CRANIAL KINESIS IN GEKKONID LIZARDS

A. HERREL1,* , F. DE VREE1, V. DELHEUSY2 AND C. GANS3

1Department of Biology, University of Antwerp (UIA), Universiteitsplein 1, B-2610 Antwerp, Belgium, 2Institut de Zoologie, Université de Liège, 22 Quai Van Beneden, B-4020, Liège, Belgium and 3Department of Zoology, College of Natural Sciences, University of Texas, Austin, TX 78712, USA

*e-mail: aherrel@uia.ua.ac.be

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Summary

Cranial kinesis was studied in two species of gekkonid lizard, Gekko gecko and Phelsuma madagascariensis, using cineradiography and electromyography. The skull of these geckoes showed the three types of kinesis described by Versluys at the beginning of this century: streptostyly, mesokinesis and metakinesis. In accordance with the later model of Frazzetta, the skull of these animals can be modelled by a quadratic crank system: when the mouth opens during feeding, the quadrate rotates forward, the palato-maxillary unit is lifted and the occipital unit swings forward. During jaw closing, the inverse movements are observed; during crushing, the system is retracted beyond its resting position. The data gathered here indicate that the coupled kinesis (streptostyly + mesokinesis) is most prominently present during the capture and crushing cycles of feeding and is largely absent during late intraoral transport, swallowing, drinking and breathing. The electromyographic data indicate a consistent pattern of muscular activation, with the jaw opener and pterygoid protractor always active during the fast opening phase, and the jaw closers active during closing and crushing. Our data generally support the model of Frazzetta. Although the data gathered here do not allow speculation on the functional significance of the kinesis, they clearly provide some key elements required for a further investigation of the functional and adaptive basis of the system.

Key words: cranial kinesis, morphology, gekkonid, lizard, Gekko gecko, Phelsuma madagascariensis, cineradiography, electromyography.

Introduction

The function of the kinetic apparatus in the vertebrate 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, kinesis occurs whenever the upper jaw and palate, or the maxillary segment, can move relative to the braincase, or axial segment. Generally, cranial kinesis is considered as a plesiomorphic feature of the vertebrate skull and is widespread among modern tetrapods (Iordansky, 1990).

The placing of the kinetic joints varies among vertebrate groups. The early osteichthyans, both sarcopterygians and actinopterygians, developed a mode of intracranial mobility in which the ethmosphenoidal section of the braincase moved relative to the otico-occipital section (Millot and Anthony, 1965; Thomson, 1967; Nelson, 1970; Bjerring, 1973). Recent amphibians, Gymnophiona, Anura and Urodela, possess one or several types of kinesis (Iordansky, 1990). The most common form includes medio-lateral movements of the maxillo-buccal segment with respect to the central axial segment (Edgeworth, 1935; De Villiers, 1938; Wake and Hanken, 1982). In many Anura and Urodela, this pleurokinesis is supplemented by upward and downward movements of the premaxillary or rhinal segments.

Within amniotes, cranial kinesis is most prominent in the Archosauromorpha (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; Zweers, 1982). Within the lepidosaurs, varying degrees of cranial kinesis are observed, with snake craniums being the most kinetic (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): (1) movement of the quadrate or jaw suspension (streptostyly); (2) movement of the braincase relative to the rest of the skull (metakinesis); and (3) movement of the palato-maxillary unit at the frontal–parietal joint (mesokinesis). Amphikinesis is the combination of meso-and metakinesis (Frazzetta, 1962).

Frazzetta (1962) proposed a model for an amphikinetic skull that he believed to be the general condition observed in lizards. His model is based on a quadratic crank mechanism (basic four-bar linkage). If one of the links is fixed, then a force...
applied to one of the other links moves the system as a whole. In the model, the skull is divided into four units (palato-maxillary unit, pterygoid unit, parietal unit and quadrate unit; for more details, see Frazzetta, 1962, 1983). The implications of the model are that, as the jaws open, the quadrate and pterygoid units are moved forwards and the palato-maxillary unit is lifted at the mesokinetic joint. In addition, a rotation of the occipital unit is thought to take place around the metakineti c axis running through the paraoccipital processes. As the jaws close, the quadrate and pterygoid bones are withdrawn, the palato-maxillary unit is lowered (retracted) and the occipital unit rotates posteriorly.

