# Cranial Kinesis in Lepidosaurs: Skulls in Motion

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## Abstract

This chapter reviews various aspects of cranial kinesis, or the presence of moveable joints within the cranium, with a concentration on lepidosaurs. Previous studies tend to focus on morphological correlates of cranial kinesis, without taking into account experimental evidence supporting or refuting the presence of the various forms of cranial kinesis in these taxa. By reviewing experimental and anatomical evidence, the validity of putative functional hypotheses for cranial kinesis in lepidosaurs is addressed. These data are also considered with respect to phylogeny, as such an approach is potentially revealing regarding the development of various forms of cranial kinesis from an evolutionary perspective. While existing evidence does not allow for events leading to the origin of cranial kinesis in lepidosaurs to be clearly understood at the present time, the potential role of exaptation in its development for specific groups (i.e., cordylids, gekkonids, varanids) is considered here. Directions for further research include greater understanding of the distribution of cranial kinesis in lepidosaurs, investigation of intraspecific variation of this feature (with a focus on ontogenetic factors and prey properties as variables which may influence the presence of kinesis), and continued study of the relationship between experimentally proven observation of cranial kinesis and cranial morphology.

Key words: cranial kinesis, lepidosaur skull, functional morphology.

#### Introduction

Cranial kinesis, or the presence of moveable joints within the cranium, has been a subject of considerable interest to researchers for more than a century (for references see Bock, 1960; Frazzetta, 1962; Smith, 1982). Numerous types of cranial kinesis have been defined and their distribution among vertebrates reported. However, descriptions of morphological features that are correlated with the presence of a kinetic skull are less common. Additionally, the vast majority of reported cases of cranial kinesis are based upon manual manipulation of skeletal or ligamentous specimens. While this type of observation is indicative of the potential for intracranial movements, only rarely have these findings been confirmed through functional studies on living animals exhibiting naturalistic behaviors (Smith, 1980; Condon, 1987; Herrel et al., 2000). Lepidosauria, composed of the Rhynchocephalia and Squamata (see Figure 1), represents the most commonly examined group among vertebrates with regard to cranial kinesis, and numerous functional hypotheses about its potential adaptive significance have been proposed (see Throckmorton and Clarke, 1981; Schwenk, 2000a for summaries). While the diversity of kinetic mechanisms has been only partially explored for this speciose clade, lepidosaurs are the only group for which sufficient

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data exist to construct phylogenetically based hypotheses regarding the evolution cranial kinesis. This review focuses on cranial kinesis in non-ophidian lepidosaurs. Although ophidians (snakes) are phylogenetically nested within lepidosaurs and possess highly kinetic skulls, they will not be discussed because they represent an extremely derived condition with respect to cranial kinesis (see Kardong, 1994; Frazzetta, 1999; Lee et al., 1999; Cundall and Greene, 2000 for information on cranial kinesis in snakes). The various forms of cranial kinesis are defined and a mechanical model describing them for lepidosaurs (Frazzetta, 1962) is reviewed. Anatomical features correlated with intracranial movements and experimental studies of lepidosaurian cranial kinesis are described in detail. Review of these data allow for a discussion of the validity of putative functional explanations of cranial kinesis. Additionally, this topic is examined from a phylogenetic perspective in an attempt to understand some of the basic evolutionary transitions leading to kinesis in extant taxa, as much as present data allow. While existing evidence does not allow for events leading to the origin of cranial kinesis in lepidosaurs to be clearly understood at the present time, the potential role of exaptation (Gould and Vrba, 1982; Arnold, 1994, 1998) in its development for specific groups (i.e., cordylids, gekkonids, varanids) is considered.



Figure 1. Hypothesized phylogeny of Lepidosauria based on Estes et al. (1988), Frost and Ethridge (1989).

#### Definitions of Cranial Kinesis in Lepidosaurs

A short description of the major types of cranial kinesis found in lepidosaurs is warranted, although detailed definitions are available elsewhere (Frazzetta, 1962; Condon, 1987; Iordansky, 1990; Schwenk, 2000a,b). In general, cranial kinesis refers to movements between the bones of the cranium, excluding movements of or within the mandible. Although small-scale movements within sutural junctions, such as those described in mammals (Herring, 1972; Jaslow and Biewener, 1995; Herring and Teng, 2000) technically fall under the umbrella of this definition, they are not discussed in this review. The advantage of developing an all-encompassing system of definitions for cranial kinesis in vertebrates is clear; it allows for broad taxonomic comparisons to be made and evolutionary transitions to be better understood. However, this goal has proven elusive due to difficulty in establishing homologies as well as because of terminological differences related to anatomical features between taxa. In the past, types of kinesis have been defined using anatomical terminology in a developmental framework. For example, metakinesis (see later for definition) has

been described as mobility between the dermatocranium and chondrocranium, but it is defined more specifically from an anatomical standpoint as the presence of a joint between the supraoccipital and parietal bones. While the latter portion of this definition is not entirely complete, it more closely approximates the location of metakinetic movements. Inability to establish homologies between taxa is a potential difficulty when all vertebrates are considered, but is less problematic when discussing a more taxonomically restricted group such as lepidosaurs. For vertebrates in general, homology is an issue that is central to questions of evolutionary origins of cranial kinesis.



Figure 2. Cranium of Varanus salvator (Varanidae) in (A) dorsal, (B) ventral, and (C) right lateral views. Dashed lines, targets, and joints indicate locations of kinetic axes. 1, mesokinetic axis; 2a, metakinetic axis; 2b, metakinetic joint (supraoccipital slides anteroposteriorly under ventral parietal as indicated by double headed arrow); 3, streptostylic axis; 4, hypokinetic axis. bo, basioccipital; bp, basipterygoid process; bs, basisphenoid; ect, ectopterygoid; ep, epipterygoid; fr, frontal; jug, jugal; l, lacrimal; max, maxilla; n, nasal; pa, parietal; pal, palatine; pf, prefrontal; pmx, premaxilla; pop, paroccipital process; be, septomaxilla; soc, supraoccipital; sq, squamosal; stp, supratemporal; vom, vomer. Modified from Rieppel (1980), with permission  $\bigcirc$  Birkhäuser, Verlag.

Three main forms of cranial kinesis are present in lepidosaurs (see Figure 2, Table 1). Of these, streptostyly and mesokinesis are well defined. Metakinesis has been discussed often, but there remains a great deal of confusion regarding its anatomical definition. An additional form of kinesis, hypokinesis, has been mentioned occasionally (Patchell and Shine, 1986; Condon, 1987, 1988, 1998). Although it is not usually considered a distinct form of kinesis, it will be briefly defined, as it is an essential component of Frazzetta's quadric-crank model (discussed later). Amphikinesis is the occurrence of mesokinesis and metakinesis in a coupled and coordinated manner (Versluys, 1912; Frazzetta, 1962).

Streptostyly is defined as rotation of the quadrate at its dorsal articulation against the squamosal and/or supratemporal. The axis of rotation is transversely oriented, so that the quadrate swings through an anteroposterior arc. However, some species [e.g. *Varanus niloticus* (Varanidae), Condon, 1987; *Lialis burtoni* (Pygopodidae), Patchell and Shine, 1986; *Gekko gecko* (Gekkonidae), A. Herrel, personal communication] may exhibit a lateral rotation of the quadrate around an anteroposteriorly directed axis. Streptostyly is sometimes considered to be distinct from all other forms of cranial kinesis (Frazzetta, 1962; Robinson, 1967; Throckmorton and Clarke, 1981), but this is unwarranted. Like other forms of cranial kinesis, streptostyly involves quantifiable movement of cranial elements against each other.

Туре	Definition
Streptostyly	Rotation of the quadrate at its dorsal articulation against the squamosal and/or supratemporal. The axis of rotation is generally oriented transversely, but may be anterposteriorly oriented in some taxa.
Mesokinesis	Dorsoventral flexion and extension around an axis that runs transversely through the frontal-parietal suture.
Metakinesis	Curvilinear sliding movement between the parietal and supraoccipital bones. The axis of rotation is oriented transversely through the paroccipital processes of the exoccipital bones.
Hypokinesis	Dorsoventral flexion and extension around an axis that runs transversely through the palate (palatine/ectopterygoid/pterygoid suture).
Amphikinesis	Simultaneous mesokinesis and metakinesis as described in the quadric-crank model.

### Table 1. Summary of types of cranial kinesis in lepidosaurs

Mesokinesis involves dorsoventral flexion and extension. The mesokinetic axis runs transversely through the frontal-parietal suture. Because mesokinesis is the most easily visualized form of cranial kinesis, it has generally received the most attention in experimental studies.

As mentioned previously, metakinesis involves curvilinear sliding movement between the dermal bones of the skull and the ossified braincase, first defined by Versluys (1912) and confirmed by later workers (Frazzetta, 1962; Herrel et al., 1999a; Schwenk, 2000a) as being located between the parietal and supraoccipital bones. The location of the metakinetic axis of rotation is elusive; it is recognized that this axis must be located posteroventrally to the sliding region of metakinetic movement, but its exact position is difficult to determine (see Figure 2). Frazzetta (1962) emphasized the difference between the metakinetic joint and its axis of rotation, indicating that the axis passed transversely through some point on the paired paroccipital processes of the exoccipital

bones. This location has been accepted as the axis of metakinetic rotation, although experimental evidence has been unable to confirm it (see later, De Vree and Gans, 1987a; Herrel et al., 1999a). The hypokinetic axis is represented by an axis of flexion and extension that runs either obliquely or transversely through the palate. It is most likely to be located at the sutural junction between each pterygoid and the ectopterygoid and palatine elements, which are located anterolaterally and anteromedially to the pterygoid, respectively. Movement at the hypokinetic joint has never been quantified experimentally in living animals, but its presence is indicated from manipulation of preserved lepidosaur specimens and its existence is essential for dorsiflexion and ventroflexion of the upper jaw during mesokinesis.

