

CRANIAL KINESIS IN GEKKONID LIZARDS

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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 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; Zweers, 1982). Within the lepidosaurians, 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 metakinetic 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 \pm 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 \times 100 mm \times 100 mm) on a 12 h:12 h 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

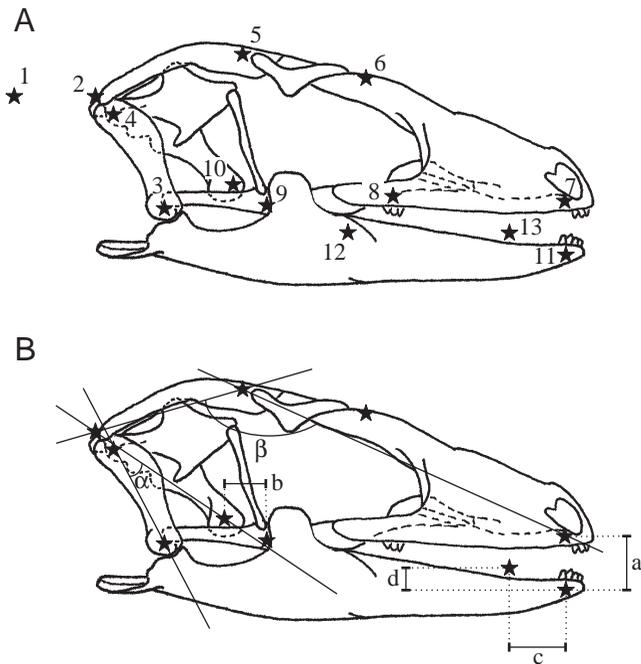


Fig. 1. (A) Schematic drawing of the skull of *Gekko gecko* to illustrate the position of the radio-opaque markers (numbered 1–13) inserted into the cranial elements to help visualise intracranial movements. (B) Variables measured to illustrate intracranial movements (see Materials and methods for details). a, gape distance; b, pterygoid–basipterygoid distance; c, antero-posterior tongue displacement; d, dorso-ventral tongue displacement; α , streptostylic angle; β , mesokinetic 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 anteroiad rotation of the quadrate during opening (strepto1), the posteroiad rotation of the quadrate during closing (strepto2), the dorsiflexion of the snout (meso1), the ventroflexion of the snout (meso2), the anteroiad displacement (sliding) of the pterygoid relative to the basipterygoid (pterygoid sliding 1), and the posteroiad 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. pseudotemporalis, 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 ($S \times A$). Muscle activity was classified as low if the activity level ($S \times A$) 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 metakinetic joint between pro-otic and parietal bones, and a typical synovial joint between the basiptyergoid 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 epiptyergoid 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–epiptyergoid 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 epiptyergoid.

