

STRAIN GAUGE MEASUREMENT OF MESOKINETIC MOVEMENT IN THE LIZARD *VARANUS EXANTHEMATICUS*

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SUMMARY

Single-element strain gauges were placed across the mesokinetic joint of the skull of the savanna monitor lizard, *Varanus exanthematicus* Bosc, in order to document the extent and timing of mesokinetic movement. In addition, rosette strain gauges were placed on various points of the palato-maxillary segment. Strain recordings and simultaneous cineradiographic films or videotapes were taken during normal feeding activities, including the strike, prey manipulation, ingestion and pharyngeal compression. Tensile strain, indicating lowering (retraction) of the palato-maxillary segment, was observed during all stages of feeding. Compressive strain, indicating lifting (protraction) of the palato-maxillary segment, generally appeared briefly in the strike and during pharyngeal compression. Maximum tensile strains were always larger than maximum compressive strains within each sequence. The highest levels of tensile strain occurred during prey manipulation periods, which were characterized by isometric biting. Strain on the palato-maxillary segment revealed a pattern of timing similar to the one at the mesokinetic joint, although strain levels were at least an order of magnitude lower. These data directly contradict conventional models of the function of the kinetic skull in lizards. We conclude that the kinetic apparatus in lizards is not a mechanism for actively moving the palato-maxillary unit and is therefore not a mechanism for increasing gape or actively controlling upper jaw movements.

INTRODUCTION

The skulls of many reptiles, including living lizards and snakes and numerous fossil forms, have specific areas of potential movement. Such movement is called cranial kinesis. Although vertebrate morphologists and palaeontologists have long been interested in the timing, amount and significance of cranial kinesis, there is no general consensus on these issues. In lizards, there are three specific types of cranial movement (Versluys, 1910). They are: (1) movement of the quadrate or jaw suspension, *streptostyly*; (2) movement of the ossified braincase or occipital unit at the paroccipital process/supratemporal junction, parietal/supraoccipital junction and basiptyergoid joint, *metakinesis*; and (3) movement of the palato-maxillary unit or snout at the frontal-parietal line, *mesokinesis* (see Smith, 1982, for a review of the morphology and literature on this subject).

Key words: Mesokinesis, lizards, strain gauge.

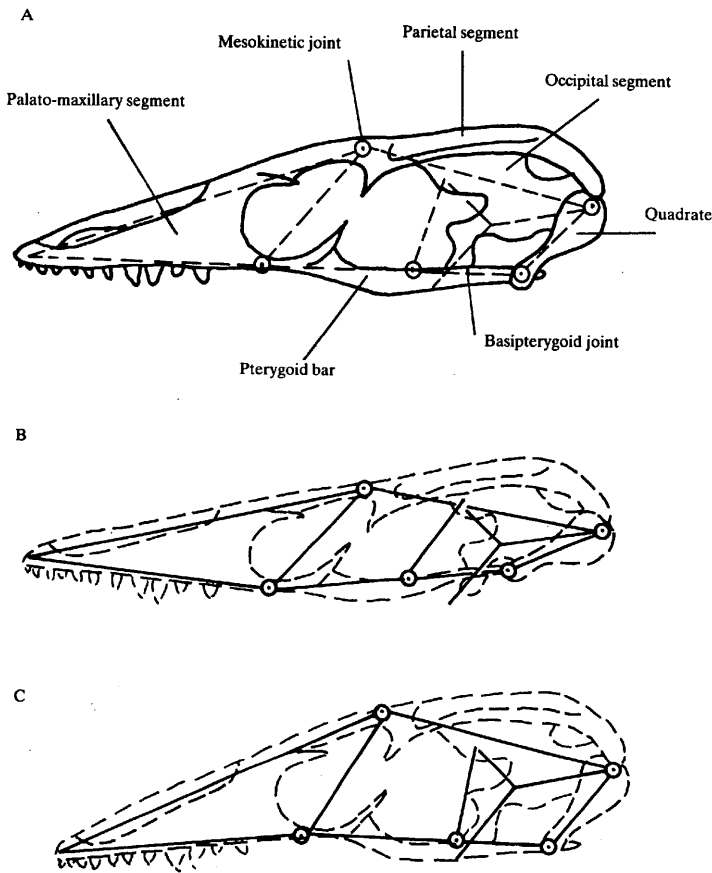


Fig. 1. The kinetic apparatus of lizards as modelled by Frazzetta (1962). (A) Resting state. The major morphological features to be discussed are labelled and the 'quadratic crank' mechanism is shown as a dashed line. The vertical bar anterior to the occipital segment is the epipterygoid bone. (B) The quadratic crank mechanism in the protracted or lifted state (jaw open); skull in dashed line. (C) The quadratic crank in retracted state; skull morphology in dashed line. The proportions and angles of the quadratic crank are duplicated exactly from Frazzetta (1962).

The most accepted model for the timing and amount of cranial kinesis in lizards was presented by Frazzetta (1962), although elements of this model go back to the work of Versluys (1910, 1912). Frazzetta proposed that as the jaw opens, the parietal segment is depressed, the quadrate is moved forward and the palato-

maxillary segment or snout is lifted (protracted) at the mesokinetic joint (Fig. 1B). This lifting is the result of a force directed anteriorly along the pterygoid bone produced by the *Mm. levator* and protractor pterygoidei. He proposed that as the jaws close, the quadrate and pterygoid bones are withdrawn and the maxillary segment is lowered (retracted; Fig. 1C). Two major features of this model are: (1) there is significant and regular lifting or protraction of the snout with a bending or hinging at the mesokinetic joint during jaw opening and (2) the three types of cranial movements are linked so that a 'quadratic crank' mechanism is formed.