#### Frazzetta's Model for Cranial Kinesis in Lepidosaurs

Frazzetta (1962) was the first to present a detailed mechanical model of cranial kinesis in lepidosaurs. Working from video observation of live animals, examination of preserved materials from numerous lepidosaurs, and construction of physical models, he described kinesis in the lepidosaur skull as a four-joint linkage, or quadric-crank, mechanism. This model was based upon the skull of the putatively highly kinetic monitor lizard, *Varanus indicus*. Under this scheme, the skull is composed of two principal segments, the occipital and the maxillary (see Figure 3). The occipital segment consists of the braincase, while the maxillary segment is made of five smaller units (parietal, quadrate, basal, muzzle, and epipterygoid), four of which attach directly to the occipital segment of the skull (see Figure 3).



Figure 3. Quadric-crank model of coupled cranial kinesis in a varanid lizard (Varanus). The skull is shown in left lateral aspect during (A) resting, (B) protracted, and (C) retracted states. Shading indicates the occipital segment of the skull. Labels indicate five units of maxillary segment of skull. Targets indicate location of kinetic axes. 1, mesokinetic axis; 2, streptostylic axis; 3, hypokinetic axis. Modified from Frazzetta (1962), with permission © Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.

In Frazzetta's model, the contact points between each of the units of the maxillary segment, and the four connections between the maxillary and occipital segments are discrete joints allowing rotation or some degree of flexion and extension. The model provides a relatively simple elucidation of kinetic movements. Protraction (anterodorsal rotation) of the quadrate pushes the basal unit forward, and elevates the muzzle unit through dorsiflexion at the mesokinetic and hypokinetic joints. Additionally, when coupled with mesokinetic dorsiflexion, rotation around the metakinetic axis (see earlier discussion for difference between metakinetic axis and joint) results in ventral flattening or depression of the parietal unit relative to the rest of the skull. Retraction of the quadrate depresses the muzzle unit as the basal unit is pulled posteriorly, causing ventroflexion at the hypokinetic and mesokinetic joints (see Figure 3). A slight amount of lateral quadrate movement may occur during ventroflexion as the pterygoids are forced laterally by the stationary basipterygoid processes of the basisphenoid. The epipterygoid unit presumably acts a central supporting strut and its ventral end translates anteroposteriorly along with the basal unit.

Frazzetta's diagrammatic description has formed the foundation of numerous subsequent studies of lepidosaurian cranial kinesis (Iordansky, 1966, 1990; Rieppel, 1978b; Smith, 1980; Arnold, 1998). While useful as a general means for understanding a particular type of lepidosaurian cranial kinesis, it is by no means clear that it represents the most common condition in lepidosaurs. The quadric-crank model only describes amphikinesis (simultaneous metakinesis and mesokinesis), presumably driven either by streptostylic movements of the quadrate or quadrate-independent protraction and retraction of the basal unit through muscular action (see later for potential mechanisms). However, while manipulations of preserved skulls indicate the potential for metakinetic movements in many lepidosaurs, experimental studies of living animals have been unable to quantify either the nature or magnitude of metakinetic movements and it remains unproven that metakinesis and mesokinesis are always correlated with each other. Additionally, several studies indicate that streptostyly can occur at the same time as mesokinesis, but that the two are uncorrelated in their kinematics [Pogona (Amphibolurus) barbata (Agamidae), Throckmorton and Clarke, 1981; Lialis, Herrel, in preparation] or that streptostyly occurs without concurrent mesokinetic movement (Throckmorton, 1976; Smith 1980, 1982; Herrel et al., 1998; Herrel and De Vree, 1999). This suggests that the quadric-crank model is only applicable in cases where amphikinesis and streptostyly are present. Several researchers have indicated that amphikinesis is the most common condition for lepidosaurs (Frazetta, 1962; Iordansky, 1990, 1996) but experimental studies do not necessarily support this assertion (see later).

## **Experimental Studies of Cranial Kinesis**

#### I. Experimental Techniques

The presence of cranial kinesis in lepidosaurs is usually confirmed through the manipulation of skeletal or ligamentous specimens. This technique allows certain types of kinesis to be excluded, but it can only indicate the potential presence of intracranial movement. Evaluation of cranial kinesis is most accurately performed through experimental studies of living animals under naturalistic feeding conditions. A variety of experimental techniques have been used for this purpose, each of which has benefits and drawbacks. The most commonly used experimental techniques are video or cinematographic observation (Frazzetta, 1962, 1983; Boltt and Ewer, 1964; Iordansky, 1966; Patchell and Shine, 1986). While these methods are non-invasive, they do not allow quantification of streptostyly or metakinesis. Cineradiography has also been used to determine the nature and magnitude of intracranial movements (Throckmorton, 1976; Rieppel, 1978b; Smith, 1980, 1982; Throckmorton and Clarke, 1981; Herrel et al., 1999a). The primary advantage of this technique is its ability to quantitatively assess the degree of streptostyly and

possibly metakinesis, especially when radio-opaque markers are implanted prior to filming. However, placement of markers is invasive and the use of only one x-ray source, the typical experimental setup, limits analysis to sequences without significant amounts of out-of-plane movement from the experimental subject. Two other techniques have been used to assess mesokinesis only. Smith and Hylander (1985) placed single-element strain gauges across the frontal-parietal joint of the savanna monitor lizard, Varanus exanthematicus (see Herring and Mucci, 1991; Herring and Teng, 2000 for in vivo sutural strain studies in mammals). Assuming that bending of the muzzle unit occurs in a sagittal plane, tensile and compressive strains across the joint indicate ventroflexion and dorsiflexion of the snout, respectively. Use of strain gauges has the potential to very accurately measure mesokinetic movements, but there are some potential problems with this technique. In addition to potentially inhibiting movement at the joint (since the gauge is firmly bonded across it), surgical placement of strain gauges may alter natural feeding behavior (Frazzetta, 1986). Additionally, interpretation of strain data may be ambiguous, as possible out-of-plane buckling of the gauges may mimic strains due to flexion/extension. Condon (1987) employed a goniometer apparatus affixed to the frontal and parietal bones to measure flexion and extension at the mesokinetic joint of Varanus niloticus. This methodology has a high resolution for measurement of angular excursions, but the size and mass of this devise make its use on smaller lepidosaurs, for which data regarding cranial kinesis are most badly needed, impractical. Additionally, it can only measure mesokinetic movements and cannot yield information about streptostyly or metakinesis.



Figure 4. Right lateral view of cranial musculature of the gekkotan Gekko gecko indicating (A) superficial and (B) deeper levels of dissection. Shaded areas indicate bony or connective tissue structures. Muscles discussed in text are labeled. MAME, m. adductor mandibulae externus; MLPt, m. levator pterygoidei; MPPt, m. protractor pterygoidei; MPt, m. pterygoideus; MSCa, m. spinalis capitis. Modified from Herrel et al. (1999a), with permission © The Company of Biologists Limited.

The primary goals of studies investigating cranial kinesis in lepidosaurs have been to (1) identify the presence or absence of specific forms of kinesis, (2) determine the nature and timing of kinetic movements relative to stages of the feeding and gape cycle, and (3) elucidate the muscular activation patterns causing these movements (see Figure 4 for diagram of cranial musculature relevant to later discussion). Most research has focused on the first two goals; there have been few electromyographic studies (although see De Vree and Gans, 1987a; Herrel et al., 1999a for exceptions) to support the muscle recruitment hypotheses derived largely from analysis of free-body diagrams (e.g., Frazzetta, 1962; Iordansky, 1966, 1996). Experimental studies are reviewed here within a broad phylogenetic framework (rhynchocephalian, iguanian, scleroglossan), aiding in later discussion of phylogenetic aspects of lepidosaur cranial kinesis. The presence of kinesis has been evaluated once experimentally using cineradiography in the rhynchocephalian *Sphenodon* (the tuatara). *Sphenodon* is known to utilize propalinal movements of the lower jaw as a means of shearing food items during feeding. However, this fore-aft motion is accommodated not by rotation of the quadrate, but instead by sliding of the mandible anteroposteriorly against the immobile quadrate. Gorniak et al. (1982) indicated that there was no evidence for mesokinesis or metakinesis in *Sphenodon*. These results were in contrast to the findings of Ostrom (1962), who reported the presence of the constrictor dorsalis muscles (protractor pterygoidei and retractor pterygoidei), thought to be active during kinetic movements (especially mesokinesis, see later). However, the presence of these muscles in *Sphenodon* is probably variable and at best represents circumstantial evidence that the tuatara has functional cranial kinesis during feeding. Additionally, examination of juvenile specimens confirmed the akinetic nature of the tuatara cranium (Gorniak et al., 1982), contrary to Ostrom's assertion of a possible role of ontogenetic factors in allowing kinesis in young individuals.

# III. Iguania

Numerous studies have investigated cranial kinesis in iguanian lizards. In general, iguanians do not show mesokinetic or metakinetic movements, but some taxa are streptostylic. However, in contrast to the idea that all squamates are streptostylic (Romer, 1956; Robinson, 1967; Carroll, 1988; Pough et al., 1998), an assertion usually based upon the manipulation of ligamentous specimens, experimental studies indicate that many iguanians have no functional kinesis of any kind. Among the Iguanidae, Iguana iguana was found by Throckmorton (1976) to lack all types of kinesis. Ctenosaura similis, studied through cineradiography, has functional streptostyly but no indication of mesokinesis or metakinesis (Smith, 1982; Smith and Hylander, 1985). Agamids are the other major group of iguanians that has been assessed for the presence of cranial kinesis. Similar to Iguana, no intracranial movements were observed in Plocederma (Agama) stellio (Herrel and De Vree, 1998). However, in the related agamid Pogona (Amphibolurus) barbatus, Throckmorton and Clarke (1981) reported definitive streptostyly and possible mesokinesis. Overall streptostylic movements averaged 7°, and there was a low correlation between streptostylic angle and gape angle. Small mesokinetic movements were observed during feeding, averaging less than 1° and never exceeding 5°. Ventroflexion at the frontal-parietal joint was correlated with anterior rotation of the quadrate, a finding that is completely opposite to Frazzetta's quadric-crank model and unsupported by any other mechanical model or anatomical evidence. However, the resolution of the experimental system was claimed by the authors to be no greater than 3-4°, so this mesokinetic data may be error prone (Schwenk, 2000a). In the agamid Uromastix aegyptius (Leiolepididae), anterior rotation of the distal quadrate (up to 25°) occurred simultaneous with jaw opening and was qualitatively associated with an increase in the ability to crop foods relative to the non-streptostylic Iguana (Throckmorton, 1976). Herrel and De Vree (1999) performed a more detailed analysis of streptostyly in Uromastix acanthinurus, comparing the degree of quadrate movement during different feeding stages (intraoral transport vs. swallowing) and during feeding on different prey items (endive vs. locusts). Their results confirmed the basic findings of Throckmorton (1976): maximum streptostylic protraction correlating with maximum gape. Evaluation of prey type or feeding stage effects indicated that the streptostylic angle only differed significantly between intraoral transport and swallowing when feeding on locusts. In general, streptostylic excursions in U. acanthinurus were slightly less than in U. aegyptius, and no other form of cranial kinesis was found in either species (Throckmorton, 1976; Herrel et al., 1998).

