

CRANIAL KINESIS IN LIZARDS; CONTRIBUTION TO
THE PROBLEM OF THE ADAPTIVE SIGNIFICANCE OF SKULL KINESIS

by N. N. Iordansky

Zoologicheskii Zhurnal
(Zoological Journal)

volume 45, number 9
pp. 1398-1410

1966

Translated by Dr. Leon Kelso
Edited by Carl Gans

SMITHSONIAN HERPETOLOGICAL INFORMATION SERVICES
1968

Additional copies available from:

Division of Reptiles and Amphibians
United States National Museum
Washington, D. C. 20560

The term kinesis, when used as a reference to the skulls of tetrapods, is defined either as the movement of the upper jaw accompanied by specific elements of (or the entire) dermatocranium, or as movement of the olfactory region of the neurocranium with respect to the rear part of the axial skull (i.e., of the brain case formed of cartilage-replacement bones). This phenomenon was first described by Nitzsch in 1822, according to Bradley (1903), who discovered that the lizard skull was capable of movement in the fronto-parietal suture and in the articulation of the parietal bone with the occipital. Bradley studied the chewing musculature and accompanying movements in the skull of lizards. He formulated the first hypothesis of the functional significance of the movement of the upper jaw in relation to the axial skull (see below) and made the first attempt to correlate these movements with the functions of specific muscles. The term "cranial kinesis" was introduced by Versluys (1910) for a construction of the skull in which such movements would be possible, as well as the movements of the lower jaw. Versluys (1910, 1912, 1922, 1927) made a more thorough analysis of tetrapod cranial kinesis. He pointed out the prevalence of kinesis among most of the tetrapod groups, recent and extinct; classified various forms of kinesis, and proposed a theory of cranial kinesis, according to which the tetrapod skull was primitively kinetic; kinesis was inherited by the ancient tetrapods from fish-like ancestors and secondarily lost in several lines of tetrapod evolution.¹ From Versluys comes one of the most widely accepted hypotheses to date on the functional significance of cranial kinesis. Later contributions to the study of kinesis were made by Lakjer (1927), Marinelli (1928, 1936), de Jong and Brongersma (1927), Hofer (1960) and various other authors. Kinesis in crossopterygian fishes was shown by Romer (1937 per Frazzetta 1962) and in some stegocephalians (Pfannenstiel, 1932; according to Frazzetta, 1962). An exceptional amount of work on kinesis was devoted to the more specialized and unusual forms of birds and snakes. Comparatively little attention was given to kinesis in the more primitive forms of cranial kinesis (in lizards). A valuable contribution to the study of cranial kinesis in lizards was the work of Frazzetta (1962). Frazzetta by using motion pictures, demonstrated the connection between the movement of the upper jaw and the seizing and consumption of prey, and made the first biomechanical analysis of the work of the jaw muscles,

-- p. 1399 --

responsible for movement of the upper jaw. Frazzetta presented a new hypothesis on the functional significance of cranial kinesis (see below). However, Frazzetta, in his analysis of cranial kinesis, focused his attention on one form (Varanus), giving less attention to the features of cranial kinesis of other forms studied by him. The type of cranial kinesis exhibited by Varanus, as our work has shown, cannot be considered as either the most primitive or the most widespread among lizards. For a clear presentation of the evolution of skull kinesis and its functional significance, a comparison of kinesis in various skulls beginning with the more primitive forms, is necessary.

