a prescribed movement pattern (based on cineradiography of both species). The position of the quadrate at rest (angle 115°) is shown. The system is then spring/dashpot-adjusted until relevant depressor forces are obtained. See text for further details. (B,C) The output of the model for the two species. The horizontal line indicates the position of the quadrate at rest. As long as the joint forces act in front of the quadrate (filled circles below horizontal line), depression of the lower jaw tends to rotate the quadrate forwards. Moreover, quadrate protraction implies that this horizontal line will shift upwards along these curves. ▲, depressor forces; ■, joint forces; ●, orientation joint forces.

oriented away from the plane perpendicular to the occlusal plane (Tables 1–3; Fig. 3A). Similarly, in both geckoes studied here, joint forces also tend to be lower for anteriorly directed food reaction forces and highest for posteriorly directed food reaction forces (Tables 1–3; Fig. 3C). Taking into account that counterclockwise moments are considered positive (see Herrel et al., 1998a), the generally positive sign of the moments required to keep the skull in static equilibrium (Tables 1–3; Fig. 3B) indicates a tendency to rotate the quadrate posteriorly for nearly the entire range of food reaction forces considered. In contrast to other lizards (Herrel et al., 1998a), no ligaments or bony struts are present that could generate these required moments. Thus, actual displacement of the quadrate is expected, and observed, to occur.

These results also indicate that retraction of the cranial system (as observed during feeding; Herrel et al., 1999) results in an increase in bite forces for the complete range of food reaction forces considered (Tables 1–3; Fig. 3A). However,

the bone-to-bone joint forces also increase during retraction of the kinetic system (Tables 1–3; Fig. 3C).

Discussion

From the results of the bite-modelling approach used in this study, it is clear that the relative positions of different cranial elements have an important effect on the bite force, the bone-to-bone joint forces and the moments occurring at the jaw and quadrato-squamosal joints. Similar trends are observed in the two species examined. One of the major observations is that the bite force increases by as much as 30% in *P. madagascariensis* and up to 15% in *G. gecko* as the result of the retraction of the kinetic system. In addition, the calculation of the ratios of joint forces to bite forces (Tables 1–3) indicates a more unfavourable situation for the skull in a more protracted configuration (i.e. a relatively high joint force for a given bite force). As indicated by the moments calculated about the quadrato-squamosal joint, the retraction of the kinetic system

Table 1. Output of the static bite model with the skull in the resting configuration

	AFRF (degrees)	FRF (N)	JF (N)	AJF (N)	RemM (Nm)	JF/BF
<i>Gekko gecko</i>	-138	16.97	37.18	130.75	0.22	2.19
<i>Phelsuma madagascariensis</i>		3.20	9.55	116.04	0.017	2.98
<i>G. gecko</i>	-126	13.78	33.96	125.65	0.18	2.46
<i>P. madagascariensis</i>		2.67	9.08	111.95	0.014	3.40
<i>G. gecko</i>	-114	12.04	31.86	121.43	0.16	2.65
<i>P. madagascariensis</i>		2.37	8.77	108.64	0.011	3.69
<i>G. gecko</i>	-102	11.13	30.3	117.62	0.13	2.72
<i>P. madagascariensis</i>		2.23	8.53	105.70	0.0088	3.83
<i>G. gecko</i>	-90	10.78	29.04	113.87	0.11	2.69
<i>P. madagascariensis</i>		2.19	8.33	102.86	0.0067	3.81
<i>G. gecko</i>	-78	10.91	27.92	109.88	0.094	2.56
<i>P. madagascariensis</i>		2.24	8.16	99.86	0.0047	3.63
<i>G. gecko</i>	-66	11.56	26.89	105.26	0.072	2.33
<i>P. madagascariensis</i>		2.41	7.99	96.41	0.0024	3.31
<i>G. gecko</i>	-54	12.89	25.92	99.39	0.047	2.01
<i>P. madagascariensis</i>		2.74	7.82	92.01	-0.00043	2.86
<i>G. gecko</i>	-42	15.32	25.09	91.01	0.014	1.64
<i>P. madagascariensis</i>		3.33	7.67	85.68	-0.0043	2.30

AFRF, angle of the food reaction forces; AJF, angle of the joint forces; BF, bite forces; FRF, food reaction forces; JF, joint forces; RemM, remaining moment at the quadrato-squamosal joint.

Bite forces are calculated for one side only and are only a rough estimate of the actual bite forces.

Positive moments indicate a tendency to rotate the quadrate backwards.