# IV. Gekkota

Among Gekkota, three pygopodids and two gekkonids have been examined experimentally for cranial kinesis. Based on video analysis, Patchell and Shine (1986) reported a large degree of flexure at the frontal-parietal joint in *Lialis burtoni* (up to 40°), and possible lateral rotation of the quadrates. No kinesis of any kind was seen in the more closely related species *Pygopus lepidopodus* (Pygopodidae) and *Delma inorrata* (Pygopodidae). Cineradiographic films of *Lialis* (Herrel and Meyers, in preparation) show a very unique and baffling pattern of kinesis in this species. Both streptostyly and mesokinesis are present, but there is no consistent correlation in the kinematics of these movements (e.g., anterior rotation of the quadrate only sometimes functionally linked to dorsiflexion of the muzzle unit). This would represent the first time that large-scale excursions of the kinetic apparatus were observed to occur in an uncoordinated manner, requiring the development of a new mechanical model to explain these movements since the quadric-crank model does not consider this scenario.

Recently, two gekkonids (Gekko gecko and Phelsuma madagascariensis) were studied through cineradiography and electromyography, and the fast opening and slow closing/power stroke phase of the gape cycle were biomechanically modeled to investigate the possible function of kinesis in these taxa (Herrel et al., 1999, 2000). In the cineradiographic study (Herrel et al., 1999a), cranial kinesis was qualitatively compared among the stages of the feeding cycle (capture, intraoral transport, swallowing), and was examined quantitatively during intraoral transport. Overall, these two gekkonids were found to follow Frazzetta's model of coupled streptostyly, mesokinesis, and metakinesis. Anterior rotation of the quadrate was closely linked with muzzle dorsiflexion, as were posterior quadrate rotation and muzzle ventroflexion. Kinesis was most prominent during prey capture and least during swallowing cycles and was less pronounced during feeding on soft vs. hard prey items (newborn mice and crickets vs. grasshoppers). Interspecific analysis revealed that all kinetic variables were greater in Phelsuma than in Gekko. During transport cycles, muzzle dorsiflexion was consistently less than ventroflexion, with a total rotation of approximately  $50^{\circ}$ around the mesokinetic axis. Quadrate retraction and muzzle ventroflexion both extended beyond the resting point (muzzle angle when feeding is not occurring) at the end of the slow close/power stroke phase, which was followed by slow anterior recoil of the quadrate. Electromyography indicated that during jaw opening/muzzle dorsiflexion, the m. depressor mandibulae (MDM), m. protractor pterygoidei (MPPt), and m. spinalis capitis (MSCa) were all active (De Vree and Gans, 1989; Herrel et al., 1999a). It is likely that the MPPt pulls the pterygoid anteriorly, increasing pterygoid/basipterygoid distance and dorsiflexing the snout. Stabilization of the occipital unit, hypothesized to be required for muzzle dorsiflexion (Smith and Hylander, 1985; Herrel et al., 1999a), may be accomplished by simultaneous activity in the m. spinalis capitis (MSCa). Muscle activity in the m. levator pterygoidei (MLPt) during muzzle elevation was also reported by De Vree and Gans (1987a) for Gekko gecko. Based on static bite modeling techniques utilizing muscle orientation and physiological cross-sectional area data, Herrel et al. (1999a) hypothesized that the m. adductor mandibulae externus (MAME) and m. pterygoideus (MPt) bring about pterygoid retraction and muzzle ventroflexion. During the slow closing/power stroke phase, the MDM and MPPt are also active, possibly to stabilize the quadrate-squamosal joint during braking of the retracting system.

### V. Scincomorpha

No scincomorphs (sensu Estes et al., 1988) have been shown to exhibit any type of cranial kinesis except streptostyly, and even that is not universally present. Among the scincids that have been studied, *Tiliqua scincoides* and *Corucia zebrata* both lack functional streptostyly (Herrel et al., 1998), but the Australian skink *Trachydosaurus rugosus* exhibits overall streptostylic excursions of

approximately 6° (De Vree and Gans, 1987b). Muscle stimulation experiments indicate that quadrate retraction occurs during stimulation of the MAME, a pattern similar to that found in gekkonids (De Vree and Gans, 1987b; Herrel et al., 1999a). Cineradiographic films of the teiid *Tupinambis nigrapunctata* (Smith 1980, 1993) and observational study of various gymnopthalmids (e.g. *Gymnothalmus, Neusticurus, Pantodactylus,* and *Proctoporus*) indicate at least some degree of streptostyly, with the possibility of lateral quadrate movement in the latter group (MacLean, 1974). The cordylid *Pseudocordylus* may be mesokinetic, but this needs to be confirmed (Arnold, 1998).

## VI. Anguimorpha

Experimental investigations have focused upon anguimorph lizards, with a particular concentration on varanids. Frazzetta (1983) performed a high-speed cinematography analysis of cranial kinesis in the anguid *Gerrhonotus multicarinatus*. He concluded that *Gerrhonotus* followed the pattern of coupled and coordinated mesokinesis and streptostyly. However, interpretation of Frazzetta's data is problematic. Data are not quantified and examination of Vanguard analysis tracings (see Figures 10 and 11 from Frazzetta, 1983) indicates that in some feeding sequences, quadrate rotation is not always correlated with mesokinetic movements and that mesokinesis is sometimes absent even when streptostyly is not. However, this study and others that rely solely on videography for the quantification of streptostylic movements may be problematic due to the low accuracy of this technique. The only other non-varanid anguimorph that has been examined, *Heloderma horridum* (Helodermatidae) shows no indication of any type of cranial kinesis (Herrel et al., 1997; A. Herrel, personal communication).

Although varanid lizards are often used as model organisms for describing lepidosaur cranial kinesis, there has been little consensus regarding the nature of their intracranial movements. The major points of contention among researchers are whether specific types of kinesis actually occur, as well as the timing and magnitude of these movements. Streptostyly is present in varanids but it is unclear how consistently it occurs (Rieppel, 1979; Smith, 1982). Smith (1982) analyzed intracranial movements in Varanus exanthematicus during intraoral transport only. During prey prehension, unpredictable head movements that were not completely in lateral view made quantification of kinesis impossible. Smith reported that although quadrate protraction usually occurs during jaw opening, this was not always the case. Additionally, the magnitude of streptostyly was variable. In fact, during some inertial transports, maximum gape corresponded with maximum quadrate retraction. There was no indication of mesokinesis during any stage of the feeding cycle, and Smith indicated that previous accounts of mesokinetic activity might instead be unrecognized movement at the craniocervical joint. In a similar study, Rieppel (1979) reported that Varanus bengalensis followed Frazzetta's quadric-crank model. Contrary to observations in gekkonids (Herrel et al., 1999a), quadrate protraction was greater than retraction (21° vs. 5.5°) and muzzle dorsiflexion was greater than ventroflexion (9° vs. 6°). Studies of mesokinesis in varanids provide conflicting results. The results of Condon (1985, 1987) show that mesokinesis is correlated with gape angle in Varanus niloticus, as predicted by Frazzetta (1962), with magnitudes of dorsiflexion and ventroflexion remaining relatively small (on average approximately 5°). Using data recorded from single-element strain gauges, Smith and Hylander (1985) reported a rapid rise in tensile strain (which would theoretically be correlated with ventroflexion, but see earlier discussion of potential problems with using strain gauges) that peaked at maximum gape. Tensile strain decreased as the jaws closed, but there was no transition into compressive strain during transports. Translation of strain values into angular movement resulted in very low mesokinetic excursions, no greater than 1.4%. Rotation of the muzzle unit in varanids has also been linked to backward and forward rotations of the craniocervical complex during inertial feeding (Boltt and Ewer, 1964). However, Smith and Hylander (1985) proposed the same hypothesis but based it on completely opposite data:

during backward rotation of the head (jaw opening), inertia of the muzzle unit gives it the tendency to remain in place, possibly explaining their finding of increasing tensile strain. Schwenk (2000a) noted that during mesokinesis, dorsiflexion of the muzzle unit beyond the rest point only occurs at the moment before prey prehension (see later). This assertion is generally supported for varanids, although Rieppel (1979) indicates that the muzzle is routinely dorsiflexed beyond the resting state.

### VII. Summary

In summary, there does not appear to be any experimental evidence supporting the hypothesis that lepidosaurs are in general amphikinetic, with coupled mesokinetic and streptostylic movements. Streptostyly is the most widespread type of kinesis among squamates, appearing to some degree in all of the major clades. Reports of mesokinesis are quite variable, and although some groups appear to conform to the quadric-crank model (i.e., gekkotans, anguids), in some cases repeated experimental studies have been unable to even confirm the nature of mesokinetic movements (i.e., varanids), and some taxa may directly contradict the idea that mesokinetic movements are quadratedriven at all (Lialis). Methodological differences may account for a large portion of this disagreement, but it is probable that even within a single individual, the extent of mesokinesis may vary widely depending upon a number of factors, including stage of the feeding cycle and properties of the prey item. Ontogenetic factors may also have a profound influence on the degree of cranial kinesis present in various lepidosaurs. Although few studies have investigated this, growth of the skull may allow for the development or loss of kinetic joints. Additionally, studies have not been able to determine the nature of metakinesis. Finally, few electromyographic studies have been conducted to investigate the role of muscles in driving intracranial movements. It is thought that the constrictor dorsalis muscles (m. levator pterygoidei and m. protractor pterygoidei) play a large role in protraction of the kinetic system and that the adductor musculature (primarily m. adductor mandibulae externus and m. pterygoideus) retract it, but this has not been confirmed for most kinetic taxa.