MATERIALS AND METHODS

We have studied skull structure in Sphenodon punctatus and the following lizards: Cyclura macleanyi, Iguana sp. (Iguanidae), Agama caucasica*, A. lehmanni, A. sanguinolenta*, Phrynocephalus reticulatus (Agamidae), Lacerta media*, L. agilis*, Eremias arguta, E. grammica (Lacertidae), Eumeces schneideri*, Mabuya aurata, Trachysaurus rugosus (Scincidae), Varanus griseus*, V. niloticus (Varanidae), Teratoscincus scincus*, Gecko gecko*, Platydactylus guttatus, Gymnodactylus caspius* (Gekkonidae), Ophisaurus apodus* (Anguillidae), Tupinambis sp. (Teiidae), Zonurus cordylus* (Zonuridae) from the material of the Zoological Institute of the Akademii Nauk USSR, the Zoological Museum of Moscow University, the Chair of Vertebrate Zoology of Moscow University and from our own collections. We studied the details of cranial kinesis in the alcoholic (wet) connective tissue preparations of skulls of 11 species of lizards² (with skin removed) and also in the skulls of freshly killed species of Varanidae. In addition, the jaw musculature of nine other species of lizards was studied. Motion pictures of the eating of prey by Agama caucasica and Lacerta agilis were taken by an aide [assistant, or probationer] at the Paleontological Institute of the ANSSSR, N.N. Kalandadze, to whom the author is very indebted for his help in the work. We also wish to express our sincere thanks to B. S. Mateev and F. Ya. Dzerzhinskij (chair of vertebrate zoology, Moscow University) for discussion of our results and for critical remarks, and for giving the opportunity to work with museum materials, the head of the herpetology division of the Zoological Institute ANSSSR, I. S. Darevskii, and head of the evolutionary morphology division, Zoological Museum, Moscow University, D. N. Hofmann.

¹An alternate hypothesis of the antiquity of the akinetic skull and independence of development of kinesis in various lines of vertebrate evolution was developed by Edgeworth (1935). Edgeworth's views do not survive serious criticism and have not received general acceptance.

²The names of these [11] lizards are designated by an asterisk in the list given above.

CRANIAL MOVEMENT OF LIZARDS

Following Bradley's work (1903), on lizard skulls, three fundamental segments [units] were distinguished: the occipital, maxillary, and mandibular. The occipital segment was reinforced in vertebrates and is considered to be immovable. It is formed of the occipitals and otic bones, and also the basi- and parasphenoids. The two other segments are movable relative to the occipital. Of interest to us here primarily is the movability of the maxillary segment, which is signified by the term "cranial kinesis". The relationships between the maxillary and occipital sections have already been described by Bradley, Versluys, Hofar, Frazzetta, Oelrich (1956) and Webb (1951) and we have confined ourselves only to their enumeration. These relationships include: the union of the quadrate, squamosal and the supra-temporal bones with the lateral ends of the paroccipital processes ("metakinetic axis" of Frazzetta), the parietal with the supra-occipital, the pterygoids with the basiptyergoidal processes, sometimes of the epiptyergoids with the prootic bones. Besides this, both segments are joined by the cartilaginous and membranous orbito-temporal elements of the brain case. All these connections allow a limited degree of movement of the maxillary segment relative to the occipital: first, as a whole, it turns around the metakinetic axis with the anterior end upward and forward (protraction) or downward and backward (retraction). Besides this, the maxillary segment during pro- and retraction changes configuration since it consists of a series of related divisions -- paired: (1) quadrate bones, (2) epiptyergoids,

-- p. 1400 --

(3) palatal divisions; -- and unpaired: (4) parietal division, and (5) the snout [muzzle], which always breaks down further into (5a) central and paired (5b) lateral parts. The composition of all these divisions with the exception of the quadrate and epiptyergoid, differs as also differ the peculiarities of kinesis in the various forms of lizards (see table).