Despite intensive investigations during the last decade or two (for an overview, see Smith, 1993), no consensus has been reached concerning the applicability of the model of Frazzetta (1962) to all lizards. One of the major drawbacks in the analysis of cranial kinesis is that comparative analyses are extremely limited and, if present, are generally based on manipulations of ligamentous preparations (e.g. Iordansky, 1990), which often overestimate the level of kinesis observed in vivo (A. Herrel, personal observations). Some groups of lizards with loosely constructed skulls, such as gekkotans, have never been examined in detail (but see Patchell and Shine, 1986; De Vree and Gans, 1989); an analysis of these animals might provide fruitful insights into the evolution of intracranial kinesis within lizards (see Smith, 1993).

The aim of this study is to examine cranial kinesis in this group of lizards, because the presence of a pronounced kinesis was indicated previously (Gekkonidae; De Vree and Gans, 1989). In the present study, the movements of the kinetic system and the muscular activities that cause these movements will be examined in detail for two species of gekkonid lizard: Gekko gecko and Phelsuma madagascariensis. These data will provide the basis for a functional analysis of the kinetic system in geckoes, allowing speculations on the origin and adaptive significance of intracranial kinesis in geckoes.

Materials and methods

Specimens

Three adult specimens of the species Gekko gecko (snout–vent length, SVL, 130±3 mm; mean ± s.d.) and three adult Phelsuma madagascariensis (SVL 110±3 mm) were used in the experiments. Each lizard was isolated in an acrylic cage (300 mm×100 mm×100 mm) on a 12h:12h L:D photoperiod 2 or 3 weeks before filming and was offered water and food consisting of grasshoppers, crickets and mealworms ad libitum. The environmental temperature varied from 26°C during the day to 20°C at night. An incandescent bulb provided the animals with a basking place at higher temperature (35°C). During the recording sessions, live prey items (grasshoppers, Locusta migratoria, 3.0–4.0 cm; crickets, Acheta domestica, 1.5–2.5 cm; newborn mice, Mus musculus, 3.0–4.0 cm) were placed less than 5 cm from the lizard. Drinking behaviour was recorded under similar circumstances after placing 3–5 drops of water just in front of the animal’s head. Breathing was observed between feeding trials, and threat behaviour was readily elicited by approaching the animals and opening the door of the cage.

Anatomy

Fresh and preserved specimens of adult G. gecko (N=7) and P. madagascariensis (N=5) were used for dissection, to describe the skull morphology and to characterize jaw muscles. Drawings were made using a Wild M3Z dissecting microscope provided with a camera lucida.

Cineradiography

Cineradiography was accomplished with a Siemens Tridoros-Optimatic 880 X-ray apparatus equipped with a Sirecon-2 image intensifier. Feeding bouts were recorded laterally with an Arriflex 16 mm ST camera equipped with a 70 mm lens at a film speed of 50 frames s⁻¹. Before cineradiography, small metal markers were inserted subcutaneously in the neck (1), on the occipital bone (2), at the base (3) and the top (4) of the quadrate, on the parietal (5) and frontal (6) bones, at the front (7) and back (8) of the upper jaw, on the pterygoid bone (9), on the basiptyergoid process (10), at the front (11) and back (12) of the lower jaw, and in the tongue (13) (Fig. 1A). All skeletal markers were glued into small holes drilled into the respective bone (dental drill, Supra Combi, model 27 195c). During the implantation of the radio-opaque markers, animals were anaesthetised using an intramuscular injection of Ketalar (200 mg kg⁻¹ body mass). Placement of the markers was checked using dorsoventral and lateral X-rays before and after the recording sessions and by dissection in two animals. Results were obtained for more than 10 feeding sequences for each species.