### Morphological Correlates of Cranial Kinesis

Although studies have demonstrated the presence of cranial kinesis in lepidosaurs, few have discussed anatomical parameters that might be correlated with these movements (see Iordansky, 1966; Condon, 1988; 1998; Arnold, 1998; Schwenk, 2000a for exceptions). In this section, the anatomical evidence supporting or refuting putative claims of kinesis will be discussed for each of the forms outlined earlier. Evaluation of morphological features can allow the exclusion of kinesis, but can only indicate the potential for movement and cannot definitively prove its presence. Unfortunately, histological studies of the morphology of kinetic joints that may shed light on this issue are limited.

In streptostyly, the dorsal quadrate joint with the squamosal and/or supratemporal must allow rotation, and the ventral end must be free to move anteroposteriorly. There appear to be few bony obstructions to rotation of the dorsal quadrate in lepidosaurs. Histological study of this joint in *Varanus* indicates that a synovial joint is present between the quadrate and the intercalary cartilage, facilitating rotation (Rieppel, 1978a, 1993; Condon, 1988, 1998). There has been little histological study of the joint in other taxa that have been experimentally shown to be streptostylic, but presence of a synovial cavity may be a good indication that rotation is at least possible. It is less clear, based on morphology, whether lateral rotation of the quadrate is possible. The articulation of the cephalic condyle of the distal quadrate to the pterygoid via medial and lateral quadratopterygoid ligaments (Throckmorton, 1976) in some lepidosaurs argue against it. Ventral quadrate morphology can be expected to vary depending upon whether streptostyly occurs as an

isolated form of kinesis or occurs in conjunction with amphikinetic movements. The articulation of the ventral end of the quadrate with the pterygoid may be an indicator of the potential for streptostyly. First, the presence of a complete lower temporal fenestra and associated lower temporal arch precludes the possibility of streptostyly. *Sphenodon* is the only living lepidosaur with a lower arch, composed of portions of the fused squamosal, jugal, quadrate, and quadratojugal posteriorly and the jugal bone anteriorly, so this parameter does not apply to most taxa. However, all other lepidosaurs, which have lost the lower temporal arch, may exhibit changes in the morphology of the quadrate-pterygoid joint which are associated with functional streptostyly. Throckmorton (1976) used cineradiography to examine cranial kinesis in two iguanian lizards, reporting the presence of streptostyly in *Uromastix aegyptins* and absence in *Iguana iguana*. Dissections of these two lizards indicated significant differences in the morphology of the quadrate-pterygoid joint with a streptostyle of the sections of these two lizards indicated significant differences in the morphology of the quadrate-pterygoid joint with a streptostyle of the sections of these two lizards indicated significant differences in the morphology of the quadrate-pterygoid joint (see Figure 5).



**Figure 5.** Left quadrate-pterygoid joint (medial view) in (A) Uromastix acgyptius and (B) Iguana iguana. Anterior is to the right. Note the presence of quadratopterygoid ligament in (A). Q, quadrate; P, pterygoid; L, quadratopterygoid ligament. Modified from Throckmorton (1976), with permission © Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.

In Uromastix, the posteriorly directed quadrate ramus of the pterygoid does not directly contact the medial surface of the quadrate. Instead, these elements are connected by the quadratopterygoid ligament, an attachment which allows considerable anteroposterior quadrate movement. However, in *Iguana iguana* the quadrate and pterygoid meet at a fibrocartilaginous joint that is firmly bound on either side of the quadrate ramus of the pterygoid by a ligament. Additionally, the medial ligament was reported to partially ossify in some specimens. This joint has been described in *Varanus bengalensis* as being composed of a synovial anterior part and a fibrous posterior part that tightly binds the quadrate ramus of the pterygoid to the distal quadrate (Rieppel, 1978a). This is the expected joint morphology if this species is amphikinetic with correlated streptostyly, although the presence of a moveable synovial joint is somewhat puzzling. Histological sectioning of this joint in a wider range of lepidosaurs and investigation of ligamentous connections between the pterygoid and quadrate is warranted in light of these findings, and may reveal much about morphological parameters which correlate with functional streptostyly.

Functional mesokinesis is typified by (1) rotation about a transverse axis through the frontal-parietal suture, (2) protraction and retraction of the basal unit (pterygoid, ectopterygoid, jugal, and posterior palatine bones) against the basipterygoid processes of the basisphenoid, (3) flexion through the hypokinetic region (see earlier discussion) of the palate, and (4) flexion in the elements lateral to the frontal-parietal joint. There has been no systematic analysis of these joints across lepidosaurs.

Although a full review of these features is beyond the scope of this paper, specific examples will be discussed, focusing on taxa that have been examined experimentally for the presence of mesokinesis.



Figure 6. Dorsal view of frontal-parietal joint of Lacerta lepida (AMNH 57770). Anterior is towards the top of the page. Note interdigitation of suture and anteriorly directed tabs of parietal that slide under ventral surface of frontal. Scale = 1 cm.

The frontal-parietal joint is quite variable among lepidosaurs, ranging from a highly interdigitated sutural junction (i.e., Sphenodon, Lacerta) to a linear joint with significant erosion on the ventral surface (i.e., Gekko gecko). Several features of this joint have been linked to mesokinesis. Most commonly, the linear or non-linear nature of the frontal-parietal joint has been cited as reflecting the potential for flexion and extension (Patchell and Shine, 1986; Arnold, 1998; Schwenk, 2000a, in preparation). This is an important parameter by which extinct taxa have been assumed to possess kinetic skulls (Sullivan, 1986; Carroll, 1988; Gauthier et al., 1988; Mead et al., 1999). Additionally, Schwenk (2000a, in preparation) noted that functional mesokinesis may be associated with significant erosion on the ventral surface of the frontal-parietal joint accompanied with the presence of loose connective tissue. However, the relationship between frontal-parietal joint morphology and mesokinesis may not be quite so straightforward. Although certain lepidosaurs that are thought to have a relatively high degree of mesokinesis, such as Varanus and Gekko, have a linear and ventrally eroded joint, some taxa that are also thought to be mesokinetic have joint morphologies that would apparently contraindicate this type of movement. For example, Lacerta, claimed by Impey (1967) to be mesokinetic, has a highly interdigitated frontal-parietal suture that does not appear to allow flexion or extension (see Figure 6). No studies have carefully examined frontal-parietal joint morphology, and while it is thought that interdigitation of this sutural junction would resist any motion at it, this has not been conclusively demonstrated; some authors have argued that movement is possible even with an interdigitated suture (Arnold, 1998). Schwenk (2000a, 2001) has also commented that the location of the parietal foramen may be related to mesokinesis. This foramen indicates the position of the parietal (pineal) eye and is variably located within either the frontal or parietal bones or within the suture itself; even within a single species, its placement can vary significantly (Estes et al., 1988). Notably, in all species which show

experimental evidence of mesokinesis, the parietal foramen is almost always located in the parietal bone and is never found in the frontal-parietal suture (Jollie, 1960; Estes, 1988; Schwenk, 2001). As placement of the parietal eye in the joint of a functionally mesokinetic lizard might cause either damage or interference with its proper function, location of the foramen within the suture, or considerable variation in foramen location may prove to be a good indication that mesokinesis is not present.





Figure 7. Ventral view of basipterygoid-pterygoid joint morphology in (A) Pogona sp. (AMNH 76571) and (B) Varanus sp. Anterior is towards the top of the page. In Pogona, the anterior end of the quadrate ramus of the pterygoid has a medially directed process that overlies the basipterygoid process. Note the bony process at the anterior end of the pterygoid notch. bp, basipterygoid; pt, pterygoid. Scale = 1 cm.

Protraction and retraction of the basal unit, and specifically of the pterygoid bones against the basipterygoid processes of the basisphenoid, is also required for muzzle dorsiflexion and ventroflexion. Variation in the morphology of the pterygoid-basipterygoid joint is common among lepidosaurs (see Figure 7). Typically, the basipterygoid processes are directed anteromedially and lie in the medially concave pterygoid notch (after Oelrich, 1956; Rieppel, 1978a) which runs along the quadrate ramus of the pterygoid. A bony process is often located at the anterior end of the pterygoid notch. The nature of this process, as well as the orientation and arthrology of the pterygoid-basipterygoid articulation are of importance in establishing the potential for anteroposterior sliding at this joint. At first glance, the process at the anterior end of the pterygoid notch might appear to be a barrier to retraction of the palate against the basipterygoid processes, preventing muzzle ventroflexion (Schwenk, in preparation). Gekko gecko and Varanus niloticus, both mesokinetic, show a marked reduction of this process; its reduction may indicate a propensity for mesokinesis. However, some species which have been reported to lack mesokinesis (i.e., Ctenosaura, Smith and Hylander, 1985; Tupinambis, Smith, 1980) also show some degree of reduction. Finally, in some iguanians without mesokinesis (i.e., Uromastix, Thockmorton, 1976, Herrel and De Vree, 1999; Plocederma stellio, Herrel et al., 1995), this process forms a thin flange that lies ventral to the basipterygoid process, but probably does not restrict fore-aft movement significantly (see Figure 7). The relative importance of pterygoid translation is unclear. The gekkonid Phelsuma madagascariensis, which exhibits greater mesokinetic excursion than any other lepidosaur studied to

date (approximately 50°) was found to have a relatively small degree of pterygoid translation relative to the basipterygoid processes (averaging 2 mm total), much smaller than the total length of the pterygoid (Herrel et al., 1999a). Muzzle elevation is more likely due to changes at the hypokinetic joint than anteroposterior movements at the pterygoid-basipterygoid joint (A. Herrel, personal communication). Further experimental evidence may indicate that basal unit mobility is of such a small magnitude that restriction of movement may not be significant.

Orientation of the basipterygoid processes and the quadrate ramus of the pterygoid may also be important indicators of functional mesokinesis, although this has not been quantified across a wide variety of lepidosaurs. Typically, taxa thought to be mesokinetic have anteroposteriorly oriented basipterygoid processes, whereas they are directed more anteromedially in akinetic taxa. Certain orientations of these processes would require greater palatal flexibility (in the form of lateral spreading of the pterygoids) for an equivalent amount of palatal translation. Histologically, the pterygoid-basipterygoid joint has been variably described as either a synovial joint or a cartilaginous articulation, but broad taxonomic accounts are lacking (Jollie, 1960; Condon, 1998).