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

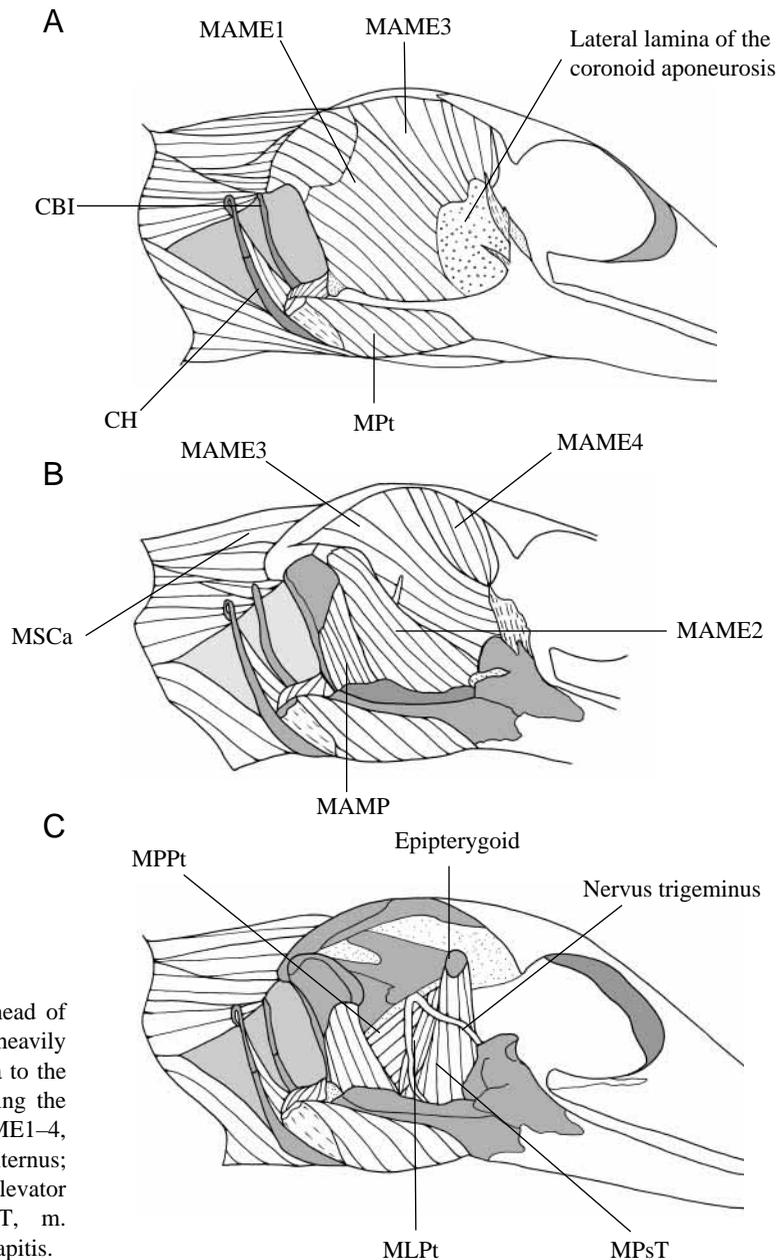


Fig. 2. (A–C) Sequentially deeper dissection levels of the head of *Gekko gecko* to illustrate the major jaw-closer muscles. The heavily shaded areas indicate bony structures; the lightly shaded area to the back of the head represents the connective tissue surrounding the oesophagus. CBI, ceratobranchial 1; CH, ceratohyal; MAME1–4, functional subdivisions of the m. adductor mandibulae externus; MAMP, m. adductor mandibulae posterior; MLPt, m. levator pterygoideus; MPPt, m. protractor pterygoideus; MPST, m. pseudotemporalis; MPt, m. pterygoideus; MSCa, m. spinalis capitis.

laterally, as observed for crocodylians (Cleuren and De Vree, 1992). 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

Table 1. Kinematic characteristics of intraoral transport cycles in *Phelsuma madagascariensis* eating large grasshoppers and *Gekko Gecko* eating crickets

Variable	<i>P. madagascariensis</i>	<i>G. gecko</i>
Jaw cycle variables		
SOI (ms)	120.8±42.9 (32)	108.0±33.5 (5)
SOII (ms)	1349.0±531.1 (32)	648.0±197.8 (5)
FO (ms)	48.1±10.5 (32)	68.0±11.0 (5)
FC (ms)	53.7±14.0 (32)	60.0±10.0 (5)
SC/PS (ms)	70.0±28.0 (32)	112.0±106.4 (5)
GD/GA (mm degree ⁻¹)	9.4±1.5 (32)	28.1±3.6 (5)
TMG (ms)	1498.4±552.1 (32)	824±208.5 (5)
Variables directly related to the movements of the cranial units		
Strepto1 (degrees)	9.7±2.5 (12)	4.8±3.2 (5)
Strepto2 (degrees)	13.2±5.2 (12)	5.6±3.6 (5)
Meso1 (degrees)	23.5±8.7 (12)	5.9±1.9 (5)
Meso2 (degrees)	25.8±8.2 (12)	6.0±2.3 (5)
Pterygoid sliding 1 (mm)	0.9±0.2 (12)	
Pterygoid sliding 2 (mm)	1.1±0.2 (12)	

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*.

FC, duration of the fast closing phase; FO, duration of the fast opening phase; GA, gape angle; GD, gape distance; Meso1, dorsiflexion of the snout unit; Meso2, ventroflexion of the snout unit; pterygoid sliding 1, anteroiad translation of the pterygoid; pterygoid sliding 2, posteroiad translation of the pterygoid; SC/PS, duration of the slow closing/power-stroke phase; SOI, duration of the first part of the slow opening phase; SOII, duration of the second part of the slow opening phase; Strepto1, anteroiad rotation of the quadrate during jaw opening; Strepto2, posteroiad rotation of the quadrate during jaw closing; TMG, time to maximal gape.

and SOII) on the basis of jaw and tongue movements. During SOI, the tongue moves forwards and upwards, and the jaws are opened slowly, but during SOII, the tongue moves little and the jaws are held at a more-or-less fixed gape angle (see also Bramble and Wake, 1985; Herrel et al., 1996).