To describe the different types of cranial kinesis, vertical (y) and horizontal (x) coordinates of each marker were recorded frame by frame, and the following angles and displacements were calculated for both species (Fig. 1B). Streptostylic angle (α), the angle subtended by the lines created by the markers on the quadrate and the markers on the supraoccipital and basiptyergoid process. A decrease in α corresponds to a forward movement of the quadrate relative to the occipital unit. Mesokinetic angle (β), the angle subtended by the lines created by the markers on the supraoccipital and the parietal, and those on the frontal and premaxillary bones. An increase in β corresponds to a lifting of the palato-maxillary unit relative to the parietal. Gape distance and gape angle, the distance between the anteriormost markers of the upper and lower jaw, and the angle subtended by the lines created by the markers on the upper and lower jaws, respectively. Relative displacement between the pterygoid and basiptyergoid bones, the distance between the markers on the basiptyergoid and pterygoid bones indicating sliding of the pterygoid relative to the occipital unit, was measured in P. madagascariensis only. Anterior-posterior and dorso-ventral tongue movements relative to the anterior marker on the lower jaw were measured in P. madagascariensis only.

On the basis of plots of the above variables and the y
performed on the kinematic data from the three individual lower jaw markers; cycles were retained if the change was less (indicated by slight changes in the distance between the two of the animal away from the lateral plane during most cycles. Analysis of the kinetic movements because of a slight deflection. Unfortunately, only 12 of these could be used for the P. madagascariensis were retained for the quantitative analysis. pt. pterygoid relative to the basipterygoid (pterygoid sliding 2), and the posteriad displacement of the pterygoid relative to the basipterygoid (pterygoid sliding 1), and the anteriad displacement of the mesokinetic angle. d, dorso-ventral tongue displacement; b, pterygoid–basipterygoid distance; c, anterio-posterior tongue displacement; d, dorso-ventral tongue displacement; α, streptostylic angle; β, mesokinetic angle. Fig. 1. (A) Schematic drawing of the skull of Gekko gecko to illustrate the position of the radio-opaque markers (numbered 1–13) inserted into the cranial elements to help visualise intracranial movements. (B) Variables measured to illustrate intracranial movements (see Materials and methods for details). a, gape distance; b, pterygoid–basipterygoid distance; c, anterio-posterior tongue displacement; d, dorso-ventral tongue displacement; α, streptostylic angle. Coordinates of the anterior upper and lower jaw markers versus time, a number of additional variables were determined: the duration of the kinematic phases slow opening I and II (SOI, SOII), fast opening (FO), fast closing (FC), slow closing/power-stroke (SC/PS), the maximal gape distance at the end of the FO phase (GD), the time to maximal gape (TMG), the anteriad rotation of the quadrate during opening (streptostylic), the posteriad rotation of the quadrate during closing (strepto2), the dorsiflexion of the snout (meso1), the ventroflexion of the snout (meso2), the anteriad displacement (sliding) of the pterygoid relative to the basipterygoid (pterygoid sliding 1), and the posteriad displacement of the pterygoid relative to the basipterygoid (pterygoid sliding 2).

Thirty-two intraoral transport cycles from three individual P. madagascariensis were retained for the quantitative analysis. Unfortunately, only 12 of these could be used for the analysis of the kinetic movements because of a slight deflection of the animal away from the lateral plane during most cycles (indicated by slight changes in the distance between the two lower jaw markers; cycles were retained if the change was less than 5%). As a multivariate analysis of variance (MANOVA) performed on the kinematic data from the three individual P. madagascariensis indicated no individual effects (Rao’s r=0.49, d.f.=14,44; P=0.22), data for all individuals were pooled (Table 1). As the G. gecko specimens used during the experiments showed a strong tendency to tilt their heads during grasshopper feeding sequences, no quantitative analysis was possible. As lateral head movements were restricted during one of the feeding sequences where a cricket was offered to an animal, a quantitative description of the intracranial displacements during cricket feeding in one animal is represented in Table 1. In addition, at least one perfectly lateral cycle for each animal feeding on grasshoppers was obtained, and the qualitative patterns could therefore be compared with those for P. madagascariensis. Here too, movements about intracranial joints were highly similar for all individuals.

Electromyography

Before electrode implantation, the animals were anaesthetised using an intramuscular injection of Ketalar (200 mg kg⁻¹ body mass). Bipolar 25 cm long electrodes were prepared from Teflon-insulated 0.065 mm Ni–Cr wire. The insulation was scraped away at the tip, exposing 1 mm of electrode wire. The electrodes were implanted percutaneously into each muscle belly, using hypodermic needles with 2 mm of the electrode bent back as it emerged from the needle barrel. Electrode inter-tip distances were approximately 1 mm. Electrodes were placed in the following muscles: the m. depressor mandibulae, the m. adductor mandibulae externus (all parts), the m. pterygoideus medialis and the m. pterygoideus lateralis, the m. protractor pterygoidei, the m. genioglossus and the m. spinalis capitis. Electrode placement was checked using dorsal and lateral X-rays and by dissection in two animals.