Cinematographic data published by various workers are said to support the above model (Bolt & Ewer, 1964; Frazzetta, 1962, 1983; Impey, 1967; Rieppel, 1979), although quantitative data given by Frazzetta (1983) suggest that the movements are less regular than he has previously claimed. This model has recently been challenged by workers analysing cineradiographic film of feeding in a variety of lizards (Smith, 1980, 1982; Throckmorton, 1976; Throckmorton & Clarke, 1981). In the cineradiographic studies, lifting of the palato-maxillary segment was not observed, although streptostyly, independent of movement of the palato-maxillary segment, was seen. Thus, there are two conflicting hypotheses about cranial kinesis, and each claim supporting data. In one, kinesis is seen as a mechanism for regular lifting and lowering of the maxilla around the mesokinetic joint during jaw opening. This movement is thought to be linked to movements of the quadrate and occipital units. In the second, it is claimed that lifting of the palato-maxillary unit is slight or non-existent and cranial movements, when observed (i.e. streptostyly), are not necessarily linked with movements of the other cranial segments. Because cinematographic and cineradiographic techniques have yielded conflicting data, we propose to test these hypotheses using an entirely different technique.

In this study we used single-element strain gauges to measure strain at the mesokinetic joint in order to detect the nature of the movements at that joint. This approach has certain advantages over previous ones, e.g. these gauges can measure very small strains, give a continuous record and do not require particular alignment of an animal relative to any filming plane. Employing this technique should circumvent methodological problems involved in measuring slight deformations at the mesokinetic joint from either cinematographic or cineradiographic films (Smith, 1982). We have recorded strain at the mesokinetic joint during a range of activities including the strike, manipulation and ingestion of food. Further, in order to obtain information on the mechanical environment near the mesokinetic joint, we have conducted a number of experiments where single-element strain gauges were placed on either side of the joint, or where rosette strain gauges were placed at various points along the frontal bone.

MATERIALS AND METHODS

Experimental animals

Twelve experiments were conducted on the savanna monitor lizard, *Varanus exanthematicus*. The animals were obtained from commercial animal dealers and maintained in the laboratory for up to 5 years before experiments were conducted. Animals used in experiments weighed between 453 and 2800 g. Monitor lizards are

active predators and scavengers and eat a variety of vertebrate and invertebrate food (i.e. Auffenberg, 1981; Cissé, 1969; Pianka, 1969, 1971). By most accounts, their skull is highly kinetic, (e.g. Frazzetta, 1962; Iordansky, 1966, 1970; Mertens, 1942; Rieppel, 1978, 1979; Versluys, 1910, 1912) capable of streptostyly, mesokinesis and metakinesis.

Strain gauge bonding procedure

In eight instances foil single-element strain gauges (BAE-06-031CC-120TE, William T. Bean, Inc.) were bonded directly over the mesokinetic joint, and in eight instances rosette strain gauges (WA-06-030WR-120, Micro-Measurements) were bonded on the frontal bone (Fig. 2). In addition, in nine instances single-element or rosette strain gauges were bonded along the parietal, nasal or maxillary bones. In most cases, two gauges were placed on an animal in each experiment. Following general anaesthesia, induced with an intramuscular injection of sodium Brevitol (Smith, 1982), the thin layer of skin over the strain gauge site was removed. The periosteum was scraped from the bone surface and, following adequate haemostasis, the area was degreased with a 2:1 chloroform-methanol solution and neutralized with a weak solution of ammonium hydroxide. Methyl-3 cyano-acrylate adhesive was applied to the gauge and the gauge was bonded to the surface of the bone. For additional details on strain gauge bonding procedures, see Hylander (1979).

Recording procedure

The lizards were kept unrestrained in a large Plexiglas box or glass aquarium and fed live adult laboratory mice during the recording procedure. Strain gauge data were recorded directly on a six-channel Gould chart recorder during experiments and usually on FM tape (Bell & Howell 4020A). Quantitative data presented in this paper are from sequences recorded on FM tape at 38.4 cm s^{-1} and later played back onto the Gould chart recorder at 4.8 cm s^{-1} . This ensured that the recording equipment exhibited an adequate frequency response (320 Hz full-scale deflection) to record and reproduce the strain data. In some cases, strain gauge and electromyographic data were recorded simultaneously, and in all cases either cineradiography or videotapes recorded the simultaneous behaviour of the animal during the experiment. An electronic pulse corresponding to each frame of cineradiographic film was recorded simultaneously with strain data to allow precise frame-by-frame synchronization of strain and behaviour. See Smith (1982) for further details on electromyographic and cineradiographic techniques. During experiments in which behaviour was recorded using videotape, one camera was focused on the subject while a second camera was focused on the chart-recorder tracing. Using a videotape recorder and special-effects generator, a split-screen recording was made of the subject and the chart-recorder tracing. The videotape was later played back at slow speeds so that simultaneous behaviour and bone strain records could be precisely correlated (Hylander, 1979). After all recordings were completed the gauges were removed and the animals recovered with no apparent change in health.