Because the orientation of the food reaction forces is unpredictable, results are given for an entire range of orientations (AFRF).

Table 2. Output of the static bite model with the skull in a protracted configuration

	AFRF (degrees)	FRF (N)	JF (N)	AJF (N)	RemM (Nm)	JF/BF
<i>Gekko gecko</i>	-138	15.17	36.07	134.79	0.16	2.38
<i>Phelsuma madagascariensis</i>		2.69	9.31	123.41	0.013	3.46
<i>G. gecko</i>	-126	12.32	32.97	130.48	0.13	2.68
<i>P. madagascariensis</i>		2.24	8.85	120.24	0.010	3.95
<i>G. gecko</i>	-114	10.77	30.91	126.91	0.11	2.87
<i>P. madagascariensis</i>		1.99	8.52	117.69	0.0084	4.27
<i>G. gecko</i>	-102	9.95	29.34	123.70	0.095	2.95
<i>P. madagascariensis</i>		1.87	8.27	115.40	0.0069	4.42
<i>G. gecko</i>	-90	9.64	28.02	120.49	0.081	2.91
<i>P. madagascariensis</i>		1.83	8.04	113.17	0.0055	4.38
<i>G. gecko</i>	-78	9.76	26.83	117.06	0.066	2.75
<i>P. madagascariensis</i>		1.88	7.83	110.79	0.0040	4.15
<i>G. gecko</i>	-66	10.34	25.66	113.04	0.051	2.48
<i>P. madagascariensis</i>		2.02	7.61	108.20	0.0025	3.75
<i>G. gecko</i>	-54	11.53	24.45	107.84	0.033	2.12
<i>P. madagascariensis</i>		2.30	7.37	104.43	0.00053	3.20
<i>G. gecko</i>	-42	13.70	23.21	100.20	0.0095	1.69
<i>P. madagascariensis</i>		2.80	7.08	99.09	-0.0021	2.53

AFRF, angle of the food reaction forces; AJF, angle of the joint forces; BF, bite forces; FRF, food reaction forces; JF, joint forces; RemM, remaining moment at the quadrato-squamosal joint.

Bite forces are calculated for one side only and are only a rough estimate of the actual bite forces.

Positive moments indicate a tendency to rotate the quadrate backwards.

Because the orientation of the food reaction forces is unpredictable, results are given for an entire range of orientations (AFRF).

Table 3. Output of the static bite model with the skull in a retracted configuration

	AFRF (degrees)	FRF (N)	JF (N)	AJF (N)	RemM (Nm)	JF/BF
<i>Gekko gekko</i>	-138	17.70	38.35	125.95	0.27	2.17
<i>Phelsuma madagascariensis</i>		3.67	10.53	97.43	0.027	2.87
<i>G. gekko</i>	-126	14.37	35.28	120.37	0.22	2.45
<i>P. madagascariensis</i>		3.06	10.28	92.50	0.022	3.36
<i>G. gekko</i>	-114	12.56	33.34	115.82	0.19	2.65
<i>P. madagascariensis</i>		2.72	10.14	88.70	0.018	3.72
<i>G. gekko</i>	-102	11.61	31.94	111.77	0.16	2.75
<i>P. madagascariensis</i>		2.55	10.05	85.47	0.015	3.94
<i>G. gekko</i>	-90	11.24	30.84	107.85	0.14	2.74
<i>P. madagascariensis</i>		2.50	10.01	82.45	0.012	3.99
<i>G. gekko</i>	-78	11.38	29.91	103.74	0.12	2.62
<i>P. madagascariensis</i>		2.57	9.99	79.39	0.0088	3.89
<i>G. gekko</i>	-66	12.06	29.09	99.06	0.090	2.41
<i>P. madagascariensis</i>		2.76	10.01	76.1	0.0056	3.62
<i>G. gekko</i>	-54	13.45	28.38	93.24	0.061	2.11
<i>P. madagascariensis</i>		3.14	10.07	71.91	0.0017	3.21
<i>G. gekko</i>	-42	15.99	27.93	85.19	0.023	1.75
<i>P. madagascariensis</i>		3.82	10.24	66.38	-0.0038	2.68

AFRF, angle of the food reaction forces; AJF, angle of the joint forces; BF, bite forces; FRF, food reaction forces; JF, joint forces; RemM, remaining moment at the quadrato-squamosal joint.

Bite forces are calculated for one side only and are only a rough estimate of the actual bite forces.

Positive moments indicate a tendency to rotate the quadrate backwards.