Electrical signals were amplified 2000 times with Tektronix (Beaverton, OR, USA) 26A2 differential preamplifiers (range 100 Hz to 10 kHz) and Honeywell (Denver, CO, USA) Accudata 117 d.c. amplifiers and recorded on a Honeywell 96 FM 14-channel tape recorder (medium bandpass) at a speed of 19.05 cm s⁻¹.

More than five feeding sequences for all individuals (both G. gecko and P. madagascariensis) were obtained. Electromyographic recordings from 6–8 muscles were obtained simultaneously during all recording sessions. Muscles were considered active if the level of activity recorded exceeded the baseline activity by more than threefold. Increases in the intensity of muscle activity are considered as an increase in both the amplitude (A) of the signal and the number of spikes (S) observed (SxA). Muscle activity was classified as low if the activity level (SxA) was less than 30% of the maximal activity level of that muscle during that recording session. Medium activity levels were considered to be between 30% and 60% of the maximal activity, and high activity levels were those exceeding 60% of the maximal activity observed for that muscle during a particular recording session. Because activity levels may vary among recording sessions, animals and species (e.g. due to electrode placement), no statistical comparisons were made. However, qualitative patterns show strong similarities (both among individuals and species) in the way that the muscles are recruited.
Results

Morphology

Only a short description of the predominant osteological features, intracranial joints and functional properties of the jaw musculature in geckoes will be provided here. A detailed analysis of these elements will be published elsewhere.

Osteology

The general shape of the skull in the geckoes studied here is broad, flat and elongated. The widest part of the skull is situated at the level of the pterygoid bone, just caudal to the orbit. There is a significant reduction of the bones in the temporal and orbital regions (absence of supratemporal; reduction of jugal and squamosal bones, and fusion of postorbital and postfrontal bones; see Camp, 1923; Webb, 1951; Kluge, 1967), creating a lateral fenestra occupied by the adductor musculature and the highly developed eyes. The different types of kinesis are reflected in a number of intracranial joints in the skull of adult animals: (1) a synchondrosis between the paraoccipital and quadrate bones, and between the squamosal and quadrate bones, and a syndesmosis between the pterygoid and quadrate bones; (2) the mesokinetic joint (synchondrosis) between the frontal and parietal bones; (3) the metakinetonic joint between pro-otic and parietal bones, and a typical synovial joint between the basipterygoid and pterygoid bones.

Myology

The jaw muscles in lizards have been described in a number of reviews (Brock, 1938; Haas, 1973; Gomes, 1974) and will be discussed briefly below. The traditional nomenclature of the external adductor, which is based on the position of the jaw muscles relative to the basal aponeurotic complex (Lakjer, 1926; Haas, 1973; Gomes, 1974), will not be followed here because of the strong reduction of the basal aponeuroses. However, four functional subdivisions of the external adductor could be recognised on the basis of differences in the origin and insertion of groups of muscle fibres.

The most superficial part of the m. adductor mandibulae externus (MAME1) (Fig. 2A) originates in the temporal region (supratemporal, parietal and posterior side of the postorbitofrontal bone) and inserts on the dorsolateral side of the lower jaw. The muscle is covered by the superficial aponeurosis. MAME2 (Fig. 2B) originates at the dorsal aspect of the quadrate bone and inserts at the posteromedial side of the lower jaw. The third part of the external adductor (MAME3, Fig. 2A,B) originates at the neurocranium, the parietal and the squamosal bones. One portion of this muscle inserts at the ‘bodenaponeurosis’ (=coronoid aponeurosis sensu Lakjer, 1926) and the other part inserts at the posteromedial part of the lower jaw. MAME4 (Fig. 2B) is a short muscle that runs just posterior and medial to the eye. Its insertion is restricted posteriorly by the bodenaponeurosis, and the fibres originate on the parietal bone and insert onto the most superficial aponeurosis of the coronoid.

The posterior adductor (MAMP, Fig. 2B,C) is strongly reduced in geckoes. It originates at the quadrate bone by means of a short aponeurosis and inserts at the medial aspect of the lower jaw.