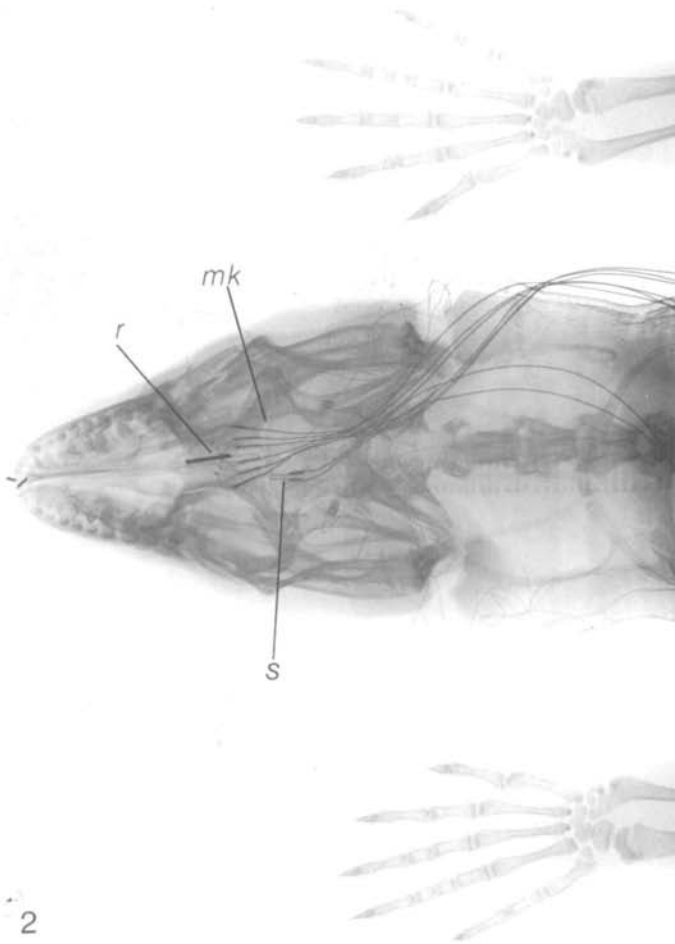


Fig. 2. X-ray of an anaesthetized *Varanus exanthematicus* after the placement of a single-element (s) and a rosette strain (r) gauge. The visible portions of the gauges represent wire leads and terminals – the sensing elements are not visible. The sensing element of the single-element gauge is immediately anterior to the visible portion, and is exactly over the mesokinetiC joint (mk). The visible large wire along the rosette is parallel to the long axis of the middle strain gauge element. Magnification, $\times 1$.

Measurements of strain

Strain gauges bonded to a bone surface enable one to measure surface deformations due to muscle or reaction forces. Strain is defined as the change in length of an object divided by the original length ($\Delta L/L$). It is expressed in units of microstrain ($\mu\epsilon$), where 10000 $\mu\epsilon$ equals a 1% deformation. Conventionally, tensile strain is expressed as a positive value and compressive strain as a negative value (i.e. Hylander, 1977; Lanyon, 1973). Single-element gauges detect only strain directed along the long axis of the gauge. Strain on a given surface can be better characterized using rosette strain gauges. In a rosette gauge, three single-element gauges are aligned at a known orientation to one another. The three independent measures of strain allow the maximum and minimum principal strains as well as the directions of these principal strains to be determined (Dalby & Riley, 1965). In this study, the maximum principal strain (ϵ_1) is the largest tensile strain, while the minimum principal strain (ϵ_2) is usually the largest compressive strain value, although ϵ_1 and ϵ_2 need not always be tensile and compressive strain respectively; in some recordings in this study, both ϵ_1 and ϵ_2 were tensile.

RESULTS

Predicted strain patterns

In the experiments discussed here, single-element gauges were placed directly on the mesokinetic joint and aligned so that their long axes were parallel to the mid-sagittal plane (Fig. 2). A gauge aligned in this manner detects strain associated with axial loading along the snout or from sagittal bending at this joint. Fig. 3A illustrates that compressive strain at the mesokinetic joint would result from either pushing the snout caudally (axial loading) or bending the palato-maxillary segment upwards. Conversely, tensile strain would occur if the palato-maxillary segment were pulled anteriorly, or if it were bent downwards. According to conventional models, mesokinetic movement should involve a combination of these two general types of loading conditions, because a force directed anteriorly along the pterygoid bone is supposed to push the palato-maxillary unit so that the end of this segment lifts (protracts) causing bending at the mesokinetic joint. The reverse type of bending (i.e. lowering or retraction of the palato-maxillary unit) is thought to be due to a backwards pull on the pterygoid bone (Frazzetta, 1962).

In order to determine the effect of various loads along the mesokinetic joint, we manipulated the skulls of dead or anaesthetized animals on which we had bonded gauges on the mesokinetic joint. Anaesthetized animals were manipulated immediately before or after recording to test each specific gauge placement. Gauges were also placed on fresh skulls which were stripped of some musculature, but no ligaments. In these manipulations mesokinetic movement was produced by pushing (1) the anterior end of the snout up and down or (2) the palato-maxillary bar at the pterygoid-ectopterygoid junction anteriorly and posteriorly. Other manipulations, such as twisting and pushing the tip of the snout were performed in order to simulate other potential loading patterns.