Because the orientation of the food reaction forces is unpredictable, results are given for an entire range of orientations (AFRF).

is caused simply by the activation of the jaw closers during biting (see also Iordansky, 1996). Moreover, it seems to be a self-reinforcing system: the more the system is retracted, the more it will tend to retract itself.

One unexpected conclusion that can be drawn from the model is that, in the protracted configuration, food reaction forces pointing anteriorly correspond with a relatively efficient bite. Similarly, in the retracted configuration, food reaction forces pointing posteriorly correspond with a relatively efficient bite. Since these species possess small peg-like teeth oriented perpendicular to the lower or upper jaws, either anteriorly or posteriorly food reaction forces will be induced simply by the configuration of the cranial system, which will result in relatively low joint forces for a given bite force. Low joint forces are probably advantageous because they reduce the stress on the kinetic joints.

The other, rather unexpected, finding is that simple jaw opening (i.e. activation of the m. depressor mandibulae) automatically induces protraction of the kinetic system. The fact that the m. protractor pterygoidei (which also protracts the kinetic system) is actually activated simultaneously with the jaw opener (Herrel et al., 1999) suggests that skull mobility is actively exploited and indicates some functional advantage to the protraction of the kinetic system.

Functional implications

As noted by Smith (1993), any explanation of the functional

significance of cranial kinesis (being a cyclical and active phenomenon) should address both the protraction and the retraction of the system. Previous hypotheses often provided an explanation for only the retraction component (e.g. Rieppel, 1979). Moreover, any discussion of a proposed functional significance should be related to the use of the system. Because cranial kinesis is most pronounced during prey capture and prey reduction stages (Herrel et al., 1999), functional explanations should focus on the actions of cranial kinesis during these stages. Given the output of our mathematical models, we can speculate on the functional significance of coupled kinesis in the geckoes examined here. The retraction component of the system seems to be a relatively easy phenomenon to explain. Not only does this increase the bite forces that can be exerted on the prey, it also decreases the joint forces relative to the bite forces for the food reaction forces most likely to be encountered.

Although the function of protraction of the system might seem less obvious at first sight, our model indicates that m. protractor pterygoidei activity is not essential, but will probably increase the protraction speed considerably. The functional advantages associated with a coupled four-bar linkage system are much faster jaw opening and closing (possibly allowing the animals to exploit more agile prey items). Kinematic data for geckoes indicate that the jaw cycle time is reduced by as much as 30% (e.g. compare data for *P. madagascariensis* in Herrel et al., 1999 with data in