The pseudotemporal muscle (MPsT, Fig. 2C) is separated from the external adductor by the trigeminal nerve, as in other lizards. It originates at the upper part of the epipterygoid bone and inserts at the inner side of the lower jaw.

The pterygoid muscle (MPt, Fig. 2A) can be divided into a deep, medial part and a superficial, lateral part. The deep part runs from the ventral side of the pterygoid to the medioventral side of the articular bone. The superficial part runs posterolaterally and curves around the ventral edge of the mandible to insert on the lateral surface of the articular bone.

The musculus depressor mandibulae (MDM, not shown on Fig. 2) consists of two bundles. The superficial bundle inserts on the postarticular region of the mandible, and its fibres originate at the anterolateral side of the superficial aponeurosis covering the m. spinalis capitis (MSCa, Fig. 2B). The thin deeper bundle (=m. paraoccipitomandibularis) originates on the outermost edge of the parietal bone and inserts on the retroarticular process by means of a short tendon.

The musculus levator pterygoidei (MLPt, Fig. 2C) originates on the ventral side of the parietal bone and inserts on the dorsal side of the pterygoid at the pterygoid–epipterygoid articulation.

The musculus protractor pterygoidei (MPPt, Fig. 2C) originates on the basisphenoid and pro-otic bones and inserts on the dorso-medial side of the pterygoid bone, posterior to the epipterygoid.

Cineradiography

General

Movements of the cranial units were examined in both species during a number of behavioural patterns such as breathing, drinking, feeding and the typical threat posture. Significant movements of the different units relative to one another were observed only during threat display and during feeding. Within a feeding bout, kinesis was most prominent during the capture cycle (as indicated by a qualitative analysis of the cineradiographic recordings in both species) and the first 2–3 intraoral transport cycles. The extent of the movements of the cranial units was also strongly dependent on the type of food eaten. While eating relatively soft prey, such as newborn mice or crickets, the movements were less prominent than during feeding cycles in which large grasshoppers were offered as prey (e.g. compare data in Table 1 for G. gecko feeding on crickets and P. madagascariensis while eating large grasshoppers). As these observations could have been due to interspecific differences, they were confirmed by qualitative analyses of cineradiographic recordings of P. madagascariensis eating crickets and of G. gecko eating grasshoppers.

During a feeding bout, the animals always captured prey items by using the jaws only. Lingual prehension was never observed. A typical feature of a capture cycle is the pronounced lateral head deflection that results in the prey being grasped.
Cranial kinesis in gekkonid lizards

The subsequent intraoral transport stage is characterised by a number of crushing bites (recognisable by the intensity of activation of the jaw closers) interspersed with transport and/or repositioning cycles. Once the prey is adequately reduced (which may involve vigorous lateral head-shaking), the swallowing stage starts. During swallowing, intracranial movements are strongly reduced and the prey is pushed into the oesophagus by repeated tongue protraction–retraction cycles. Swallowing cycles are kinematically different from intraoral transport cycles because of a reduced gape distance and the absence of the FO and SC/PS phases. The following description of the movement patterns is based upon intraoral transport cycles, with an emphasis on crushing cycles. No quantitative analysis of the cineradiographic recordings during capture was possible because of the lateral deflection of the head described above. Consequently, the movement patterns of the cranial units during capture will not be described in any detail here. However, a considerable amount of movement between the cranial units was obvious from a qualitative analysis of such capture cycles.

Intraoral transport cycles during feeding can be divided into five distinct phases, primarily on the basis of the velocity changes during mouth opening (see Bramble and Wake, 1985). During the slow opening phase (SO), the mouth is opened slowly. This phase is followed by fast mouth opening (FO). When maximal jaw opening is reached, the jaws are closed rapidly (fast closing phase, FC) until the jaws touch the prey, which initiates the slow closing/power-stroke phase (SC/PS). The SO phase can usually be subdivided into two parts (SOI...
Variables directly related to the movements of the cranial units