-- fig. 1 --

In general, in the skull of a typical lizard, the following movements take place (figs. 1-5). During retraction, the lower ends of the quadrate bones turn back and to the side [posterioro-laterally]. The palatal segments, movably joined with the quadrates, are drawn to the back and side, sliding along the basiptyergoidal processes and spreading the latter to the sides (drawing the palatine sections from the center line) [abduction]. The epiptyergoid, attached by the articular hollows [surfaces] to the dorsal surface of the pterygoid, rotates its lower end back and to the side, as does also the quadrate, but at a lesser angle than the latter. The snout, as a whole, rotates its anterior end downward around the transverse axis, passing along the fronto-parietal suture ["mesokinetic axis" of Frazzetta]. The angle between the central part of the snout and the palatine section is somewhat increased; the angle between the frontals and the

-- fig. 2 --

parietals below is decreased. At this point, the lateral parts of the snout, together with the palatine sections, are diverted and their lateral margins rotate upward around the longitudinal axis passing approximately along the lines of juncture of the lateral and median parts of the snout. The parietal section, as Frazzetta correctly noted, and contrary to the opinion of Versluys, rotates

-- p. 1401 --

around the metakinetic axis with its anterior end upwards.³ Finally, the lateral parts of the parietal section, participating in the movement of the entire section, also arch upwards, and, in forms with covered supratemporal fenestrae, rotate around the linear axis, passing along their articulation with the central part of the section, lateral margins upward.

In general, during retraction, the anterior end of the snout turns downward, the dorsal contour of the skull becomes more convex, the palatine arches, the lateral sections of the snout and the lower ends of the quadrate bones and the epiptyergoids are shifted to the rear, drawn aside and rotated around the linear axis with the lateral edges upward. During protraction, an

-- fig. 3 --

-- fig. 4 --

³In alcoholic connective-tissue preparations of lizard skulls may be found both variants of parietal division movements -- its rotation in the same direction as the snout, and the reverse, depending on the direction of force applied. Naturally, as examination shows, force applied to the lizard skull by the jaw muscles should be regarded as the latter variant of motion.

opposite movement of all the above-mentioned elements of the maxillary segment of the cranium takes place.

However, among the various forms of lizards, there are essential differences in the peculiarities of cranial kinesis and in the composition of the various sections of the maxillary segment (cf. table). First, the kinds of lizards studied fall primarily into two groups: (1) Cyclura, Agama, Lacerta, and Ophisaurus, in which the palatal unit is a solid shaft [core] participating in cranial movements as an indivisible integer [whole unit]--unquestionably a more primitive stage; (2) Eumeces, Varanus, Teratoscincus, Gecko, Gymnodactylus, and Zonurus, in which the palatine unit is articulated along the palato-pterygoidal juncture to the anterior and posterior parts, movable relative to one another. In lizards of the first group, the palato-pterygoidal articulation is a suture running as a whole very obliquely from postero-anteriorly medially and solidly uniting the two bones (Fig. 2), while lizards of the second group, a very loose syndesmosis runs more directly laterally [transversely], permitting rotation around the transverse axis (Fig. 4). In geckos, the palatine bone and the pterygoid hardly adjoin directly, being separated by loose connective tissue (mentioned by Lakjer, 1927). In lizards of the second group, during retraction, the palatine section is more or less bent upward: the region of the palatal-pterygoidal articulation is raised, and the descending angle between these bones is decreased.

-- Table, p. 1402--

--p. 1403--

The interior movement of the palatine section in lizards of the second group is correlated with the greater role of mesokinesis in the amphikinetic skull (Versluys terminology) than in lizards of the first group and is in general also correlated with the greater development of kinesis.

Within both groups of lizards there are some more pronounced differences among the various forms. Thus, in Cyclura (Fig. 1) and Agama, the

--fig. 5--

postorbital bones are closely joined not with the lateral element of the parietal division as in all the other forms, but with the lateral part of the snout, and take part in its movements. In Lacerta, the link between the quadrate bone and pterygoid (mentioned by Frazzetta) is very lax and in the amphikinetic skull, movements around the metakinetic axis predominate--mesokinetism is relatively weak. The most pronounced distinctness of movements of the central part of the parietal division and the upper temporal arches is in Lacerta and Ophisaurus. In Varanus, (Fig. 5) the zygomatic bone is closely connected with the palatine division and takes part in its movements (noted by Frazzetta), and has elements of rhynchokinetism (Hofer, 1960); i.e., the movability of the premaxillary bone in relation to the nasal. In the amphikinetic skull of Varanus, movement is predominantly around the mesokinetic axis--the parietal division shifts very little (but shifts nevertheless, contrary to the opinion of Hofer) with respect to the occipital segment. The gecko (Figs. 3-4) skull is the most kinetic among the skulls of the forms studied: the vomers move together along the central part of the snout--their articulation with the palatine bones is exceedingly mobile.