The hypokinetic joint consists of a series of sutural articulations without cartilaginous sliding surfaces (Rieppel, 1978a, 1993) involving the pterygoid, ectopterygoid, and palatine elements. Mesokinetic lepidosaurs (especially gekkonids and to a lesser degree varanids) have decreased the robusticity of the hypokinetic joint, and specifically have reduced the dorsoventral thickness of this region relative to taxa without mesokinesis (i.e., *Plocederma, Iguana, Ctenosaura, Heloderma*). This so-called "flexipalatality" has also been noted in anguids, cordylids, and some scincids (Iordansky, 1990). These taxa have not been widely studied experimentally to assess for mesokinesis. Iordansky (1966) has noted qualitative differences in the orientation of this joint among lizards, with some taxa (i.e., *Agama, Cyclura, Ophisaurus*) exhibiting an obliquely directed suture between the pterygoid and palatine bones, and others (i.e., *Varanus*) having a suture which is more linear and is transversly oriented. This variation may relate to the potential for movement at the hypokinetic joint.

Cranial elements lateral to the mesokinetic joint (e.g., postorbital, postfrontal) have been noted to have specific regions of mobility. In iguanians, this flexibility is located in the postorbital-parietal and postorbital-squamosal sutures while in scleroglossans, it is found between the postorbital and jugal (Arnold, 1998). Gekkotans and varanids have lost the postorbital bar completely, possibly contributing to the evolution of mesokinesis in these groups (see later).

Because experimental studies have been unable to clearly identify and define metakinesis, its anatomical correlates are not easily established. However, if it is assumed that metakinesis involves a translational joint between the parietal and supraoccipital and concurrent rotation around an axis passing transversely through the paroccipital processes, some basic morphological features that are associated with its presence can be proposed. The processus ascendens of the supraoccipital projects anterodorsally into a corresponding depression on the ventral side of the parietal. Mobility at the supraoccipital-parietal joint may not be a requirement of mesokinesis, but is required under Frazzetta's four-bar quadric-crank model of coupled lepidosaur cranial kinesis. Histological studies of the joint are sparse, but results vary widely, even for the same genus. In Varanus, the dorsal metakinetic joint has been variably described as allowing sliding (Rieppel, 1978a; V. bengalensis) and as being a rigid connection (Condon, 1988; V. niloticus). This variability may be due to ontogenetic factors; the specimen that Rieppel (1978a) described was a juvenile. On the other hand, mobility in this joint has been described for an adult specimen of *Ctenosaura pectinata* (Oelrich, 1956), which is not considered to have metakinesis. In gekkonids, thought to follow Frazzetta's model, the processus ascendens is absent. Clearly, the nature of this joint is far from understood. There have been limited descriptions of the purported rotational metakinetic axis through the paroccipital processes of the exoccipital. In both iguanians and scleroglossans, the intercalary cartilage is lateral or ventrolateral to these processes (Oelrich, 1956; Jollie, 1960; Condon, 1988). The intercalary

cartilages are thought to facilitate rotation of the paroccipital processes on the ventrally located supratemporals.

## Functional Explanations for the Presence of Cranial Kinesis

Although the nature of cranial kinesis in most lepidosaurs is poorly understood, many hypotheses regarding its function have been proposed. More often than not, these hypotheses are based upon the potential for kinesis as deduced from examination of skeletal or ligamentous specimens, and have no foundation in experimental studies of live animals. However, considering that some experimental studies have been conducted, all hypotheses can be evaluated in light of these findings. Following Schwenk (2000a), discussion of the functional significance of different forms of cranial kinesis will be divided into a separate consideration of streptostyly and of coupled mesokinesis (mesokinesis with coordinated streptostylic movement). It is evident from numerous studies that streptostyly can occur without any other type of kinesis, thereby falsifying the idea that quadrate movement is only present to facilitate movement of the muzzle. However, when mesokinesis is present, it usually occurs as part of a coupled system that follows the quadric-crank model (see earlier discussion for possible exceptions). It is important to re-emphasize here that although numerous hypotheses for both of these types of kinesis have been proposed, they cannot currently be very widely generalized since the type of cranial kinesis that occurs in most lepidosaurs is either debated or unknown. The functional significance of metakinesis or movements at the hypokinetic joint will not be discussed. The presence of metakinesis is essentially unconfirmed for all lepidosaurs and its anatomical basis is unclear. Hypokinesis is considered here to be a requirement for movement of the muzzle unit, and will not be considered separately from coupled mesokinesis.

Proposed function	Reference				
Increased mechanical advantage for:					
m. adductor mandibulae externus	Gingerich (1971); Rieppel (1978)				
m. pterygoideus	Smith (1980)				
Gape increase	Patchell and Shine (1986); MacLean (1974)				
Efficient intraoral transport of food items	Throckmorton and Clarke, 1981				
Cropping of plant material in herbivorous lizards	Throckmorton, 1976				
Shearing of prey for processing	De Vree and Gans, 1994; Herrel and De Vree (1999)				
Accurate occlusion in agamids	Robinson (1973)				

Table 2. Functional hypotheses for streptostyly

### I. Streptostyly

Theories relating to the functional significance of streptostyly can be placed into one of three major categories (see Table 2). First, streptostyly may give an increased mechanical advantage to one or more components of the adductor musculature during jaw closing. Secondly, rotation of the quadrate around a transverse, sagittal, or dorsoventral axis might either increase gape or allow larger prey to be consumed by widening the passage to the pharynx. Finally, streptostyly may facilitate various aspects of processing and intraoral transport.

Movement of the quadrate during streptostyly can alter the lever arm of various cranial muscles that work across the lower jaw joint. This change will potentially increase the mechanical advantage of these muscles, allowing an increase in bite force. Gingerich (1971) proposed that because the quadrate rotates at both the proximal and distal ends, it can act as a link rather than as a lever, making the lower jaw system more efficient by potentially placing resultant bite and muscle force vectors in alignment and eliminating joint reaction forces. Herrel et al. (1998) addressed Gingerich's hypothesis by modeling the adductor system of various lepidosaurs, an exercise that allowed detailed input of plausible muscle forces. When food reaction force orientations were varied and placed into the model, no combination of variables resulted in zero joint reaction force, an indication that the lower jaw and mobile quadrate probably do not function as Gingerich predicted. Rieppel (1978b) focused primarily on the role of quadrate retraction, calculating that this movement results in an increased lever arm for the MAME. Rieppel's model did not address the functional advantage of anterior quadrate rotation (Frazzetta, 1986). Additionally, he determined that no increase is seen in the mechanical advantage of the pterygoideus muscle during retraction, claiming that it is primarily active during the initial phases of jaw closing and unimportant to the described system. Subsequent electromyographic analysis did not bear out this prediction, showing significant activity in MPt well into the slow close/power stroke phase (Smith, 1982; Herrel et al., 1999a). Finally, Smith (1980) reported that the function of streptostyly is to increase the muscular advantage of the MPt, allowing it to contribute significantly to bite force. This hypothesis relied upon the notion that during jaw adduction, rotation occurred around the quadrate-squamosal joint and that the lower jaw joint was stabilized by the m. adductor mandibulae externus. Later work by Smith (1982) provided evidence against this. For the quadrate-mandibular joint to be stabilized, the sum of the moments around both the dorsal and ventral quadrate joints must equal zero. Analysis of dry muscle weights and degree of pennation indicated that this was possible, but electromyographic data showed that during the power stroke both main jaw adductors (MAME and MPt) were not always synchronous in their activity, making the required stabilization unlikely.

While an increase in gape is usually cited as an explanation for mesokinesis (see later), streptostylic movements have also been implicated. Lateral movements of the quadrates have been observed in the pygopodid *Lialis* (Patchell and Shine, 1986) as well as in various gymnopthalmids (MacLean, 1974). It has been proposed that these transverse movements increase the width of the pharynx, allowing larger prey to be consumed. These species are known to consume relatively large prey, so although there is little experimental evidence to support lateral quadrate movement, this hypothesis is tenable. Similarly, quadrate retraction (without mesokinetic movements) has been hypothesized to increase gape angle during jaw opening (Robinson, 1967). Cineradiography of streptostylic iguanians (Throckmorton, 1976; Herrel and De Vree, 1999) indicates the opposite pattern during jaw opening, arguing against a role of streptostyly in increasing gape.

Finally, quadrate movement may be linked to providing a selective advantage in the transport or processing of food items. Throckmorton and Clarke (1981) suggested that streptostyly aids in the transport of food items through the oral cavity and into the pharynx during intraoral transport. Currently, there does not appear to be any support for this hypothesis. On the contrary, intraoral transport in lepidosaurs is facilitated through either movements of the hyolingual apparatus or rapid movements of the craniocervical complex (inertial transport). Movements of the quadrate are not thought to be an important factor for either of these transport mechanisms (Herrel and De Vree, 1999). Regarding its potential role in prehension or processing, it has been suggested that streptostyly is an adaptation to aid the cropping of plant materials in herbivorous lizards (Throckmorton, 1976), allow shearing of prey through propalinal movements as in *Sphenodon* (De Vree and Gans, 1994; Herrel and De Vree, 1999), or permit accurate occlusion in agamids with acrodont dentition (Robinson, 1973).

There is currently no single adaptive advantage for streptostyly that can be applied to all lepidosaurs. Several hypotheses have been shown to be unlikely (muscular advantage to MPt, intraoral transport), some are taxon specific (cropping hypothesis, occlusion in agamids), and streptostyly in some taxa (i.e., varanids, geckoes) may be a mechanism to aid protraction and retraction of the basal unit for muzzle movements as part of the quadric-crank model. The distribution of this feature needs to be better documented among lepidosaurs before any of these hypotheses can be confirmed, although the functional advantage of streptostyly may be relatively taxon-specific. Future studies need to analyze streptostylic movements in the context of food item properties and feeding and gape cycle stages; such analyses may lend additional insight into the adaptive value of this character.