<table>
<thead>
<tr>
<th>Variable</th>
<th>P. madagascariensis</th>
<th>G. gecko</th>
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</thead>
<tbody>
<tr>
<td>Jaw cycle variables</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SOI (ms)</td>
<td>120.8±42.9 (32)</td>
<td>108.0±33.5 (5)</td>
</tr>
<tr>
<td>SOII (ms)</td>
<td>1349.0±531.1 (32)</td>
<td>648.0±197.8 (5)</td>
</tr>
<tr>
<td>FO (ms)</td>
<td>48.1±10.5 (32)</td>
<td>68.0±11.0 (5)</td>
</tr>
<tr>
<td>FC (ms)</td>
<td>53.7±14.0 (32)</td>
<td>60.0±10.0 (5)</td>
</tr>
<tr>
<td>SC/PS (ms)</td>
<td>70.0±28.0 (32)</td>
<td>112.0±106.4 (5)</td>
</tr>
<tr>
<td>GD/GA (mm degree⁻¹)</td>
<td>9.4±1.5 (32)</td>
<td>28.1±3.6 (5)</td>
</tr>
<tr>
<td>TMG (ms)</td>
<td>1498.4±552.1 (32)</td>
<td>824±208.5 (5)</td>
</tr>
</tbody>
</table>

Values are means ± s.d. (N).

Note that these data represent means for three P. madagascariensis and one G. gecko.

The sliding of the pterygoid was not measured in G. gecko.

Electromyography

A generalised muscle activity pattern is described below with differences between the two species indicated where present. Because most of the data were gathered for intraoral transport cycles, detailed activation patterns in relation to intracranial movements are discussed for these cycles only. For both capture and threat displays, only a short qualitative description of the electromyographic patterns will be provided.

Intraoral transport

During the SO phase of an intraoral transport cycle, the tongue protractor (MGG, m. genioglossus) shows strong and increasing activity. During SOII, the MPPt shows low-level activity (5% of maximum activity), which increases towards the beginning of the FO phase. The MDM usually also shows low-level activity during the SOII phase (see Fig. 4). The sudden maximal recruitment of the MDM, MSCa and MPPt indicates the start of the FO phase. These muscles reach their
maximal activity (both number of spikes and spike amplitude) at the beginning (MDM), half-way through (MPPt) or near the end (MSCa) of this phase. The abrupt cessation of activity in these muscles indicates the achievement of maximal gape and...
the onset of the FC phase (Figs 4, 5). Some of the jaw closers (MAME3, MPtlat, MPtmed, MPsT) may show weak (3–15 % of maximum) but increasing activity during the SOII and FO phases. Shortly (less than 10 ms) after the end of the activity in the jaw openers, all jaw adductors show a bilaterally simultaneous activity of high amplitude (60–80 % of maximum amplitude), although in P. madagascariensis only the MPsT reaches its highest activity level during the FC phase. The other jaw adductors reach their highest activity during the SC/PS phase (Fig. 4). The activity in these muscles may last for up to 300 ms. In Gekko gecko, the SC/PS phase is characterised by repeated pulsatile activity (6–10 periods of activity of 10–35 ms duration; see Fig. 4). In P. madagascariensis, such pulsatile activity was never observed while feeding on
similarly sized food items. In *G. gecko*, the MDM and the MPPt also occasionally showed this pulsatile activation pattern (simultaneous with that in the jaw closers, but the duration of the activity bursts being shorter, 5–25 ms) during the SC/PS phase. The activity of these muscles in *P. madagascariensis* was of moderate to low intensity, but never pulsatile in the SC/PS phase. After the SC/PS phase, there is a period of inactivity in the jaw muscles, during which the cranial elements return to their resting position.

The pattern described above is characteristic of the pure crushing cycles in which pronounced adductor activity occurs during the SC/PS phase. During other intraoral transport cycles, the overall pattern is similar, but the activation of the jaw closers is less intense (mainly a decrease in amplitude) and of shorter duration, and the activation of the MPPt and the MDM is less pronounced (a decrease in the amplitude of the signal). Near the end of the intraoral transport stage, the activity in the jaw openers (MDM, MSCa), the MPPt and the jaw closers (MAME, MPt) gradually decreases.

**Capture**

The muscle activity patterns during prey capture were similar to those observed during intraoral transport, although the muscle activities during the opening and closing phases were longer during prey capture (up to 30 times longer). The onset of activity in the MPPt was notably earlier than the onset of activity in the MDM during capture. When activity began in the MDM, the MPPt had already reached near-maximal activity levels (both amplitude and number of spikes). During the vigorous lateral head-shaking that accompanies most capture cycles, the MAME and the MPt showed prolonged activity. A repositioning cycle was sometimes observed shortly (50 ms) after the start of adductor activity, as was the occasional presence of a second PS phase without previous mouth opening.