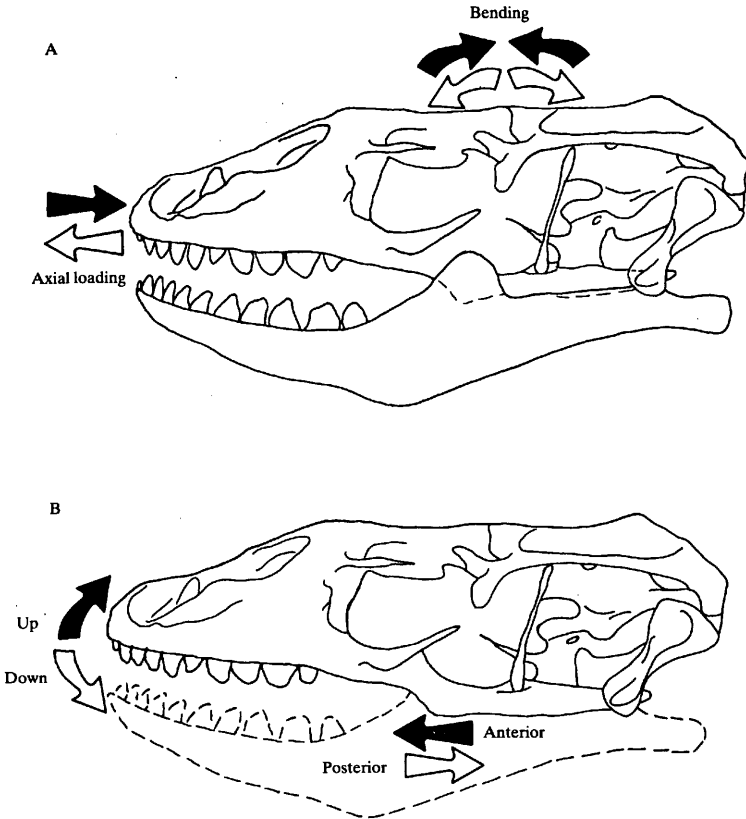


Fig. 3. (A) Expected strain patterns on the mesokinetic joint resulting from axial loading and bending. Black arrows represent loading patterns which will compress the mesokinetic joint; white arrows represent loading patterns which will tense this joint. (B) Results of experimental manipulations of skulls with strain gauges on the mesokinetic joint. Forces were applied on the tip of the snout and at the pterygoid-ectopterygoid junction. Arrows represent direction of applied force. Black arrows represent loading patterns which produced compressive strain on the mesokinetic joint; white arrows represent loading patterns which produced tensile strain on the mesokinetic joint.

Pushing either directly upwards on the tip of the snout or anteriorly on the pterygoid bar resulted in compression across the mesokinetic joint (Fig. 3B). Pushing the snout down or the pterygoid back resulted in tension. The magnitudes of tension and compression were similar given similar amounts of pressure (as judged subjectively). No other manipulations (i.e. twisting, lateral compression or pulling and pushing the tip of the snout) produced strains as large as those recorded during bending. In interpreting our recordings from strain gauges placed across this joint, we assume that bending is potentially the most important type of stress, and that tension indicates lowering (retraction) of the palato-maxillary segment and compression indicates lifting (protraction) of this segment.

Feeding behaviour

Strain recordings from along the mesokinetic joint were made during the strike, prey manipulation, inertial thrust and pharyngeal compression stages of feeding (Smith, 1982). During the strike, the prey item is grasped by the jaws. This stage is followed by a period of prey manipulation, during which the prey is orientated and subdued. Activity of jaw muscles during this period has been termed 'power phase activity' (Smith, 1982). This stage may vary from sequence to sequence in terms of length and intensity of muscle activity, although maximum levels of muscle activity generally occur in this phase. Inertial feeding, which follows prey manipulation, is a stereotyped activity during which the prey is literally thrown through the mouth and into the pharynx. In an inertial thrust, the head is pulled back as the jaws are opened rapidly; thus, the prey is pulled backwards and released. The head is then thrust forwards around the prey as the jaws close. Once a number of inertial thrusts have tossed the prey into the pharyngeal region, the hyobranchial apparatus is brought forward and then compressed against the palate so that the prey is gradually squeezed out of the pharynx and into the oesophagus (pharyngeal compression stage). The details of behaviour, intra-cranial movement and electromyographic patterns of jaw muscles during these stages can be found elsewhere (Smith, 1982).

Single-element gauges

During the strike, the mesokinetic joint usually undergoes a transient period of compressive strain as the jaws initially open and then it invariably experiences a rapid rise in tensile strain as the jaws close around the prey (Figs 4, 5). This tensile strain continues during prey manipulation and biting (which is equivalent to 'power phases' of jaw muscle activity; Smith, 1982). Compressive strains during prey manipulation periods were very rare and generally occurred when the animal was pushing the prey against the substrate. The maximum tensile strain recorded during prey manipulation was $14\,000\ \mu\epsilon$ (Table 1). During inertial feeding, the gauges also primarily sensed tension (Table 2). Two distinct peaks of tensile strain were observed in each inertial thrust. During jaw opening in an inertial thrust there is a rapid rise in tensile strain which peaks at maximum gape. As the jaws begin to close the tensile strain diminishes, and then rapidly rises again as the jaws meet the prey. In those inertial thrusts which occurred early in a feeding sequence, there was