## II. Mesokinesis

Explanations for mesokinesis have been even more numerous than those for streptostyly (see Table 3). Although it is assumed that mesokinesis is coupled with streptostylic movements, this coupling is not a requirement for most of the functional hypotheses regarding mesokinesis. Rather, dorsiflexion and ventroflexion of the upper jaw is the factor that these theories have typically involved. To date, no functional explanation of mesokinesis has been universally accepted, although there is corroborating evidence for several theories. Many hypotheses have been rejected on the basis of morphological or experimental evidence and several are plausible but have not been explicitly tested. One of the major problems plaguing the literature is that many authors have attempted to explain mesokinesis in all lepidosaurs with a single overriding hypothesis. Experimental evidence indicates significant intertaxonomic differences, and this may not be possible. In general, these explanations are linked in some way to feeding function although the evolution of this kinetic mechanism in various groups may not be (see later).

Proposed function	Reference				
Gape increase	Frazetta, 1962; Auffenberg, 1981				
Prey clamping between pterygoid bones	Bradley, 1903				
Decrease duration of gape cycle	Condon, 1987; Herrel et al., 2000				
Shock absorption	Bellairs, 1957; De Vree and Gans, 1994				
Prey subjugation	Iordansky, 1966; Rieppel, 1979				
Control during jaw prehension	Frazetta, 1962, 1983; Condon, 1987; Schwenk, 2000				
Increase bite force/ reduce joint reaction forces	Herrel et al., 2000				

Table 3. Functional hypotheses for mesokinesis

Several hypothesis regarding mesokinesis are unlikely to be correct. First, it does not appear that coupled mesokinesis and streptostyly act to affect an overall increase in gape during jaw opening. While kinesis in avian groups probably does permit a wider gape (Bout and Zweers, 2001), biomechanical modeling and kinematic analyses show that this is not the case for lizards (Frazzetta, 1962; Throckmorton and Clarke, 1981; Condon, 1987). However, it is likely that movement of the muzzle unit acts to decrease the overall duration of the gape cycle. Herel et al. (2000) reported a

30% overall reduction in gape cycle time in highly kinetic gekkonid lizards relative to an akinetic agamid (for transport cycles). While Condon (1987) found a relative time decrease of 12-18% during jaw adduction in a kinetic varanid, in absolute time this represented only 2-6 ms, a duration that may have functional significance for small prey items only. There does not appear to be any evidence supporting the idea that movement in the basal unit results in mediolateral movement of ventral skull elements, allowing prey items to be "clamped" between the pterygoid or palatine bones (Bradley, 1903). Manual manipulations of ligamentous specimens indicate little lateral palatal rotation during either protraction or retraction, and there are no cranial muscles that are positioned in such a manner as to allow a significant amount of movement in this direction. Additionally, films of Gerrhonotus show that at no time during the feeding cycle is the prey item in close contact with the roof of the oral cavity (Frazzetta, 1962). Although the presence of pterygoid teeth in some species may lend support to the clamping hypothesis, most mesokinetic species do not have pterygoid teeth, and the orientation of the teeth in those that do is not consistent with their supposed use (Arnold, 1998). Finally, Frazzetta (1962) discussed the possibility that mesokinesis acts to re-orient the jaws with respect to the prev item during capture, a function that has been suggested for birds (Bock, 1960). However, unlike in birds, the lepidosaur eye is functionally part of the muzzle unit and would most likely experience disrupting movement during upper jaw movements. In fact, observational evidence indicates that during muzzle ventroflexion the eye sinks deep into the orbit (Frazzetta, 1983; A. Herrel, personal communication).

Several theories are tenable but remain largely untested. First, coupled mesokinesis may allow shock absorption during biting (Bellairs, 1957; De Vree and Gans, 1994). Frazzetta (1962) presented a theoretical argument against this, claiming that shock absorption would require either de-activation of the jaw adductor musculature at the moment of impact with the prey or stretching of muscles from a contracted state. While Condon (1987) reported kinematic evidence that potentially contradicts this hypothesis (lack of upper jaw dorsiflexion at the moment of strike), it is unclear whether shock absorption would result in a kinematic pattern of jaw dorsiflexion or active jaw ventroflexion at the moment of prey contact. Additionally, sutures have been shown to reduce stresses during feeding activities (Herring and Mucci, 1991; Jaslow and Biewener, 1995; Metzger and Ross, 2001), although these sutures are highly interdigitated unlike the frontal-parietal joint in kinetic lizard skulls.

Rieppel (1979) proposed a link between kinesis and tooth recurvature in varanids. Highly recurved teeth allow a prey item to be held more securely, but at the same time make it more difficult for the tip of the tooth to contact the surface of the prey. In order to make penetration more easily accomplished and simultaneously ensure axial loading of the tooth, reducing shear forces that might result in tooth breakage, tooth tip contact is essential. Rotation of the muzzle via mesokinesis and dorsoventral rotation at the craniocervical joint may facilitate tooth recurvature by altering the line of action of the teeth during contact with prey items (Rieppel, 1979).

Experimental evidence has corroborated the idea that mesokinesis in various lepidosaurs either is a mechanism for fine control during prey prehension or helps to increase bite force while at the same time decreasing detrimental joint reaction forces (Frazzetta, 1962, 1983; Schwenk, 2000a; Herrel et al., 2000). It is important to recognize that these two theories are not necessarily mutually exclusive and that both may be viable functional hypotheses for certain taxa.

Various aspects of prey prehension have been linked to the use of coupled mesokinesis. As discussed earlier, while it does not increase gape angle, upper jaw movement probably does increase the speed of the gape cycle (although experimental data are generally from intraoral transport cycles). Frazzetta (1962) hypothesized that the primary advantage of mesokinesis during prey prehension is that by ventroflexing the upper jaw and adducting the mandible simultaneously, the prey item can be contacted simultaneously by both tooth rows. This was thought to reduce the risk

of deflecting the food out of the mouth before it could be gripped securely. Under this scheme, mesokinesis will only confer a selective advantage to lepidosaurs that use jaw prehension, exhibit a significant degree of cranial kinesis, and feed on small, active prey. Interestingly, large parts of this pattern were recognized long ago, and were even placed within the context of prey prehension. As Versluys (1927) stated, "The importance of cranial movements in Reptilia is that by lifting the upper jaw, grasping of moving prey (Insecta and other Arthropoda) is facilitated. This is confirmed by the [fact] that cranial movements dissappear with changing diet: herbivores, mollusk and snail eating forms have an akinetic skull." Frazzetta's hypothesis was disputed by Iordansky (1966) who quite accurately pointed out that the same advantage could be achieved by an akinetic lizard simply through movement at the craniocervical joint. In a later paper, Frazzetta (1983) refined his hypothesis and addressed this critique, expanding his argument and providing some kinematic evidence to support it. Specifically, he proposed that these movements also allow finer control of the jaws for more accurate prey capture. This was thought to be especially important during capture of prey on the ground because excessive movement of the lower jaw was limited by its proximity to the substrate. Movements at the craniocervical joint were acknowledged to act similarly to a mobile muzzle unit, but Frazzetta (1983) felt that upper jaw movements would prevent the need for coordinated motion of the jaw system and movements of the neck and body.

While there is some experimental evidence supporting the hypothesis that mesokinesis is an adaptation for precision during jaw prehension, this hypothesis is not fully supported by all experimental studies and portions of it can be disputed on theoretical grounds. Schwenk (2000a) was the first to make detailed kinematic predictions for this hypothesis. Dorsiflexion beyond the rest position is expected to occur only in the moment immediately before prehension and prey



Figure 8. Tracings of mesokinetic excursions during feeding in monitor lizards (Varanidae). Dorsiflexion beyond the rest position only occurs at strike (indicated by arrow), supporting the hypothesis that mesokinesis is an adaptation for prey prehension (see text). In both graphs, muzzle dorsiflexion is indicated when the plot is above the rest position line, and ventroflexion when it is below. Scaling of mesokinetic magnitudes and temporal scaling for the two plots are not equivalent. Legend for stage of feeding cycle (manipulation, transport, swallowing) for both plots is indicated below lower tracing. (A) Tracing modified from Smith and Hylander (1985) data collected from single-element strain gauge over the frontal-parietal joint of Varanus exanthematicus. (B) Tracing based on goniometric data from Varanus niloticus presented by Condon (1987).

contact should be simultaneous with ventroflexion past the rest position. No dorsiflexion past rest should occur throughout the rest of the feeding sequence for mesokinesis to specifically be an adaptation for accurate prey prehension. Numerous studies (Frazzetta, 1983; Smith and Hylander, 1985; Condon, 1987) have confirmed this prediction during prey capture (see Figure 8). However, in a cineradiographic study of cranial kinesis in Varanus bengalensis, Rieppel (1979) noted dorsiflexion past the resting position to occur routinely during transport sequences. Schwenk (2000a) attributed dorsiflexion past rest seen by Condon (1987) during transports to "tooth clearing" behavior, but cyclic and repeated movements can probably not be explained in this way. In fact, the presence of dorsiflexion past rest during any stage besides prey prehension (as seen in some geckoes and varanids) may argue against the prey prehension hypothesis. From a more theoretical standpoint, "decoupling" of the cranial and postcranial kinematics, while potentially reducing the necessity for neuromotor coordination, is probably not a requirement. For example, most studies of varanid lizards indicate some degree of mesokinesis. However, these taxa are also known to use inertial transport, a form of intraoral transport which requires coordination of cranial and postcranial movements in order to effectively move food items from the rostral jaw tips into the pharynx (Gans, 1969; Smith, 1982; Elias et al., 2000). If this integration is possible during the transport stage of feeding there is no reason to believe that it cannot occur during prey acquisition. Despite these criticisms, the prey prehension hypothesis remains a viable explanation for the presence of cranial kinesis in at least some groups. Obviously, this can only be applied to lepidosaurs that use jaw prehension as opposed to lingual prehension, which has been demonstrated to include only the Scleroglossa (Schwenk and Throckmorton, 1989; Schwenk, 2000a). As Schwenk (2000a) notes, this hypothesis is not falsified by the lack of mesokinesis in a scleroglossan (as has been shown for several species, see earlier discussion), but only by its presence in a lepidosaur which uses lingual prehension (iguanians). Studies of mesokinesis among Iguania are lacking, but there does not currently appear to be any evidence of significant mesokinetic movements in this clade.