**Threat display**

During threat display, the jaws are opened extremely wide (60°), and the maxillary unit is maximally elevated. During such display, the MPPt and the MDM are the only muscles to show any activity. Both muscles stay active throughout the display. No adductor activity is observed during jaw closing.

**Discussion**

**Comparisons with other studies**

The skulls of *Gekko gecko* and *Phelsuma madagascariensis* clearly show the three types of cranial kinesis described by
Versluys (1910, 1912): streptostyly, mesokinesis and metakinesis. When these geckoes open their mouth during capture or intraoral transport cycles, the quadrate rotates forwards at its joint with the paroccipital (streptostylic angle decreases; Figs 3, 6), and the palato-maxillary unit (premaxillary, maxillary, prefrontal, frontal, nasal, vomer and palatine bones) lifts up at the mesokinetic joint (mesokinetic angle increases) relative to the parietal unit (parietal and squamosal bones) (Figs 3, 6). As a result of these movements, a forward displacement of the pterygoid relative to the basipterygoid bone is observed (Figs 3, 6). During jaw closing (FC, SC/PS), the elements of the kinetic apparatus execute the opposite displacements (Figs 3, 6). Ventröflexion beyond the resting position is usually observed while the prey is crushed between the jaws (SC/PS stage). These displacements are very similar to those described for Gerrhonotus multicarinata (Frazzetta, 1983).

These results for geckoes can be compared with those published for other species. However, it should be noted that a direct comparison is difficult because different researchers used different techniques and the animals ate different food items. In addition, the age of the individual will influence the degree of kinesis in several species. In P. madagascariensis during intraoral transport, the palato-maxillary unit shows a mean dorsiflexion of 23.5±8.7° during mouth opening (Table 1). In contrast, Condon (1987; Varanus niloticus) and Rieppel (1979; V. bengalensis) reported a maximum of 1–2° and 9° of dorsiflexion, respectively, during the inertial feeding cycles when the mouth opens. In all species studied, ventroflexion seems to be larger than dorsiflexion (P. madagascariensis: 25.8±8.2°; V. niloticus: 1–4°, Condon, 1987; V. bengalensis: 15°, Rieppel, 1979). In accordance with Frazzetta’s model (1962) and the results described above, Smith and Hylander (1985) measured tensile stresses at the mesokinetic joint that indicated a retraction (ventroflexion) of the palatomaxillary unit during isometric biting in V. exanthematicus.

Whereas experimental results related to meso- and metakinesis are rather scarce, streptostyly has been reported for several species. In Uromastix aegyptius, Amphibolurus barbatus (Agamidae; Throckmorton, 1976; Throckmorton and Clarcke, 1981), Gerrhonotus multicarinatus (Anguidae; Frazzetta, 1983), V. exanthematicus (Smith, 1982) and the gekkonids examined in the present study, antero-posterior movements of the quadrate are observed. In all lizards studied, the quadrate rotates forwards during mouth opening and backwards when the jaws are closing. However, in A. barbatus, V. exanthematicus and U. aegyptius, streptostyly seems to be independent of the other types of kinesis. Thus, meso- and metakinesis are not necessarily linked with streptostyly, contradicting the model of Frazzetta (1962). In P. madagascariensis and G. gecko, at least, mesokinesis and streptostyly are present and occur in fixed patterns relative to one another (an anteriad rotation of the quadrate invariably corresponds with dorsiflexion). Nevertheless, streptostyly in general may be a plesiomorphic character for lizards, related to the opening of the inferior zygomatic arch (see Rieppel and Gronowski, 1981; Iordansky, 1996), and is probably not coupled to mesokinesis in the majority of lizard families.

In both P. madagascariensis and G. gecko, streptostyly and mesokinesis are coupled, as indicated by the mechanical (morphological) links between the cranial elements and the observed movement patterns. Manipulations of ligamentous preparations clearly indicate that the movement of one segment (e.g. pushing the quadrate forwards) automatically leads to movements of the other elements (e.g. the lifting of the snout). The interspecific differences observed here in the amount of streptostyly versus mesokinesis (see Table 1) indicate either that these species differ in the geometry of the system (i.e. differences in the size of the links within the four-bar system) or that the freedom of movement of the intracranial joints...
differs between these species. The morphological data indicate that the observed interspecific difference is largely due to differences in the free movement space of the quadrate, which is larger in *G. gecko*.