If we illustrate in the lizard skull lateral view, in a very simplified pattern, the leverage mechanism, in which straight lines represent individual units of the latter (movable only in relation to other units of the skull) and circles to represent the transverse axes around which the possible rotations of these units take place (not unlike the sketches Frazzetta presented for Varanus), then we obtain the following fundamental variants of the mechanisms (Fig. 6). In Varanus, in contrast to the simplified diagram of Frazzetta, we notice lines of flexion [folding] between the nasal and premaxillary bones, between the vomer and the premaxillary bones, and between the palatines and pterygoids. As is seen in the diagram, the cranial mechanism of Varanus is unique and significantly different from the primitive forms of cranial mechanisms to which lizards of the first group (among the forms studied) stand closest of all, especially Cyclura.

KINESIS IN LIVING LIZARDS

MOVING FORCES OF CRANIAL KINESIS

Hofer (1960) correctly pointed out that the anatomical data on the possibilities of motion in the skull, like data on kinesis, obtained on alcoholic connective-tissue preparations, cannot show the actual presence of correspondingly active motion in the cranium during the life of the animal, but show only the possibility of passive [enforced] motion.

--p. 1404--

In favor of the actuality of the motion observed in connective-tissue preparations of the skull is the fact that analogous movements on a much larger scale are more noticeable in the head of a freshly killed animal with fully preserved muscles, ligatures, etc., than in the connective tissues of preparations. Thus, the length of the skull of Varanus griseus from

--Fig. 6--

the end of the snout to the occipital condyle, varies accordingly: as much as 8.97% of median skull length (71.3 mm) during protraction and retraction in "fresh" heads, in three wet connective-tissue preparations of skulls of same size--on the average, only 2.45% (2.3 - 2.7).

For proof of active movement in the kinetic skull, examination of living lizards and analysis of the lines of force arising in the cranium during the contraction of cranial muscles is necessary. Direct examination of skull kinesis in lizards is difficult due to their great rapidity

--p. 1405--

of movement. Filming of eating prey by Agama caucasica and Lacerta agilis gave results that were hard to interpret; while grasping and swallowing prey these lizards repeatedly rotate the head around the longitudinal axis and to the side so that the kinetic movements of the skull are hard to pick out [distinguish] without the risk of taking the desired for the actual effect. The reason for this may be the small choice found in our selection of living forms. Both Lacerta and Agama belong to the first group of lizards, that is, they do not have movement within the palatine element and kinesis in them is generally less than in lizards of the second group. Thus in Lacerta, we see that the dominating movements of the maxillary segment are around the metakinetic axis, which is difficult to distinguish in a live lizard, and Agama has a very broad and low skull, thanks to which the dorsal contour is quite distorted during a slight lateral inclination. Frazzetta, with the aid of motion pictures, studied eating of prey by Gerrhonotus coeruleus. He noted that retraction takes place during closing of the mouth and compression of the lizard's jaws, while protraction takes place during the opening of the mouth. Frazzetta's observations were confirmed also by data of Bolit and Ewer (1964), on Varanus niloticus.