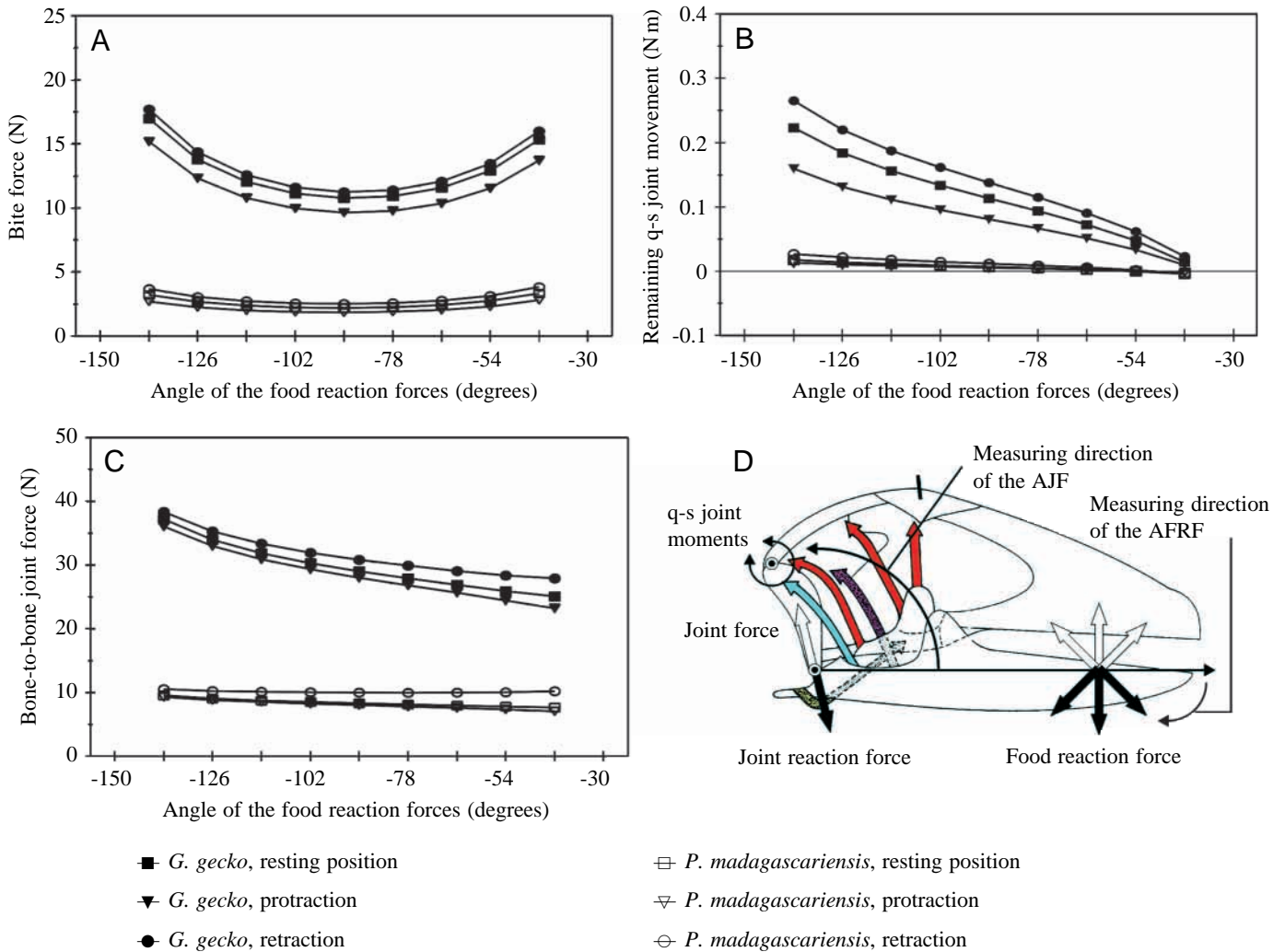


Fig. 3. Results of the static bite modelling. Although the absolute values differ for the two gecko species studied, the observed trends are similar. (A) Bite forces, (B) the remaining quadrato-squamosal joint moments and (C) the bone-to-bone joint forces for the two species studied are plotted for different food reaction force angles. (D) A schematic representation of the static bite model with the skull in the retracted configuration. Coloured arrows represent forces. Red arrows represent the external adductor complex, the purple arrow represents the pseudotemporal muscle, the light blue arrow represents the posterior adductor and the yellow arrow represents the pterygoid muscle complex. AJF, angle of the joint forces; AFRF, angle of the food reaction forces; q-s, joint moments, moments calculated about the quadrato-squamosal joint. Filled symbols, *Gekko gekko*; open symbols, *Phelsuma madagascariensis*; squares, resting position; triangles, protraction; circles, retraction. The short black line at the top of the skull in D represents the mesokinetic axis.

Herrel et al., 1996, for an agamid lizard feeding on similar prey).

Why did the skull not become fixed in its retracted state? That way, the animals could always exert relatively high bite forces. However, the resulting reduction in opening and closing speed could then only be counteracted by adjusting the moment arm of the jaw openers and/or closers at the expense of the force efficiency of the system (a trade-off between speed and force). In addition, a number of functional constraints seem to arise for a gecko skull in a retracted configuration. First, during the retraction phase, the eye is pushed into the orbit, thus obstructing normal vision. Second, fixation of the skull in a retracted position would require both strong ossifications of the intracranial joints and a strong

ligament or bony strut fixing the quadrate relative to the snout (decreasing the space available for the jaw muscles). Moreover, the height of the skull increases considerably during retraction, and this would make it impossible for the animal to hide in tight cracks or underneath the bark of trees (an ability that has been proposed to be one of the major driving forces in the evolution of kinetic skulls; see Arnold, 1998). Finally, having a high skull would tend to raise the centre of gravity away from the substratum, which is unfavourable for climbing species (Vanhooydonck and Van Damme, 1999). Yet, by making the system go through cyclical protraction–retraction cycles, the animals are able to exploit the advantages of having a flat head (climbing, hiding in cracks), fast jaw opening (feeding on agile, elusive prey,

possibly correlated with an arboreal lifestyle) and high bite forces (feeding on larger, harder prey). Although this might provide a mechanistic explanation for the kinetic cranial system in geckoes, the origin of the system remains to be investigated further.