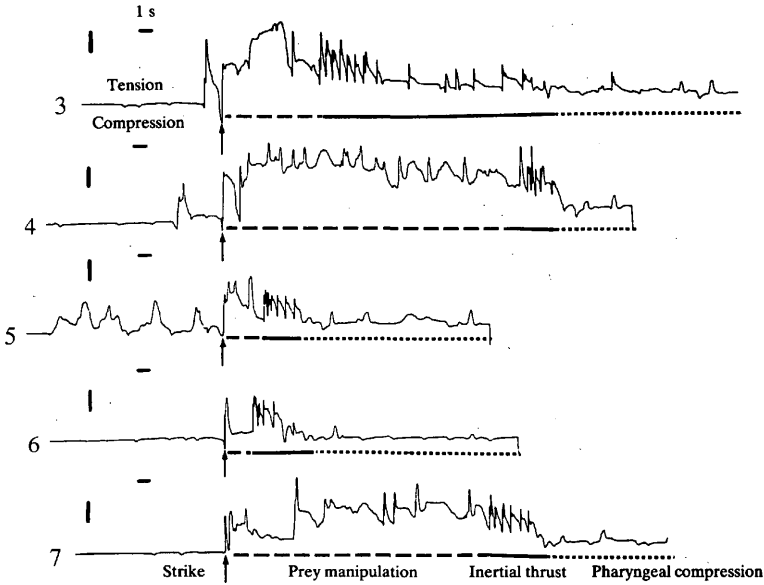


Fig. 4. A series of five tracings of consecutive sequences from a single-clement gauge placed on the mesokinetiC joint. Vertical bars on the left represent $400\ \mu\epsilon$; horizontal bars represent 1 s. In each case a zero level baseline is shown at the beginning and end of each sequence. Movement above that baseline represents tension, and below that baseline represents compression. The strike in each sequence is represented by an arrow. Activity before the strike is either 'missed' strikes (3,4) or pushing the snout against the sides and bottom of the enclosure (5). Prey manipulation, inertial thrusts and pharyngeal compression stages are represented by the dashed, solid and dotted lines respectively at the bottom of each tracing. Tracing 6 is shown as (A) in Fig. 5. These tracings represent gauge number 1 in Tables 1 and 2.

often a third peak in tension, which may reflect brief bites which often occur during inertial feeding. In general maximum strain was lower in inertial feeding than in prey manipulation. During the pharyngeal compression stage, strain levels were low relative to prey manipulation and inertial feeding. Tensile and compressive strains were registered during this stage.

For each individual strain gauge site, the levels of strain were consistent throughout all sequences. However, the levels of strain were quite variable between each individual site (Table 1). Some gauges experienced very low levels of strain (e.g. less than $500\ \mu\epsilon$ in either tension or compression), and rarely deflected from the zero baseline. In other instances the strain gauges experienced higher levels of strain. The very low strain levels may have been a result of gauge position, as in one experiment, a low strain level occurred simultaneously with a high strain level (two gauges placed on the same animal; Fig. 5).

There are at least two features of gauge placement which could lead to these low

Table 1. *Quantitative data from four single-element gauges placed on the mesokinetiic joint*

Gauge	N	Strike		Power		Pharyngeal Compression	
		Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
1	5	-2015 (-234 to -4219)	7947 (6681 to 9025)	3512 (1406 to 4806)	12864 (9963 to 14652)	-1335 (-351 to -2461)	2109 (820 to 3047)
2	5	3 (-51 to 85)	236 (17 to 513)	40 (0 to 68)	260 (85 to 393)	30 (0 to 51)	105 (66 to 136)
3	5	-256 (-573 to -98)	426 (65 to 1503)	-541 (-890 to -257)	811 (375 to 1186)	—	—
4	4	-1749 (-3000 to -1166)	3833 (2000 to 5833)	500 (166 to 1000)	4874 (2000 to 6666)	—	—

The algebraically smallest (minimum) and algebraically largest (maximum) value for each stage in $\mu\epsilon$ (strike, prey manipulation and pharyngeal compression) was taken from a number of sequences (N). The mean maximum or minimum value and the range of these values (in parentheses) are given.

Tape recordings were not continued into the pharyngeal compression stage for gauges 3 and 4, so these data were not available.

Gauges 1 and 2 were on the same animal during the same sequences; their difference illustrates the types of differences which may be due to gauge placement. They are illustrated in Figs 3 and 4.

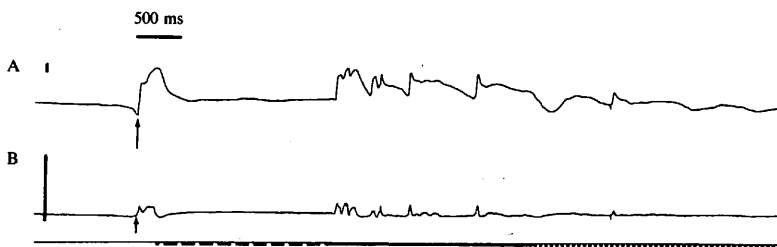


Fig. 5. A sequence showing simultaneous activity of two strain gauges placed on the mesokinetic joint. (A) represents the higher level of strain discussed in the text, while (B) represents a low level. Note the direction and pattern of strain is identical. Vertical bar in each represents 200 $\mu\epsilon$; the amplification of gauge B is eight times that of A. Tracing above neutral baseline represents tension, below that baseline, compression. Gauge A is tracing 6 in Fig. 4 (with time base expanded); A and B represent gauges 1 and 2 in Tables 1 and 2. Strike, prey manipulation, inertial thrusts and pharyngeal compression stages as in Fig. 4.

Table 2. Quantitative data on strain levels during inertial feeding for the same gauges shown in Table 1

Gauge	N	Inertial thrust 1	Inertial thrust 2
1	28	7028 (5274-9377)	7749 (4102-11 135)
2	28	241.4 (102-427)	239 (0-804)
3	9	164 (0-543)	368 (59-791)
4	19	1859 (333-3333)	2473 (500-4166)

Inertial thrust values 1 and 2 represent the peak strain level corresponding to the maximum gape and jaws meeting the prey respectively (see text and Figs 3 and 4). Several inertial thrusts for each sequence were analysed (N). As in Table 1, the mean and range of values in $\mu\epsilon$ are presented.

strain levels. Although every effort was made to place the gauge parallel to the mid-sagittal plane, placement of the gauge oblique to the mesokinetic joint and thus the axis of bending would cause the gauge to be improperly aligned to detect maximum strains. Reduced strain would also result if the gauge was placed so that the sensing element was positioned slightly anterior or posterior to the joint. In this case a recording of bone strain, rather than a combination of bone strain and mesokinetic joint tissue strain would result. Although both of these factors possibly influenced our recordings, we suspect that the latter was the most important.