Frazzetta made a graphic analysis of the lines of force arising during the contraction of the jaw muscles in the cranium of Varanus. This analysis seems fundamentally accurate, but somewhat superficial, since Frazzetta did not study the jaw musculature of the lizard in detail, and did not try to assign a role to all the muscular parts. Protractors of the jaw mechanism in lizards appear in M. protractor pterygoidei and M. levator pterygoidei; retractors are primarily the fibers of the large M. adductor mandibulae externus (but never M. pterygoideus, despite Frazzetta's assertions). Various parts of the M. adductor mandibulae externus play completely different roles in the movements of the cranial mechanism: a large part of the fibers of the muscle have a retractive effect, some are neutral in relationship to the cranial mechanism and some manifest themselves as protractors. The summary effect of contraction of M. adductor mandibulae externus is retraction. Our studies of the jaw musculature of lizards showed that parts of M. adductor mandibulae externus, accepted in the works of Lakjer (1926), Lubosch (1933), I. Poglayen-Neuwall (1954), Oelrich (1956) and others, do not correspond with the functional and topographic units of the muscles. Furthermore, he (Frazzetta?) does not succeed well in identifying these parts in various forms in the order Sauria and, moreover, with parts with the same names in other reptiles. The scope of this article, unfortunately, does not allow us to add here a detailed analysis of the structure and function of lizard jaw muscles; we hope to do this in future publications.

In his analysis of the functions of the cranial mechanism of lizards, Frazzetta made one important error: according to his opinion, M. pterygoideus is a retractor, at least in the closing of the jaws on the prey. Actually, this muscle in lizards is neither a retractor or protractor of the cranial mechanism. Its force is applied to the pterygoids and to the lower jaw, forward and downward posteriorly of the jaw articulation. By such attachments, the contraction of M. pterygoideus does not change in conformity to the cranial mechanism. The movements associated with kinesis are in no way affected by the length of M. pterygoideus (Fig. 7; it corresponds to Fig. 11 in Frazzetta's paper). M. pterygoideus might be a retractor with fulfillment of two conditions: (1) flexibility of the palatine arch (at least in the juncture of the palatine bone and the pterygoids); (2) the origin of M. pterygoideus anterior of the hinge line of the palatine arch from the palatine bone or the bones of the snout. (*cf. Geologicheskii Slovan-Sofiano, p. 223). The second condition is not fulfilled in lizards. The role of M. pterygoideus in retraction of the maxillary segment lies in the transfer of the retraction force component in the contraction of M. adductor mandibulae externus from the lower jaw to the palatine arch (for birds - see Marinelli, 1936).

--p. 1406--

THE PROBLEM OF THE FUNCTIONAL SIGNIFICANCE OF CRANIAL KINESIS

The phenomenon of cranial kinesis has been known for about 150 years, but one problem has not been finally solved--what is the functional significance of this wide-spread complex adaptation in vertebrates? In general, all are agreed that kinesis is correlated with feeding and chiefly with the capture of food. But, in regard to the definite value of cranial kinesis, there are several different hypotheses.

Frazzetta convincingly showed the inadequacy of Versluys' hypothesis, according to which cranial kinesis served as a means of increasing the size of the gape of predatory animals, through a greater spread between the upper and lower jaws. In the monokinetic metakinetic cranium, protraction does not change the vertical range of the gape, and during amphikinesis or in the monokinetic-mesokinetic skull, it decreases the gape.

--Fig. 7--

Bradley's hypothesis is also untenable; it proposed that kinesis, during the opening of the mouth for grasping prey, permits adduction of the palatine elements for holding the prey between them. The evolution of lizards has gone particularly in the direction of increasing the width of the inter-pterygoidale cavity [depression] and the reduction of the palatal teeth, that is, in a direction diametrically opposed to that which would have been expected if such a kinetic function were present. In addition, the protractor muscles are comparatively weak and cannot produce the considerable compressive force between the left and right elements of the palatine arch necessary for holding of prey between them.

Romer's hypothesis on the amortizational role of kinesis (1937) on the impact of jaws cannot be discarded so decisively. Frazzetta was inclined to display skepticism as regards this hypothesis, since in the capacity of amortizers in the kinetic cranium, one must include the contraction of the retractor muscles, i.e., the above-noted jaw adductors. The flexibility of the cranial bones in the lower forms of lizards might, according to Frazzetta, with the same success play the amortizational role without the aid of the complex structure provided by kinesis. But, skull kinesis is strongly developed even in small lizards. We can add that from the point of view of this hypothesis incomprehensible is the role of the protractor muscles according to which, during the opening of the mouth (before the clamping of the jaws) the maxillary segment of the skull is elevated and thus bending the spring at the end.