Evolutionary reconstruction

As suggested by the currently available data on lizard cranial kinesis, true coupled kinesis has been demonstrated in a limited number of groups only (Impey, 1967; Throckmorton, 1976; Throckmorton and Clarke, 1981; Smith, 1980, 1982, 1984; Frazzetta, 1983; Smith and Hylander, 1985; Patchell and Shine, 1986; Condon, 1987). What allowed these groups, and in particular geckoes, to develop a highly kinetic skull? An answer might be found by examining the evolutionary history of geckoes. Apparently, three constructional novelties arose in the evolutionary history of geckoes: (i) the quadrate was freed from the snout unit through the loss of the lower temporal bar (a plesiomorphic character for all lizards, see also Rieppel and Gronowski, 1981); (ii) the supratemporal bar was lost; and (iii) the postorbital bar was lost. On the basis of the mechanics of the system (i.e. forceful biting), all these might induce mobility in the skull. Whereas the lower temporal bar braces the quadrate to the snout, the upper temporal bar connects the jugal to the back of the skull, decreasing the potential for flexion of the skull at the mesokinetic axis. The postorbital bar, which consists of the jugal and postorbital bones, firmly attaches the maxilla to the parietal, again reducing the potential for, or even preventing, flexion at the mesokinetic axis in primitive lizards such as iguanians (see El Toubi, 1947; Jollie, 1960; Herrel et al., 1998a,b).

The origin of these losses of cranial elements can largely be explained by constructional constraints. To increase the amount of force produced by the jaw muscles, at least two options exist. First, by acquiring a high degree of pennation, the total amount of force produced for a given muscle volume can be increased. Second, the total muscle volume can increase, which implies a reduction of those cranial elements (such as the lower and upper temporal bars) that limit the increase in jaw adductor volume (for an elaboration on this argument, see Rieppel and Gronowski, 1981; Herrel et al., 1998a). Whereas in most lizards both options are used (i.e. extreme pennation and loss of the lower temporal bar), in geckoes the degree of pennation of the jaw adductors remains low, but the upper temporal bar is lost. The advantage of reducing (the primitive condition being a high degree of pennation; see Gomes, 1974) the basal aponeuroses is an increase in the individual fibre lengths, creating relatively fast, yet strong, muscles (see also Rieppel and Gronowski, 1981).

The loss of the postorbital bar, in contrast, cannot readily be explained by constraints imposed by an increase in jaw adductor mass. However, it might be explained by examining the ecology of the lizards in question. It has been demonstrated that nocturnality is a primitive trait for geckoes (see Autumn et al., 1994, 1997) and nocturnal geckoes have larger eyes than

diurnal ones (Werner, 1969), so the loss of the post-orbital bar might be the result of its constraint on the size of the eye. For nocturnal animals that actively hunt for prey (Autumn et al., 1994), the ability to see in low light conditions seems crucial and, because an increase in eye size improves night vision (Werner, 1969), this might have been a considerable selective drive in ancestral gekkonoids. The only way that the size of the eye can increase considerably without compromising other sensory functions is by the loss of the postorbital bar.

Although the driving forces discussed above remain speculative, early geckoes probably possessed a skull without lower temporal, upper temporal and postorbital bars. This must have induced an enormous, and potentially deleterious, mobility in the skull, given the magnitude of the joint forces observed during forceful biting (see Tables 1–3). By creating flexion zones within (e.g. the palatine) and between (e.g. between the parietal and frontal bones) bones, these forces could be absorbed by the system. By coupling the cranial units with the quadrate, and thus the lower jaw, a derived weakness was turned into a functional advantage for the animals (fast jaw cycle, high bite forces and a flat skull).

Still, this evolutionary scenario holds only in the case of geckoes and cannot, as a whole, be extrapolated to other lizards. This leaves the coupled kinesis in varanid lizards and other anguimorphs (see Smith, 1980, 1982; Frazzetta, 1983; Smith and Hylander, 1985; Condon, 1987) to be explained. Other constraints probably operated on the system in these groups because these animals are generally not nocturnal and do show a high degree of pennation in the jaw adductors. One element that might be involved in the reduction of skeletal elements in the skull of varanids might be their kinetic inertial feeding mode (see Smith, 1982). Considerable accelerations have to be imparted upon the prey, so a decrease in the overall weight of the skull, as observed in crocodylians (Cleuren, 1996), would undoubtedly be advantageous for these lizards. Again, this would imply that kinesis in these animals is not so much functional *per se* but, instead, a consequence of the reduction of cranial elements. More experimental data need to be gathered on a wider range of lizards before conclusive remarks on the functional significance of lizard cranial kinesis can be made.

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