Movement patterns during intraoral transport

The patterns described here are general patterns observed for both species (see Fig. 3). Although bite-to-bite differences in the details of these patterns occur, the overall pattern is highly similar within and between species (e.g. a forward movement of the quadrate is always accompanied by a dorsiflexion). During the SOI and SOII stages, the tongue moves forwards and upwards into the buccal cavity. The distance between the markers on the pterygoid and basipterygoid bones increases, together with the mesokinetic angle. In contrast, the streptostylic angle decreases, indicating an anteroiad rotation of the quadrate. During the FO stage, the tongue moves backwards and downwards, whereas the quadrate bone still rotates forwards. The frontal bone, or rather the whole palato-maxillary unit, is further elevated with respect to the parietal bone. The distance between the pterygoid and basipterygoid

Fig. 3. Representative kinematic profiles of the changes in the distance between the basipterygoid and pterygoid bones (A), the mesokinetic angle (B), the streptostylic angle (C), the horizontal (x; top, an increase in the values indicates an anteroiad displacement of the tongue) and vertical (y; bottom, an increase in the value indicates a dorsoad displacement of the tongue) displacement of the tongue relative to the lower jaw (D), the vertical displacement of upper (top) and lower (bottom) jaw relative to a fixed background (E) and the gape distance (F) during two successive intraoral transport cycles in a single *Phelsuma madagascariensis* while eating a grasshopper. Vertical lines indicate the kinematic stages recognised within a typical intraoral transport cycle. FC, fast closing phase; FO, fast opening phase; SC/PS, slow closing/power-stroke phase; SOI, SOII, slow opening phases I and II.

bones increases slightly or remains constant. During the two closing stages (FC, SC/PS), the tongue continues to move backwards and downwards. The mesokinetic angle and the pterygoid–basipterygoid distance decrease and the streptostylic angle increases, indicating a backward rotation of the quadrate.

In summary, during opening of the mouth (SOI, SOII, FO), the quadrate rotates forwards (streptostylic angle decreases), the frontal bone is elevated with respect to the parietal (mesokinetic angle increases) and the pterygoid–basipterygoid distance increases. During the closing stages (FC, SC/PS), we observe the opposite movements: the quadrate swings backwards, the frontal bone moves downwards and the distance between the markers on the pterygoid and basipterygoid bones decreases. During most cycles, the quadrate is retracted beyond its resting position at the end of the SC/PS stage. Dorsiflexion (lifting) of the palato-maxillary unit is always less than ventroflexion (compare meso1 and meso2 in Table 1). Despite the large standard deviations observed, these observations seem to indicate a slow recoil of the quadrate and the palato-maxillary units to their resting position after the end of the SC/PS stage.