A detailed study of cranial kinesis in gekkonid lizards (Gekko gecko and Phelsuma madagascariensis) by Herrel et al. (1999a) has resulted in the other major functional explanation for mesokinesis. Although gekkonids are scleroglossans, this study could neither support nor refute the prehension hypothesis because out of plane rotation of the head rendered quantification of intracranial movements during prey capture impossible. Herrel et al. (2000) applied cineradiographic, electromyographic, and physiological cross-sectional area data to dynamic jaw opening and static bite models in order to elucidate whether a potential mechanical advantage was achieved through movements of the muzzle unit. For the bite model, orientation of food reaction force was varied and magnitudes of bite force and joint reaction forces were calculated for protracted, rest, and retracted positions. A higher bite force is known to relate to increased feeding performance and to convey an adaptive advantage (Herrel et al., 2001a,c). High joint reaction forces, on the other hand, are thought to be detrimental, as they are transferred into the cranium from the mandible and would be likely to increase stress on kinetic joints (Herrel et al., 2000). At the most common food reaction force angles, the ratio of joint reaction force to bite force is lowest during retraction, allowing a more powerful bite with relatively lower joint reaction forces. Protraction during jaw opening was thought to increase the speed of the gape cycle (see earlier discussion). Experimental confirmation of these results on actively feeding animals is difficult; although bite forces and orientations can potentially be measured, joint reaction forces can not be quantified directly (Herring and Liu, 2001). However, at least for gekkonid lizards with a particular type of coupled mesokinesis and streptostyly (following Frazzetta's model), this is a realistic adaptive hypothesis. Determining the adaptive and functional value of the complex coupled system of kinesis in lepidosaurs has proven to be a challenge. While a number of explanations has been shown to be incorrect, previous studies have not provided data that can conclusively address most hypotheses. It must be stressed that many of these theories are not mutually exclusive. For example, the jaw prehension hypothesis may prove to be correct, but this does not necessarily mean that coupled mesokinesis does not simultaneously decrease the ratio of joint reaction to bite force. Clearly, further experimental data need to be collected in order to apply most functional hypotheses to more inclusive clades.

### Cranial Kinesis in a Phylogenetic Framework

Mapping functional and morphological cranial characters onto a cladogram can potentially help reveal some of the evolutionary pathways that led to various forms of cranial kinesis in lepidosaurs. Once again, here we are confronted with the problem that experimental studies are conflicting in their results. Nevertheless, if some assumptions are made regarding characters that are likely to be correlated with the potential for various forms of intracranial movements, this exercise becomes an informative one. Figure 9 shows the distribution of various functional and morphological attributes of lepidosaurs. Assessment of cranial kinesis for this purpose is based on evidence from experimental studies only.

The most serious challenge to correlating feeding or anatomical features with mesokinesis or streptostyly is the lack of data regarding the type of cranial kinesis in most of these groups. However, several conclusions can be reached. For streptostyly, there does not appear to be any link between the type of prehension or transport mechanism used and the potential for functional mobility of the quadrate. At the present time, it is difficult to attempt to link morphological

		Meso- kinesis	Strepto- styly	Prehension mechanism	Intraoral transport	Parietal foramen	F-P joint	S-T bar	P-O bar
RHYNCHOCEPHALIA	Sphenodon	No	No	Lingual	Hyolingual	Parietal	Complex	Present	Present
	Iguanidae	No	Variable	Lingual	Hyolingual	Variable	Variable	Present	Present
IGUANIA	Agamidae	No	Variable	Lingual	Hyolingual	Variable	Variable	Present	Present
	Leiolepididae	No	?/Yes	Lingual	Hyolingual	In suture	Variable	Present	Present
	Chamaeleonidae	No	?	Lingual	Hyolingual	Frontal/Abs.	Variable	Present	Present
	Pygopodidae	?/Yes	Variable	Jaw	Hyolingual	Absent	Simple	Absent	Absent
	Gekkonidae	Yes	Yes	Jaw	Hyolingual	Absent	Simple	Absent	Absent
	Teiidae	?	?/Yes	Jaw	Both	Variable	Complex	Present	Present
	Gymnopthalmida	ie ?	?/Yes	Jaw	Both	Absent	Complex	Present	Present
	Lacertidae	?	?	Jaw	Hyolingual	Parietal	Complex	Present	Present
b	Xantusiidae	?	?	Jaw	?	Parietal/Abs.	Complex	Present	Present
	Scincidae	?/No	Variable	Both	Hyolingual	Parietal/Abs.	Variable	Present	Variable
	Cordylidae	?	?	Both	Hyolingual	Parictal/Abs.	Variable	Present	Present
	Anguidae	?/Yes	?/Yes	Jaw	Hyolingual	Parietal	Simple	Present	Variable
ch	Xenosauridae	?	?	Jaw	?	Parietal	Simple	Present	Present
	Helodermatidae	No	No	Jaw	Hyolingual	Absent	Simple	Absent	Present
	Lanthanotidae	?	?	?	?	Absent	Simple	Present	Present
L	Varanidae	Yes	Yes	Jaw	Inertial	Parietal	Simple	Present	Absent
L	Serpentes	No	Yes	Jaw	Other	Absent	Fused	Absent	Variable

Figure 9. Phylogeny of Lepidosauria with functional and morphological characters shown for each clade. Nodes on cladogram indicate (a) Gekkota, (b) Scincomorpha, and (c) Anguimorpha. Assessment of mesokinesis and streptostyly from review of experimental studies. Prehension mechanism and intraoral transport data from Schwenk (2000a). Parietal foramen indicates location of foramen (parietal bone, frontal bone, frontal-parietal suture, foramen absent, or position variable), from Estes et al. (1988). F-P (frontal-parietal) is complex or simple, based on presence of parietal tabs and sutural interdigitation, from Estes et al. (1988) and personal observations. S-T (supratemporal) and P-O (postorbital) bars present or absent.

features, beyond the absence of a lower temporal bar, with streptostyly. Histological studies of the quadrate-squamosal and quadrate-pterygoid joints across a wide variety of taxa and synthesis of information regarding quadratopterygoid ligaments might help in this effort.

More can be said about the distribution of phenotypic traits with regard to mesokinesis (see Figure 9). As noted by other authors (Schwenk, 1994, 2000a) there is a clear relationship between the existence of functional mesokinesis and prehension mechanism. No iguanian lizards, all of which use lingual prehension, show clear evidence of significant mesokinetic movements. Instead, this character is limited solely to the jaw prehending Scleroglossa. This tends to support the hypothesis of Frazzetta (1962, 1983) that mesokinesis may be an adaptation for prey prehension (see earlier discussion). Examination of the distribution of anatomical characters is also revealing. In all mesokinetic taxa, the parietal foramen is either absent or entirely enclosed within the parietal bone. Schwenk (2001) relates this to the presence of internal selection for consistency in the positioning of this foramen in kinetic taxa, and the data tend to support this assertion. Complexity of the frontal-parietal joint was assessed by the presence of either ventral parietal tabs underlying the frontal bones or increased interdigitation at this sutural junction. Presence of these characters would be an indication that mesokinesis is unlikely to possibly occur. Once again, there are no mesokinetic taxa that exhibit a complex frontal-parietal joint, although the presence of a simple joint is not necessarily an indication that a group shows functional mesokinesis (i.e., Helodermatidae). Finally, taxa were evaluated for the presence of the supratemporal (S-T) and postorbital (P-O) bars, as the loss of these struts has been linked to the development of structural instability in the lepidosaur skull and the advent of coupled cranial kinesis (Herrel et al., 2000). There does not appear to be a relationship between the presence of a supratemporal bar and functional mesokinesis. While it is absent in the kinetic gekkotans, some taxa without mesokinesis lack it (Helodermatidae, Serpentes) and it is present in some groups which are clearly mesokinetic (Varanidae). Absence of the postorbital bar may be a better indicator of the potential for mesokinesis. This makes sense from a structural standpoint; loss of the postorbital bar would facilitate muzzle movement by allowing mobility in the lateral postorbital area. All taxa which have been demonstrated to be mesokinetic have either lost the bar or reduced it significantly. In Gerrhonotus, the only anguid that is known to be kinetic, the bar is decreased to dorsal and ventral postorbital processes which are barely in contact with each other and would still allow significant lateral movement in the postorbital region.

Can any conclusions be reached from these distributional data about the origin of either streptostyly or mesokinesis? By recording the presence of these forms of kinesis on a cladogram (see Figure 10), several patterns become apparent. The development of streptostyly probably occurred near the origin of squamates. The reduction of the lower temporal bar, while seemingly associated with quadrate movement, may not be causally linked to it. Fossil sphenodontians show both complete and incomplete lower temporal bars, but the quadrate is always firmly sutured to the quadrate ramus of the pterygoid, preventing movement (Carroll and Currie, 1991). It has been proposed that instead of being an adaptation for streptostyly, reduction of the lower temporal bar may allow for elaboration of lateral adductor musculature. Determination of more anatomical correlates of streptostyly is necessary before evolutionary deductions can be further confirmed, but it is clear that if it originated near the origin of squamates, the ability for functional streptostylic movements has been lost in many groups and that it cannot be used as a synapomorphy for Squamata.



Figure 10. Phylogeny of Lepidoauria with possible origination and loss of streptostyly and mesokinesis indicated. Character states for most clades are generalizations. Nodes as indicated in Figure 9.

Mesokinesis has been considered limited to the scleroglossan lineage (Schwenk, 1994, 2000a; Arnold, 1998). Distributional evidence supports this hypothesis and an evolutionary mechanism (as part of an "evolutionarily stable configuration", see later discussion) has been proposed for its origin. However, although data are equivocal for many groups, the distribution of mesokinesis may be even more limited. Current evidence does not indicate that mesokinesis is present in any scincomorph (although see Arnold, 1998 for a possible exception). There are two possible scenarios that are suggested by this conclusion. First, coupled mesokinesis may have originated early in the scleroglossan lineage and was subsequently lost for the Scincomorpha. An equally parsimonious solution is that it arose independently in both the Anguimorpha and the Gekkota. Current morphological and experimental evidence does not give any indication whether coupled kinesis in gekkotans is significantly different from that in anguimorphs, although both show indications of following the quadric-crank model. Regardless of which hypothesis is correct, examination of fossil scleroglossans could shed light on this issue. Functional mesokinesis is lost relatively easily, as evidenced by its presence in the Varanidae and absence in the closely related snakes and helodermatids, as well as by the variable state among pygopodid lizards.