*Functional roles of the cranial muscles*

During mouth opening, in the SOI phase, the three types of kinesis are observed in both *P. madagascariensis* and *G. gecko*, but no activity is present in most of the jaw muscles at this stage. This indicates that the cranial apparatus undergoes largely passive movements during the muscle relaxation that occurs after their contraction during the previous cycle. The low activity levels in the m. protractor pterygoidei (MPPt) alone may aid in returning the system to its resting position. The m. genioglossus is generally the first muscle to become active during mouth opening, and tongue protraction under the prey probably causes the opening of the jaws during the SOI phase (see also Herrel et al., 1996, 1997). The activity in the MPPt, however, ceases rapidly and then restarts simultaneously with that of the jaw opener (MDM) during the FO stage (Figs 4–6). The contraction of the MDM pulls down the lower jaw. Simultaneously, the activity of the MPPt presumably pulls the pterygoid bone forward relative to the basipterygoid and, through the links between the pterygoid and palatine bones, causes elevation of the snout. Additionally, through the link between the pterygoid and quadrate bone, the base of the quadrate moves forwards (streptostyly; see Fig. 6). During these movements, the contraction of the m. spinalis capitis elevates the parietal bone and stabilises the occipital unit (which is crucial if the MPPt is to protract the pterygoid, see Smith and Hylander, 1985; K. K. Smith personal communication).

During mouth closure, the adductor muscles (MAME, m. pseudotemporalis and the m. pterygoideus medialis and lateralis) show two bursts of activity corresponding to the two closing stages FC and SC/PS (Figs 4–6). The strongest (i.e. high-amplitude activity showing maximal numbers of spikes) activity is observed during the SC/PS stage when the prey is crushed between the jaws. The MAME and the MPsT mainly produce the lifting of the mandible. Judging by the orientation of the muscle fibres, the MAME, together with the MPs, causes the backward displacement of the pterygoid bone and, thus, the ventroflexion of the snout unit and the backward rotation of the quadrate (see also Iordansky, 1966, 1970). The activity observed in the MDM and the MPPt during the SC/PS (Figs 4, 5) is probably related to the stabilization of the quadrate-squamosal joint during crushing of the prey. In addition, the activity of the MPPt during the SC/PS stage could play an important role in braking the kinetic system once it has passed its resting position. The contraction of the m. spinalis capitis observed during this stage would again tend to stabilize the cranium. It can therefore be concluded (1) that the forward displacement of the palato-maxillary unit relative to the occipital unit is most likely to be the result of m. protractor pterygoidei activity, and (2) that the m. adductor externus, pterygoideus and pseudotemporalis lift the mandible and presumably simultaneously retract the kinetic system (see also Frazzetta, 1962, 1983; Iordansky, 1970).

*Generality of the observations*

According to Frazzetta (1962) and Iordansky (1990), most lizard families except the chameleons have an amphikinetic skull. However, in three agamid lizards, *A. barbatus* (Throckmorton and Clarke, 1981), *U. aegyptius* (Throckmorton, 1976; Herrel et al., 1998a,b) and *P. stellio* (Herrel et al., 1996, 1998a,b), and two scincids, *T. rugosa* (De Vree and Gans, 1987) and *C. zebrata* (Herrel et al., 1998a,b), no significant movement was detected at the fronto-parietal joint by cineradiography. Results concerning the extent of kinesis in varanid lizards are rather inconsistent because of differences in the species studied, the food items presented and the techniques used (Condon, 1987; Rieppel, 1979; Smith, 1980, 1982; Smith and Hylander, 1985). Studies on gekkonid lizards (De Vree and Gans, 1989; present study) show that, at least in this family, streptostyly and mesokinesis are present and coupled. The hypothesis that the amphikinetic skull is a general feature in lizards should be investigated using standardised experimental methods on live animals and within a strict phylogenetic framework, rather than by manipulations on preserved specimens. In addition, further experimental work on the exact nature of the metakinetic movements in the skull is badly needed.

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*References*