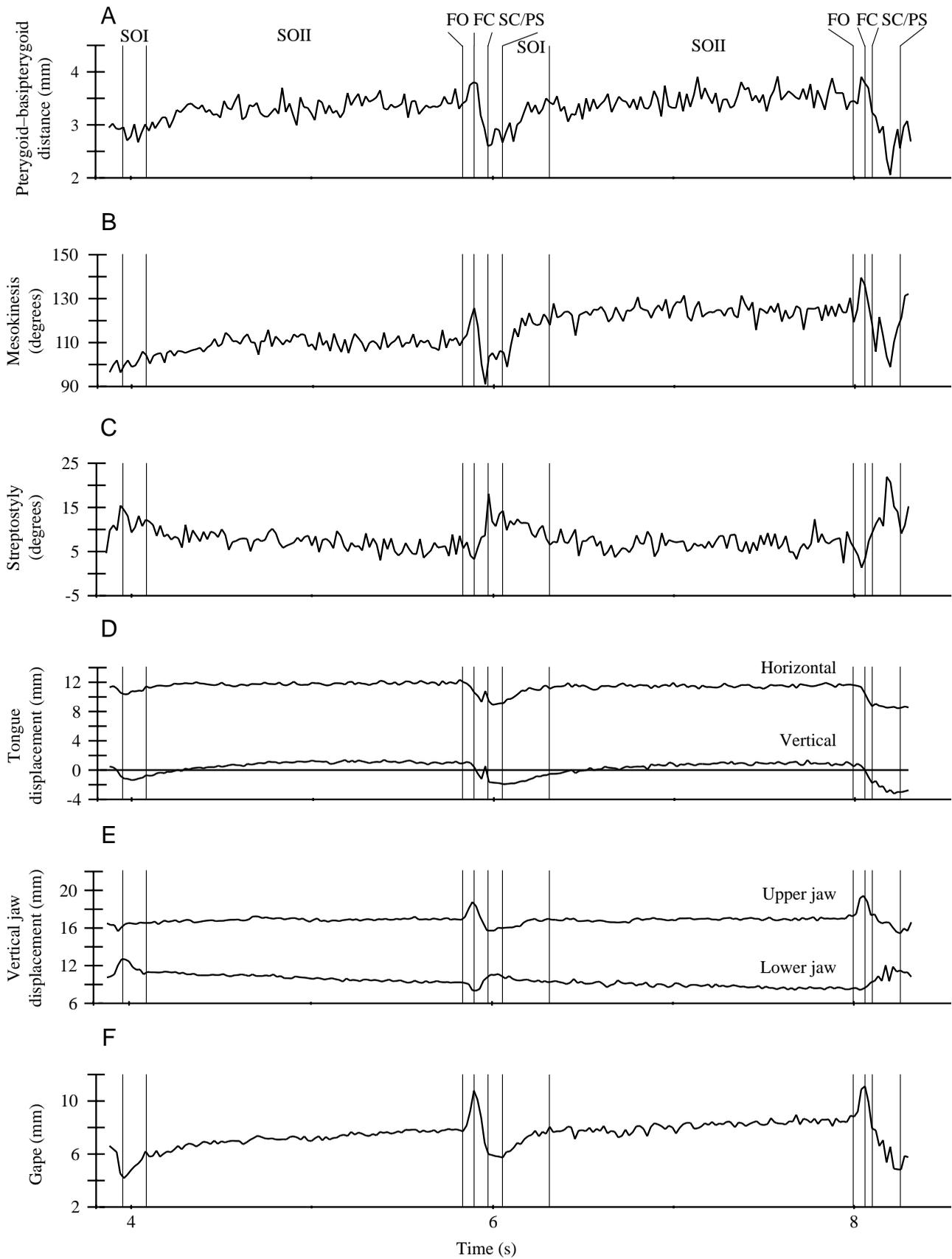
Electromyography

General

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

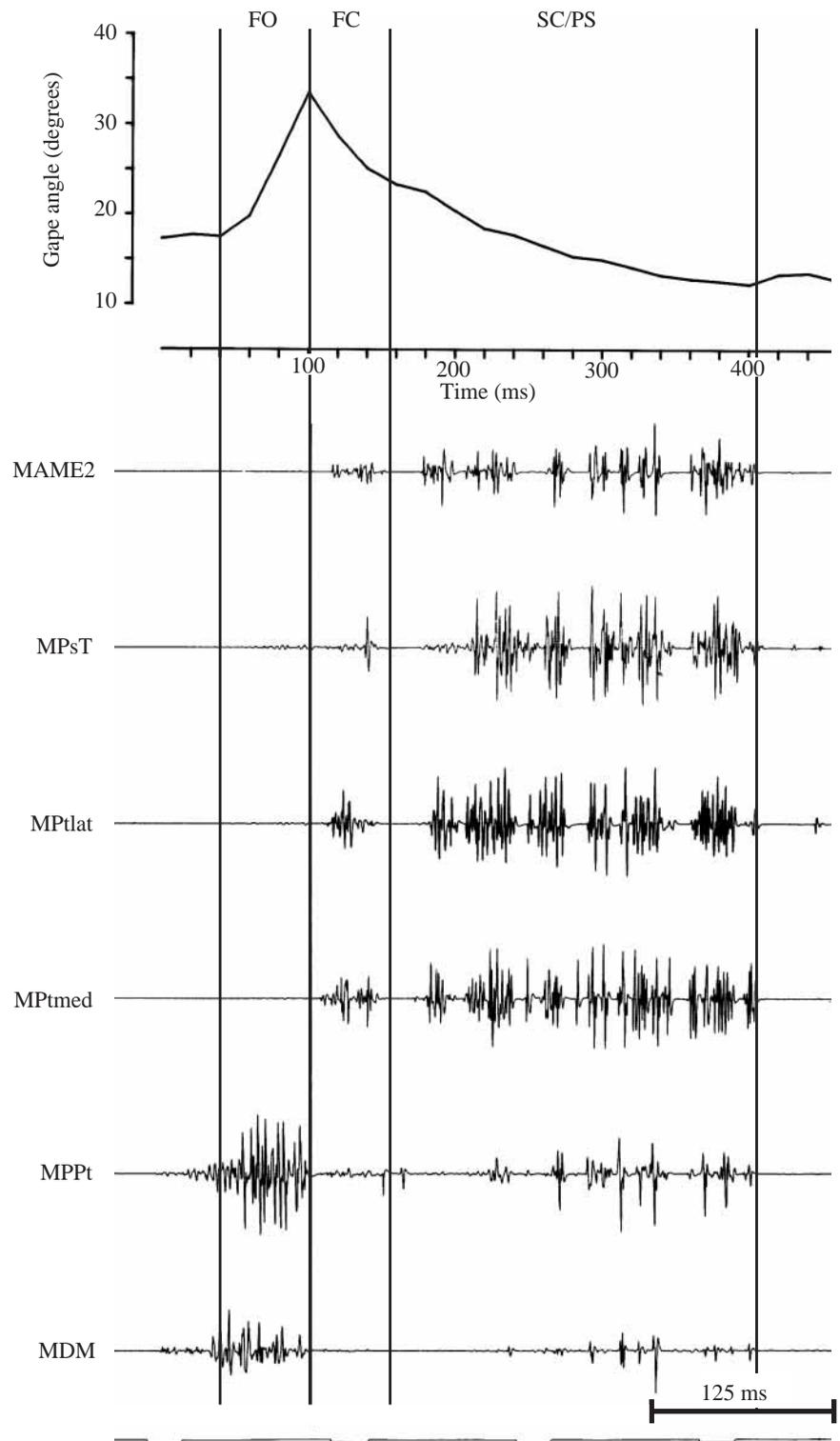


Fig. 4. Representative original electromyograms from simultaneous recordings of several muscles in *Gekko gecko* while eating a large grasshopper. The upper panel shows changes in gape angle over the same period. The vertical lines indicate kinematic phases within a jaw cycle. Note the pulsatile activation of the jaw closers (MAME2, MPST, MPtlat, MPtmed) during the power-stroke phase. FO, fast opening phase; FC, fast closing phase; MAME2, m. adductor mandibulae externus 2; MDM, m. depressor mandibulae; MPPt, m. protractor pterygoideus; MPST, m. pseudotemporalis; MPtlat, m. pterygoideus pars lateralis; MPtmed, m. pterygoideus pars medialis; SC/PS, slow closing/power-stroke phase. Note the low-level activity in MDM and MPPt during the slow-opening phase (SOII).