According to Frazzetta's hypothesis, cranial kinesis serves for attaining the simultaneous closing of the jaws in seizing the prey. The gape is oriented so that the rising lower jaw and lowering upper jaw are simultaneously applied to the prey, by which means the risk of the prey's escape is lessened, as compared with the condition in the akinetic skull, where the prey is "caught" by the lower jaw only. It seems to us, however, that Frazzetta lost sight of the fact that the orientation of the jaws in relationship to seizing the object is not attained by kinetic movements, but by movements of the neck and by turning the head at the occipito-cervical joint, i.e., movements which take place also in the akinetic cranium. The simultaneity (or near simultaneity) of contact with the prey by the upper and lower jaws might be attained in the akinetic skull by the lowering of the head simultaneously with the raising of the lower jaw. It is unlikely in predators with an akinetic skull (and of such there are very many, discounting the mammals),

--p. 1407--

that, after contact of the prey by the upper and lower jaws, sufficient time elapses for the escape of the prey. Even in rushing at concealed prey from ambush a predator discloses itself sooner than its jaws (both together or one of them a split second earlier) grasp the prey. It seems to us that kinesis is not of any essential benefit either in gaining a "moment of surprise" in seizing prey nor for the catching of prey in general.

--Fig. 8--

In movements of the kinetic skull, the inequality of the forces produced during protraction and retraction is significant. The protractors are two very comparatively weak muscles, while the retractors are powerful jaw adductor muscles. Therefore, the active movement bearing the functional load should likely be retraction. Strange as it seems, beginning with Bradley and Versluys, most scientists have sought the functional significance in protraction. Only Marinelli (1936) hinted at the functional significance of the closing of the beak in birds, since the opening of the beak (according to his opinion) was only a preparatory step in the process of movement in the upper jaw. Kinesis, according to Marinelli, is permissible in the case of necessity of shifting the place of principal pressure by the jaws closed on the prey closer to the end of the beak or corner of the mouth.

It seems to us that the advantage of the kinetic skull in comparison to the akinetic is not in any kind of capture, but in holding the still living, moving prey. The kinetic and akinetic jaws can be identically effective in catching prey. But it is easier for kinetic jaws to hold it. We can note that akinetic straight jaws during the holding of prey will push forward on the object caught (Fig. 8-1); and the resultant forces applied by them to the object held will also be directed forward. In the akinetic skull this load lies in holding prey by the teeth. This may be avoided by the convex form of jaw, but then the jaws would always be "bent down" to some prey of limited size and could not hold smaller prey. Kinesis provides the predominantly bent jaws with more effective jaw pressure on any item seized, and eliminates their [the jaws] deficiencies (Fig. 8, 2). Akinetic jaws may be analogized to claws; the kinetic, to fingers; since fingers are more suitable than claws for holding objects, so kinetic jaws are more suitable than the akinetic for the same purpose. The complexity of the movements of cranial kinesis is a result of the complexity of the cranial structure.

In grasping prey, the kinetic skull has other advantages over the akinetic (analogous to the advantages of fingers over claws): the kinetic upper jaw can transfer the prey along the lower jaw, crushing its resistance and killing it. During squirming of the prey, the kinetic jaws holding it can relax slightly, without releasing the victim, and finally exhausting it in the struggle (the "spinning? principle"). The amortizational hypothesis also does not contradict this role of kinesis. All these functions of kinesis can exist together, as kinesis has a complex significance, serving as the best means of holding prey.