Rosette strain gauges

The magnitude and direction of strain on the frontal bone varied widely from experiment to experiment and for the rosette data only the most general points of our results will be discussed. As in the single-element strain gauge recordings, the

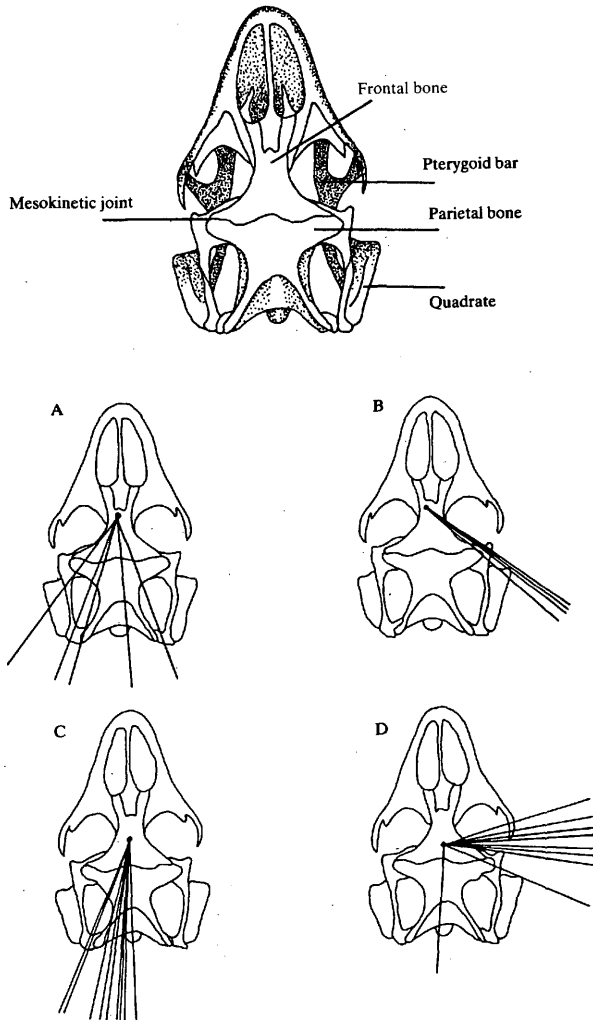


Fig. 6. Results from rosette strain gauge experiments. Top drawing is for orientation; major morphological features are labelled. A, B, C and D represent four different rosette strain gauge experiments. (A) indicates peak strains from an inertial thrust sequence, while (B)–(D) represent peak strains during prey manipulation. The lines represent the direction of the maximum principal strain (ϵ_1) for each peak. The direction of minimum principal strain (ϵ_2) is at 90° to this.

maximum principal strains (maximum tension) were highest during prey manipulation. Two peaks of strain were observed during inertial feeding. The timing of the peaks of strain during inertial feeding was the same as was found with the single-element gauges on the mesokinetic joint. The levels of frontal bone strain, however, were at least an order of magnitude lower than strain across the mesokinetic joint. The largest principal strain value, (ϵ_1) recorded on the frontal bone in any experiment was approximately $2000 \mu\epsilon$, although generally the strain level was between 100 and $600 \mu\epsilon$. The magnitude of the maximum principal strain was always larger than the minimum principal strain.

The direction of ϵ_1 was variable (Fig. 6). Most often, tension was directed along the long axis of the snout. Usually, strain directions were similar for a given strain gauge placement during prey manipulation and inertial feeding. The relative magnitudes of ϵ_1 and ϵ_2 were extremely variable. Occasionally both the maximum and minimum principal strains were tensile. In these cases, the dorsal surface of the maxilla was being placed in tension along the long axis of the snout and at 90° to this axis.

DISCUSSION

Rosette strain gauge data

Maximum levels of strain in the rosette strain gauge placements were of the order of several hundred microstrain. This level is similar to strains measured on the mandible of macaque monkeys during mastication (Hylander, 1979), the opercula of the bluegill sunfish during feeding (Lauder & Lanyon, 1980) and limb bones of mammals during running (Lanyon & Rubin, 1980).

The variability in level and magnitudes of ϵ_1 and ϵ_2 , and in the direction of principal strains on the frontal bone is not surprising for two reasons. First, no attempt was made to duplicate precisely the position of the strain gauge, and therefore some of the variability may reflect differences in position and orientation. Second, as shown elsewhere (Smith, 1982), there may be wide variations in behaviour from sequence to sequence, especially during prey manipulation. This variation includes occasional unilateral muscle activity or position of the prey in the jaws. Variability in bite point position or relative muscle activity would have significant effects on the loading patterns on the frontal bone and thus lead to the types of differences observed in strain magnitude, direction and ratio of ϵ_1 and ϵ_2 . Additional experiments are necessary in order to analyse the complex pattern of strain on the frontal bone.

Single-element gauges

Compressive strain was observed during pharyngeal compression and during jaw opening in the strike. The levels of compressive strain were similar in these two phases, approximately $-500 \mu\epsilon$. The maximum amount of compressive strain registered in any experiment was $-4000 \mu\epsilon$ or 0.4% strain. More often compressive strain was less than 0.1% strain, a level of strain typically measured along the *surface of cortical bone* of vertebrates during normal activities. Tensile strain,

associated with palato-maxillary retraction, was present during all stages of feeding. Maximum levels of tensile strain were considerably higher than maximum levels of compressive strain. During prey manipulation or 'power phases' of muscle activity, strains as large as $14\,000\ \mu\epsilon$ were recorded.