## The Evolution of Coupled Mesokinesis in Three Lepidosaur Groups and the Possible Role of Exaptation

Whatever the current function of coupled mesokinesis and streptostyly is in extant lepidosaurs, it is possible that this suite of features evolved for a purpose other than that for which it is currently used. Such features are termed exaptations (Gould and Vrba, 1982), and it has been proposed that they may play a role in the evolution of cranial kinesis for several groups of lepidosaurs. Arnold (1994) expanded upon this definition, calling the feature an addition exaptation if both the ancestral and present uses are retained and a transfer exaptation if the original use was subsequently lost. Identification of exaptations is problematic and often relies upon circumstantial evidence. If a group is surveyed for the function of a specific feature and an adaptive advantage which is in addition to the first known is found, exaptation is suggested. However, it is also possible that instead of this representing an exaptation, a feature can simply have evolved as an adaptation for

multiple functions (Arnold, 1998).

Arnold (1998) was the first to suggest an exaptive origin for mesokinesis. He proposed that while its current advantage may be in apprehending prey, for certain scincomorphs (especially cordylids and lacertids) mesokinesis may have originally evolved in association with a crevice-dwelling niche. The advantage of this feature for these forms is that it allows the animal to retreat into narrower fissures when being pursued by predators, since mesokinetic motions allow flattening of the cranial roof at the frontal-parietal joint. Morphological features in putatively mesokinetic rock-dwelling lacertids and cordylids, including decrease in relative head height and reduction in cranial ossification, suggest the importance of this activity in these forms. Currently, this hypothesis is relatively unsupported. Experimental evidence for mesokinesis is indeterminate for lacertids and cordylids. If applicable to all lepidosaurs, this hypothesis would be supported by the presence of certain features in extinct lizards. Specifically, we should expect to see a trend towards decreased dorsoventral skull height and reduced skull ossification in early lizards (especially scincomorphs, since this hypothesis applies mainly to them) and extinct crevice-dwelling forms. It would also be predicted that the suite of characters indicating coupled mesokinesis in extant lizards would not all be present (Arnold, 1998). Unfortunately, these anatomical features are also unclear at the present time, so corroboration of this hypothesis awaits not only adequate fossil finds but also definitive correlation of morphological features with functional mesokinesis.

Herrel et al. (2000) proposed that three structural changes in the gekkonid skull, loss of the lower temporal, supratemporal, and postorbital bars, may have facilitated the development of coupled mesokinesis in this group. Loss of the lower temporal and supratemporal bars may have removed constraints on the size of the jaw adductors (Rieppel and Gronowski, 1981; Herrel et al., 1998), but postorbital bar loss cannot be accounted for by the same explanation. The plesiomorphic activity pattern for gekkonids is thought to be nocturnality (Autumn et al., 1997); an increase in relative eye size, needed for nocturnal activity, could only be permitted by the increased space derived from the loss of this bony strut (Herrel et al., 2000). The loss of these supports would have resulted in extreme instability of the skull. Elaboration of zones of mobility (mesokinetic and hypokinetic axes), and coupling of these movements with streptostyly, is hypothesized to allow the advantage of faster gape cycle, increased bite force, and lowered joint reaction forces.

A similar circumstance may be applicable to the origin of coupled mesokinesis in varanids, the other main group of lizards that have shown strong experimental support for the presence of this form of cranial kinesis. Reduction of bony elements of the varanid skull might be linked not to an increase in eye size, as is possibly the case in gekkonids, but instead to the form of intraoral transport that these animals utilize. Instead of utilizing hyolingual transport to move food items from the jaw tips to the pharynx, varanids use inertial transport mechanisms (defined briefly earlier). Several authors have predicted that due to the high accelerations imparted on the skull during this behavior, inertial transport should be accompanied by a relative decrease in the mass of the cranium (Gans, 1961, 1969; Bramble and Wake, 1985; Cleuren and De Vree, 1992). Herrel et al. (2000) indicated that reduction of skeletal elements in the skull (i.e., supratemporal, lower temporal, postorbital bars) might be part of an exaptive origin for coupled mesokinesis in this group, just as increased eye size was for gekkonids. To test this and other hypotheses related to inertial transport, Metzger and Herrel (2001) examined representatives of a number of lepidosaur families including the Varanidae. Analyses of covariance of skull versus postcranial skeletal mass indicated that varanids did not exhibit relatively lighter skulls relative to body mass (Figure 11). Therefore, these data do not support the idea that mesokinesis in varanids is an exaptation which is a consequence of skull mass reduction for inertial transport.

It is by no means clear that exaptation played a role in the development of coupled mesokinesis in any extant lepidosaurs. One advantage of exaptive hypotheses is that they help explain the origin

of a complex morphological system such as cranial kinesis by explaining how partial development of the complex may have conferred some adaptive advantage. However, there are competing hypotheses for how different forms of cranial kinesis might have evolved. The relatively phenotypically stable lingual feeding system in lepidosaurs has been labeled as an "evolutionarily stable configuration" (ESC), which is described as a complex, functionally integrated set of characters that are coordinated for a suite of functions (Wagner and Schwenk, 2000; Schwenk, 2000a, 2001). There is evidence that after the basal split between iguanians and scleroglossans, the ESC was dissolved early in the scleroglossan lineage. It is possible that the evolution of mesokinesis, thought to be limited to scleroglossans, is intimately linked to this occurrence.



Figure 11. Plot of log (skull mass) versus log (postcranial skeletal mass) for varanids and all other lepidosaurs. Analysis of covariance run on the two regression lines results in no significant difference in slope elevation, indicating that varanid skulls are not lighter relative to the postcranial skeleton when compared to other lepidosaurs.

#### **Future Directions for Research**

Although cranial kinesis is routinely discussed as one of the defining features of the lepidosaur cranium, and has been the subject of numerous experimental studies, we still have little understanding of its functional significance. As Schwenk (2000a) aptly notes, "we are in the precarious position of having enough data to discern patterns and generate hypotheses, but not enough data in most cases to test the hypotheses." While a blanket statement regarding the necessity for more data is surely applicable in the case of lepidosaur cranial kinesis, the acquisition of specific information is needed to answer some of the most elusive aspects of this topic.

First, and probably most importantly, there is a basic lack of knowledge regarding the distribution of all forms of cranial kinesis. Information about possible movement obtained by manipulation of

ligamentous specimens needs to be confirmed through rigorous experimental work using consistent methodology. From the techniques available, cineradiography can simultaneously quantify all forms of cranial kinesis but requires limited out-of-plane movement for analysis to be accurate. Simultaneous use of strain gauges and cineradiography may allow more confident interpretation of strain patterns through correlation with cineradiographical derived data. Several criteria may be used in order to guide the selection of which taxa to evaluate. Examination of anatomical features of the kinetic system, such as those discussed above, for taxa known to be kinetic may suggest that potential unstudied taxa that share those characteristics are more likely to exhibit cranial kinesis. Alternatively, taxa can be chosen in order to test the validity of a specific functional hypothesis. Currently, only the prey prehension hypothesis (see earlier discussion) is firmly rooted in a phylogenetic framework. Testing of this hypothesis would be furthered through studies of insectivorous lizards that use jaw prehension. Additionally, Schwenk's (1994, 2000a) hypothesis that coupled mesokinesis is limited to scleroglossans could be addressed through such research. Of particular interest would be studies on representatives of the Cordylidae, Scincidae, Lacertidae, and Teiidae among scincomorphs and Anguidae among anguimorphs. All of these groups are suggested from anatomical evidence to have at least some kinetic species and are virtually unstudied with respect to cranial kinesis.

A second major avenue of research involves determination of the degree of intraspecific variability in cranial kinesis that is present. This variability can be analyzed at several different levels. First, an understanding of the nature of cranial kinesis during the different stages (prehension, processing, transport, swallowing) of the feeding cycle is needed for many functional hypotheses to be addressed. Unfortunately, many studies only report either maximum values or values during a particular stage. Next, many lepidosaurs are known to exhibit significant ability for modulation of jaw and hyolingual kinematic variables and muscle activation patterns during feeding, values that often vary with properties of the prey item such as prey item type, mass, shape, mobility, and hardness (Bramble and Wake, 1985; Bels and Baltus, 1988; Schwenk and Throckmorton, 1989; Delheusy and Bels, 1999; Herrel et al., 1999b; Herrel et al., 2001b; but see Herrel and De Vree, 1999 for exceptions). Such studies may help in understanding both the degree of stereotypy and the adaptive significance of streptostyly and coupled mesokinesis. A number of other non-kinematic feeding-related variables, such as bite force, have bearing on functional explanations that can potentially be validated by attempting to correlate them with the presence and magnitude of intracranial movements (Herrel et al., 1999a).

Finally, although dependent upon previous determination that a species is kinetic, a complete study of the anatomical correlates of cranial kinesis would be extremely valuable. Potential avenues of exploration with regard to morphological studies include the potential relevance of skull mass reduction, general morphometric analysis of skull form in kinetic vs. non-kinetic lepidosaurs (Schwenk, 2000a, in preparation), and a broad taxonomic study of joint structure, both on a gross morphological and histological level. Although it is unlikely that any single "magic trait" will allow the prediction of a functionally kinetic skull in extant or extinct species, this information will help in determining a suite of characters that allow for reasonable estimations of the potential for cranial kinesis to be made. Of particular interest would be a ontogenetically-controlled histological examination of putative kinetic joints (e.g., parietal-supraoccipital, metakinetic axis, dorsal quadrate-squamosal joint) which have been virtually unstudied to date. Through such studies, the anatomical basis for cranial kinesis in extant lepidosaurs would be better understood and these data could be extrapolated to fossil taxa, allowing a better understanding of the evolution of this distinct feature of the cranial system.

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