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

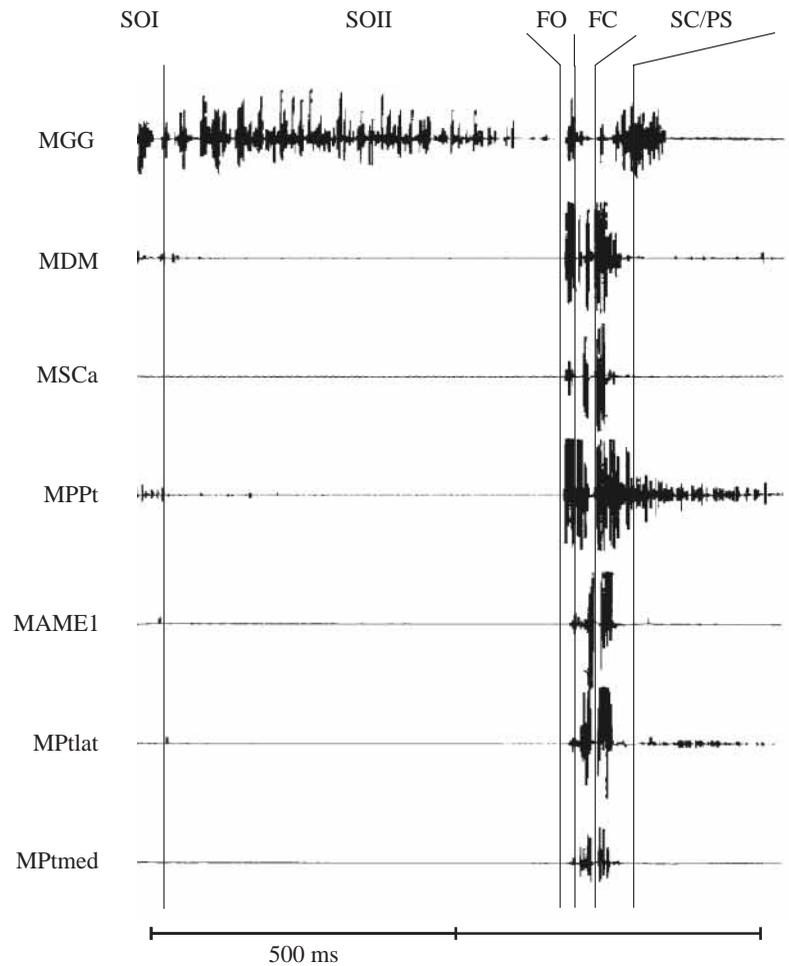


Fig. 5. Representative original electromyograms from simultaneous recordings of several muscles in *Phelsuma madagascariensis* while eating a large grasshopper. The vertical lines indicate kinematic phases within a jaw cycle. For abbreviations, see Fig. 4; MGG, m. genioglossus; MSCa, m. spinalis capitis; SOI, slow opening I phase; SOII, slow opening II phase.

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, 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

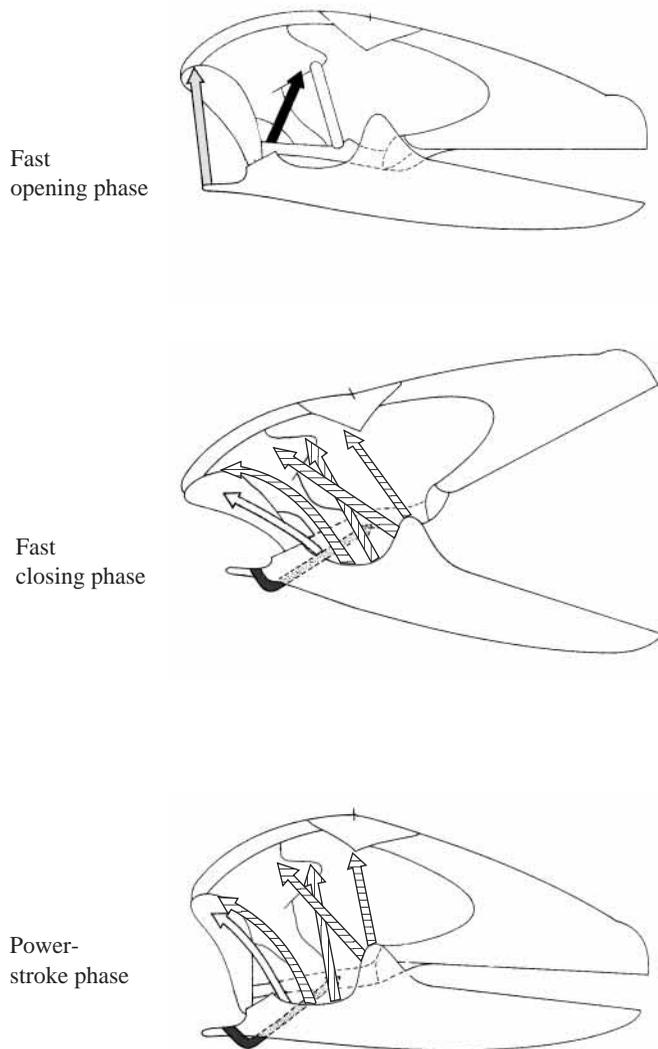


Fig. 6. Summary of jaw muscle action and the corresponding skull configurations in the geckoes examined in this study. Light grey, jaw opener; black, m. protractor pterygoidei; horizontal striping, m. adductor mandibulae externus group; vertical striping, m. pseudotemporalis; dark grey, m. pterygoideus; white, m. adductor mandibulae posterior.

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 basiptyergoid 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). Ventroflexion 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 $23.5 \pm 8.7^\circ$ during mouth opening (Table 1). In contrast, Condon (1987; *Varanus niloticus*) and Rieppel (1979; *V. bengalensis*) reported a maximum of $1-2^\circ$ 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*: $25.8 \pm 8.2^\circ$; *V. niloticus*: $1-4^\circ$, 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* (Anguillidae; 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 antero-posterior 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 basiptyergoid 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 MPpT mainly produce the lifting of the mandible. Judging by the orientation of the muscle fibres, the MAME, together with the MPt, 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 quadrato-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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