It is difficult to interpret what the levels of strain mean in terms of amount of movement. If the presence of the strain gauge had no effect on the amount of mesokinetic movement, these low levels of strain would indicate that there is little movement. For example, $14\,000\ \mu\epsilon$ (the maximum amount of strain measured) would translate to less than one degree of movement. However, we cannot be certain that the strain gauges did not significantly restrict the amount of movement at this joint by virtue of their presence. Nor can we calibrate the level of strain measured by each individual gauge with an absolute amount of movement, because of the variability in strain level between each gauge placement. For example, as discussed above, two gauges on the mesokinetic joint at the same time recorded very different levels of strain.

If we assume that the gauge itself did not restrict movement, we may translate this strain into angular movement in the following manner. The sensitive element of the strain gauge is 1 mm long. $14\,000\ \mu\epsilon$ represents 1.4% strain, which is equivalent to $1 \times 0.014 = 0.014$ mm of extension over the length of the gauge. Although it is difficult to determine the centre of rotation of the palato-maxillary segment, we may take two extremes: (1) the centre of the palato-maxillary segment, 10 mm from the gauge, and (2) the centre of the bones forming the mesokinetic hinge, 1.5 mm from the gauge. In the former case the extension indicates bending through an angle of $0.014\text{ mm}/10\text{ mm} = 0.0014$ rad, or 0.08° . Taking the latter centre of rotation, 1.4% extension indicates bending through an angle of 0.009 rad or 0.53° . These are, again, measures of tensile strain indicating retraction and represent the *maximum* strain ever recorded. The maximum compressive strain recorded, indicating protraction, was $-4000\ \mu\epsilon$ which gives much lower estimates of protractive movement, 0.02 – 0.15° .

While it may be impossible to correlate the level of strain with the amount of movement, there is no reason to believe that the direction or timing of strain would be affected by the presence of the gauge. The data on the direction and timing of the strains contradict the predictions made from traditional models of cranial kinesis. First, these data indicate that there is little lifting or protraction of the snout at any time, and none whatsoever during inertial feeding (directly contradicting the models of Boltz & Ewer, 1964 and Rieppel, 1979, for example). Second, further contradicting these models, is the fact that within any experiment, the maximum level of compression measured was always less than the maximum level of tension, indicating that the relative extent of protraction is always less than the relative amount of retraction. Third, in contrast to predictions of models by Frazzetta (1962, 1983), for example, we observed that the relative amount of tension, which reflects retraction, is less during jaw closing than during isometric biting. Of all the work on cranial kinesis in lizards, only the analyses of Iordansky (1966, 1970) would predict this result. Finally, it must be emphasized that these data support those studies in which cineradiographic data indicated that little or no movement occurs at the mesokinetic joint (Smith, 1980, 1982; Throckmorton, 1976; Throckmorton & Clarke, 1981).

Patterns of strain vary between the strike, prey manipulation, inertial thrust and pharyngeal compression stages. These behavioural stages are also characterized by distinct electromyographic patterns (Smith, 1982). As noted in previous studies, the prey manipulation stage is highly variable. It tends to have the highest levels of muscle activity, while inertial thrusts are associated with generally lower levels of muscle activity and stereotypic, rhythmic behaviour (Smith, 1982).

How do these strain patterns in the vicinity of the mesokinetic joint relate to external forces that cause the strains to occur? Deformations at the mesokinetic joint during normal feeding behaviour may be due to: (1) inertial responses to head movements, (2) muscle forces from the *Mm. levator* and protractor pterygoideii, (3) bending moments associated with the bite force, and (4) bending moments associated with jaw adductor muscle force. The stresses produced by each of these forces and the resultant strain patterns will be briefly discussed below.

The extremely rapid rise in tension during jaw opening in inertial feeding may be due in part to inertial effects resulting from the rapid lifting of the head at the atlanto-occipital joint, and the simultaneous posterior pull of the entire head and upper body (Smith, 1982). This interpretation is supported by the fact that the time course of the rise in tension corresponds exactly to head and jaw movements during fast opening. The fact that the mesokinetic joint is in tension during jaw opening in inertial feeding eliminates the possibility that it is being actively lifted by the *Mm. levator* and protractor pterygoideii, because under these conditions this joint would experience compression.

Conventional analyses of mesokinetic movement claim that the *Mm. levator* and protractor pterygoideii exert an anteriorly directed force on the pterygoid bar which lifts the palato-maxillary unit (Frazzetta, 1962; Impey, 1967; Rieppel, 1979; Versluys, 1910). We have shown that there is no evidence that this occurs during jaw opening in inertial feeding. The slight compression registered during jaw opening in the strike may be a result of the activity of these muscles. However, we believe that a re-examination of their potential mechanical effects does not support assumptions that they function as elevators of the palato-maxillary unit. Fig. 7A shows the relative components of force of both the *Mm. levator* and protractor pterygoideii. Portions of the force vector of the *M. protractor pterygoideii* pull the palato-maxillary bar anteriorly (or the occipital unit posteriorly); the *M. levator pterygoideii* will pull the palato-maxillary bar slightly posteriorly. In both cases, the major force vector is elevation of the palato-maxillary bar or depression of the anterior part of the occipital segment. Although the *Mm. protractor* and *levator pterygoideii* in lizards may be homologous with muscles which protract the pterygoid bar in birds and snakes (i.e. they are all 'constrictor internus dorsalis' portions of the trigeminal musculature; Haas, 1973; Lakjer, 1926), we suggest that these muscles in lizards do not function similarly, and that this homology has misled workers on both the function of these muscles and the kinetic apparatus since the time of Versluys.