--p. 1408--

From this point of view, the relative weakness of the protractor muscles is understandable; their fundamental role is to return the maxillary unit of the skull from the operative retractive position to the normal position necessary for compact closing of the oral cleft. Also, protraction is accomplished somewhat farther along than the "normal" central position of the maxillary segment and always accompanies the opening of the mouth and the closing of the jaws. Therein is the truth of the hypothesis of Boltz and Ewer (1964) which says that protraction serves for freeing the upper teeth, stuck in the victim during the grasping of the prey and for momentum in swallowing it.

We ought to give here an explanation of the history of the very numerous cases in the history of vertebrates of loss of cranial kinesis, which occurred independently in various lines of evolution. The loss of kinesis is to be expected in (1) animals which do not need to hold squirming prey--for them, kinesis is useless (all specialized vegetarian forms, Diadectidae and Pareiasaurs among the Cotylosauria; many Chelonina and many Ornithischia; even Versluys remarked about this, giving a different explanation, however, for the loss of kinesis in vegetarian forms); (2) those forms which require maximum pressure on the food being chewed--kinesis in this case would even be harmful (as in some forms of vegetarians, but especially in mollusk eaters and other such forms, for example Placodontia, also noted by Versluys); (3) in some situations in which the preservation of the adaptive values of kinesis would be advantageous, but when some other kind of competing adaptation is more important for a given form, excluding the possibility of retaining kinesis. This situation occurs in forms for which the development of the secondary palate has proven to be especially important, apparently eliminating kinesis; it also occurs in the case of specialized feeding on very small or large prey. Kinesis is advantageous (in its unspecialized forms) in specific forms of predation, and especially for the generalized predators that feed mainly on prey small (but not very small) relative to its own size; prey of that size may be seized in the predator's jaws, such as insects, by lizards, and small vertebrates by the larger [predators]. When prey is considerably smaller than the predator, the advantage of kinesis for seizing it is not so essential, since for seizing it, long, relatively thin, pincher-like jaws are advantageous. Typical cases of this kind are: Crocodilia, Phytosauria, Ichthyosauria, Mesosauria, dolphins and others (Iordanskii, 1963). Kinesis in the form of metakinesis cannot be maintained in the species with long jaws due to the lesser firmness of the linkage of the long jaws to the brain case (Versluys, 1912). The loss of kinesis in Pterosauria is probably associated with this. It should be pointed out that in the presence of mesokinesis and prokinesis, kinesis in that case can be preserved; an example of this would be the long-beaked avian ichthyophages. The above pertains only to the more primitive forms of kinesis, meta- and amphikinesis.

If a predator specializes in feeding on coarser prey, subequal to itself or larger, the load on the cranium during the capture, killing and chewing [of food] is so great that kinesis is disadvantageous, through lessening the solidity of the skull. Kinesis may be advantageous in absence of food mastication by the jaws but it becomes disadvantageous for more or less prolonged chewing of the food requiring, as said above, rather firm pressure on the object processed. The loss of kinesis in the Therapsida line is associated with this fact. Snakes occupy a special position. In snakes, a more highly specialized form of kinesis developed with an extreme degree of movability of elements of the maxillary segment in relation to each other, which aids in swallowing large prey whole. As a consequence, snakes in many cases kill

their prey by constriction or by poison, and the jaws do not exert mechanical pressure in holding, killing and chewing the prey.

The reduction of kinesis in chameleons is evidently correlated with feeding on small prey, captured by the aid of the tongue.