We suggest that the primary effect of these muscles in lizards is to stabilize the occipital unit and pterygoid bone at the basiptyergoid joint. This suggestion is supported by the following observations. (1) The resultant force of these muscles is primarily dorso-ventral, which makes them poorly arranged to serve primarily to

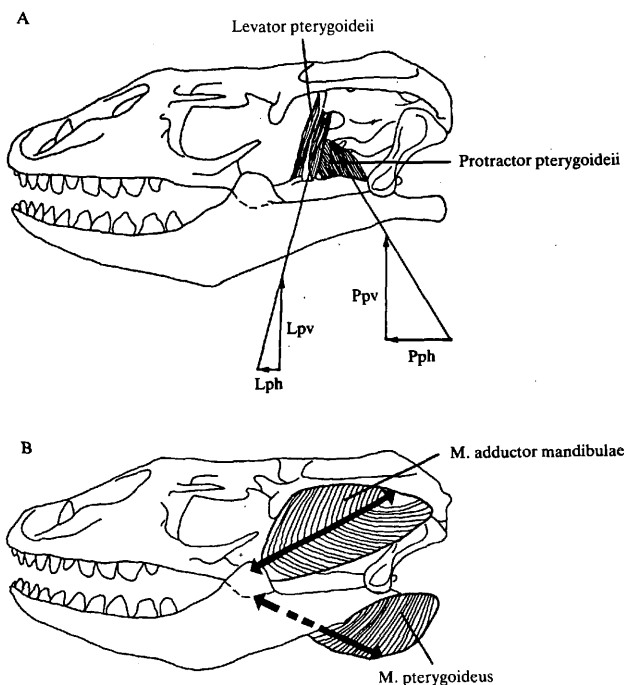


Fig. 7. The force vectors for the M. levator pterygoidei and M. protractor pterygoidei of *Varanus exanthematicus*. Lpv, vertical component of M. levator pterygoidei; Lph, horizontal component of M. levator pterygoidei; Ppv, vertical component of M. protractor pterygoidei; Pph, horizontal component of M. protractor pterygoidei. (B) Outline of the Mm. adductor mandibulae externus and pterygoideus. The double-ended arrows indicate alignment of resultant muscle forces. Dashed portion of the double-ended arrow for the M. pterygoideus represents that portion which runs on the medial side of the mandible to insert on the pterygoid bone. The M. adductor mandibulae pulls the mandible up and back and the posterior region of the parietal segment down. The M. pterygoideus pulls the mandible forward and up and the palato-maxillary segment down. The combined action of these muscles leads to cranial bending and places the mesokinetic joint in tension (see text for further discussion).

protract the palato-maxillary segment. Instead, they appear to be well aligned to resist displacements of the basipterygoid joint. (2) Their size and cross-sectional area are almost insignificant compared to the jaw adducting muscles which would be their antagonists in palato-maxillary movement (generally less than 1 % of the total adductor mass). This is important because, during jaw opening, parts of the jaw adductors are electrically active during the supposed period of activity of the Mm. levator and protractor pterygoidei (Smith, 1982). (3) The mass of the occipital unit is rather small compared to that of the palato-maxillary unit and pterygoid bar.

Unless the occipital unit were otherwise stabilized, the *M. protractor pterygoideii*, in particular, would rotate the occipital unit down relative to the basiptyergoid joint rather than push the palato-maxillary unit forward. (4) The *Mm. levator* and *protractor pterygoideii* are found in lizards which possess a well-developed basiptyergoid joint but no particular mesokinetic mobility (i.e. *Ctenosaura*, *Uromastix*). These features will be discussed in more detail elsewhere (K. K. Smith, in preparation). In summary, we conclude, from the strain gauge data and the arrangement of the cranial musculature, that the *Mm. levator* and *protractor pterygoideii* have little or no effect on the palato-maxillary segment.

A consistent observation in this study is that the region of the mesokinetic joint experiences tension directed along the long axis of the head during isometric biting. Presumably, strain in this region at this time is due primarily to bending moments associated with adductor muscle and bite forces. The external surface of the mesokinetic joint would be subject to compressive stress and strain due to bending associated with the bite force during biting. In experimental manipulations of skulls, a force directed upwards on the upper tooth row produced compression on the mesokinetic joint. However the force from the jaw adducting muscles will exert a moment which causes bending opposite to that associated with the bite force, leading to tension on the mesokinetic joint. If the mandible is stabilized, most portions of the *M. adductor mandibulae* will pull the posterior end of the parietal segment downward, producing tension at the mesokinetic joint. Likewise, with a stabilized mandible, the *M. pterygoideus* exerts a posteriorly directed force at the base of the palato-maxillary unit near the pterygoid-ectopterygoid junction (Fig. 7B). Such a force was shown to produce tension at the mesokinetic joint in experimental manipulations. During isometric biting the mandible is stabilized dorso-ventrally by the prey between the upper and lower jaws. It is stabilized antero-posteriorly by opposing muscle forces. That is, the *M. adductor mandibulae* pulls the mandible up and back, while the *M. pterygoideus* pulls the mandible up and forwards; their combined activity bends or retracts the palato-maxillary and parietal segments at the mesokinetic joint. The tension recorded at the mesokinetic joint during biting suggests that the combined bending moment associated with the adductor muscle force is greater than the bending moment associated with the bite force.

In summary, the data from this study directly contradict analyses which claim that the kinetic apparatus in lizards is a mechanism for actively moving the palato-maxillary unit (i.e. Auffenberg, 1981; Bolt & Ewer, 1964; Frazzetta, 1962; Impey, 1967; Iordansky, 1966; Rieppel, 1979). We conclude that cranial kinesis in lizards is not a mechanism for increasing gape or actively controlling upper jaw movements. The evidence obtained in this study strongly supports the need for a re-evaluation of the prevailing mechanical and adaptive explanations for cranial kinesis in lizards.

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