The question of kinesis or akinesis in Sphenodon remains open at this time. Recently Ostrom (1962) showed that in several types of Hatteria the protractor muscles are well developed and in a mature state. Ostrom suggested that in various populations of Sphenodon, kinesis can be lost or preserved in the adult state depending on the feeding peculiarities of a given population. Our study of the skulls of Hatteria leads to the conclusion that metakinesis in these forms and their ancestors must essentially be distinguished from the scheme of metakinesis proposed by Versluys (1910, 1912). Versluys proposed that in metakinesis, the maxillary segment of the skull moves as a single unit, in which the palatine arch, the bones of the snout and the skull roof are all rigidly joined to each other. However, the structure of the skull of Hatteria shows that retraction in this form should take place in the abducting elements of the palatine arch (pterygoids, palatines, epi- and ectopterygoids, and vomers). This means that in this metakinetic skull, movement of the lateral parts of the maxillary segment in relation to its central part should take place, similar to those noticed in the amphikinetic lizard skull. Whether during retraction the movements of the palatal arch and the lateral elements of the dermatocranium are independent, as in lizards, or whether those and others were displaced relative to the middle elements of the maxillary segment, we cannot determine from available museum materials. In any case, retraction of the metakinetic skull type is accompanied by diversion and rotation around the linear axis, lateral margins upward, of elements of the palatine arch, by the lateral part of the superposed skull armor. It seems to us permissible to presume that these movements might be characteristic of the metakinetic skull type in general. But examination of the problems of evolution of cranial kinesis exceeds the scope of the present paper.

CONCLUSIONS

(1) Among the various lizard species, there exist essential differences in the peculiarities of cranial kinesis and in the composition of various parts of the maxillary segment. Cranial kinesis of Varanus, used as the basis for analysis of lizard skull kinesis by Frazzetta (1962), is neither the most primitive nor the most prevalent form of cranial kinesis among lizards.

(2) The most primitive type, among the forms studied, is in the Cyclura, Agama, Lacerta, and Opisaurus, in which the palatine section of the maxillary segment is a tough core [stout shaft], taking part in the movements of the skull as a single unit.

(3) In the presence of strengthening of cranial kinesis in lizards, in the palatine unit there is developed movability of its anterior part in relation to the posterior part.

(4) The M. pterygoideus, which functions as a retractor in the cranial mechanism in Frazzetta's opinion, actually in lizards cannot produce any kind of retractor movements by the latter.

(5) It seems probable that cranial kinesis provides the best means of holding prey [which is trying to escape] in the predators jaws. Protraction can serve to release the teeth of the upper jaw during seizure of prey or in swallowing.

(6) Kinesis of the skull in its unspecialized forms is especially advantageous for the universal [generalized] predator feeding on prey [which is] small relative to its own size, but not too small prey.

(7) Most of all, in the metakinetic type of skull, retraction and protraction of the maxillary segment are accompanied by abduction and adduction of the palatal arches, and the lateral elements of the superposed skull and by their rotation around the longitudinal axes, that is, definite movement taking place within the maxillary segment of the skull, despite the pattern of metakinetism proposed by Versluys (1910, 1912).

Segments and divisions of the skull	Cyclura, Agama	Lacerta, Ophisaurus	Eumeces	Varanus	Teratoscincus, Gecko, Gymnodactylus
Occipital Segment	Basioccipital, exoccipital, supraoccipital, basisphenoid, parasphenoid, prootic, and opisthotic bones			Posterior unit	
				Pterygoid and transverse bones	Pterygoid and transverse bones
Palatine Division	Pterygoid, palatine and transverse bones, vomers, and septomaxillaries			Anterior unit	Pterygoid and transverse bones
				Vomers, palatines and septomaxillaries	Palatines
Maxillary segment					
Snout					
Lateral unit	Supramaxillaries, prefrontal, postorbital, lachrymal	Supramaxillaries, prefrontal, lachrymal			Supramaxillaries, prefrontal, and lachrymal
Median unit	Premaxillary, nasal, frontal, postfrontal	Premaxillary, nasal, and frontal			Anterior unit: premaxillary bone
Parietal Division	Parietal, squamosal, supratemporal	Supratemporal arch: squamosal, postorbital, postfrontal	Median unit: parietal and supratemporal		Parietal, squamosal, postorbital, postfrontal, and supratemporal
Epipterygoid division—Epipterygoid					
Quadrato division					
Quadrato bones					

*Broken lines designating divisions taking part to some extent jointly in skull kinesis action.

TABLE OPPOSITE PAGE 1403