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Introduction

The tongue is an essential, often dominant, component of tetrapod feeding mechanisms. Recent reviews have stressed the tongue's central role and emphasized its importance in the evolution of terrestrial from aquatic vertebrates (Bramble & Wake, 1985; Hiiemae & Crompton, 1985). Despite these and other studies, we remain ignorant about the role of the tongue in the feeding dynamics of many groups, particularly reptiles. This ignorance clouds our ability to discern evolutionary patterns in tongue structure and function. The elucidation of such patterns is critical if we are to address fundamental questions about the evolution of vertebrate feeding, including the phylogenetic generality of rhythmic feeding cycles (e.g. Hiiemae, Thexton & Crompton, 1978; Bramble, 1980; Throckmorton, 1980; Smith, 1984), the homology of feeding stages among tetrapods (Bramble & Wake, 1985), and the conservation of kinematic and motor patterns in the evolutionary transition from water to land (Shaffer & Lauder, 1988; Lauder & Shaffer, 1988).

Tetrapod feeding comprises three stages, *ingestion* (movement of food from the outside environment into the mouth), *intra-oral transport* (movement of food through the oral cavity to the oesophagus, including mastication and manipulation), and *deglutition* (swallowing) (Bramble & Wake, 1985; Hiiemae & Crompton, 1985). The role of the tongue varies both among stages in the same animal and among taxa in the same stage. Tongue use has been studied most extensively during intra-oral transport and deglutition in mammals (e.g. Ardran & Kemp, 1955; Hiiemae *et al.*, 1978; Thexton, 1981; Miller, 1982; Franks, Crompton & German, 1984; Franks *et al.*, 1985). Smith (1984) provided similar data for transport and deglutition in two squamate reptile species. In contrast, the role of the tongue during ingestion is poorly known for amniotes, although well studied in amphibians (e.g. Larsen & Guthrie, 1975; Lombard & Wake, 1976, 1977; Thexton, Wake & Wake, 1977; Gans & Gorniak, 1982*a, b*; Larsen & Beneski, 1988). Gorniak, Rosenberg & Gans (1982) documented lingual ingestion of prey in the rhynchocephalian lepidosaur, *Sphenodon punctatus*. Among squamates, however, tongue use during ingestion has been studied only in the highly derived chameleons (e.g. Gnanamuthu, 1930, 1937; Altevogt & Altevogt, 1954; Gans, 1967). Lingual prey prehension in other taxa has been mentioned only in passing (Kästle, 1965; Cooper, Poole & Lawson, 1970; Throckmorton, 1976, 1980; Smith, 1984).

Given that the tongue functions differentially among taxa in each of the three stages of feeding, any attempt to explain the evolutionary bases of variation in tongue form must consider its role in all stages (Schwenk, 1984). Therefore, ignorance about the role of the tongue during ingestion in squamate feeding seriously undermines our ability to explain the astonishing diversity of lingual morphologies present within this group. Since this variation historically has been an important, often central, element of squamate systematics (Camp, 1923; McDowell, 1972; Schwenk, 1988), an understanding of its functional basis is all the more desirable. In addition, use of the tongue during ingestion, or not, may have consequences for non-lingual features of cranial morphology (Schwenk, 1987, In prep.).

In this paper we describe the kinematics of lingual ingestion in squamate reptiles and analyse these data in the light of recent, phylogenetic hypotheses of squamate relationships. In addition, we consider the relevance of our findings to the model of generalized tetrapod feeding proposed by Bramble & Wake (1985).

Materials and methods

Phylogenetics

Conclusions regarding the phylogenetic distribution of lingual prey prehension (ingestion) are based on our extensive observations of dozens of squamate species, as well as literature accounts reporting feeding behaviour in many others. As there are thousands of squamate species, we must assume the taxa for which we have data to be representative of larger groups. Tongue morphology is correlated closely with feeding behaviour (Schwenk, 1984) and tongue morphology varies little within families (Schwenk, 1988), therefore this is probably a reasonable assumption. In any case, our conclusions are potentially falsifiable by study of additional species.

Kinematics

Kinematics of lingual ingestion were studied in 7 species of lizard by cinographic analysis. Unrestrained lizards (Table I) were filmed feeding with Bolex or Beauliere 16 mm movie cameras set at 32 or 64 frames per sec (fps). Three different cameras were used over a period of years and when the actual frame rate was measured on one of them (set at 64 fps) it was found to be only 48 fps; therefore, it is possible that absolute times measured from the films are, in some cases, an underestimation of actual times. It is indicated in Table I whether the times given are derived from actual frame rate or assumed frame rate.

Films were exposed using synchronized stroboscopic illumination (Chadwick-Helmuth Corp., Monrovia, Calif.) in all cases except for the chuckwallas, *Sauromalus obesus*, which were filmed using photofloods. Films were analysed frame by frame on L-W model 110 or Vanguard motion analysers. Kinematic profiles were derived by plotting distances measured directly from the motion analyser screen. Distances were measured either through the use of an acetate grid overlay or with a millimetre rule. The cine frame immediately preceding the start of an ingestion sequence was used to define the X, Y start point (0, 0). Head movements were measured by noting the X, Y coordinates of a fixed point on the head relative to the starting point. Gape distance and tongue protrusion distance (Fig. 1) were measured with a rule. All distances are expressed in arbitrary units. However, in any given sequence these distances are directly comparable.

Results

Phylogenetics

Figure 2a illustrates a recent phylogenetic hypothesis of squamate relationships based on a cladistic analysis of 148 characters derived from hard and soft anatomy (Estes, de Queiroz & Gauthier, 1988). This phylogeny shows a basal dichotomy that divides Squamata into two major clades, the Iguania (Iguanidae, Agamidae, Chamaeleontidae) and the Scleroglossa (all remaining squamate families). A similar pattern was found in another phylogenetic analysis (Fig. 2b) based on 36 characters drawn entirely from the tongue and adjacent tissues (Schwenk, 1988). Although these hypotheses differ in some details within Scleroglossa (discussed by Schwenk, 1988), they agree strongly in their identification of two major squamate lineages. This pattern indicates that a fundamental dichotomy in squamate cladogenesis is paralleled by a dichotomy in tongue form. The morphological dichotomy separates those squamates with thick, muscular tongues and high-profile papillae, usually referred to as 'fleshy-tongued' (the Iguania), from those squamates with thinner foretongues covered with low-profile, often keratinized papillae (the Scleroglossa) (Schwenk, 1984, 1986, 1988).

TABLE I

Quantitative aspects of the ingestion cycle in seven species of iguanian squamate. Data unavailable for *Pogona* tongue protrusion because of missing frames at beginning of ingestion sequences. Data for *Uromastyx* gape angle from Throckmorton (1980). N = number of cycles; \bar{x} = mean; S.D. = one standard deviation; CV = coefficient of variation

Species (No.) (approx. wt.)	Food item(s)			Maximum gape angle			Duration of tongue protrusion (ms) ¹			Duration of tongue retraction (ms) ¹			Maximum tongue protrusion distance ²			
	N	\bar{x}	S.D.	CV	N	\bar{x}	S.D.	CV	N	\bar{x}	S.D.	CV	N	\bar{x}	S.D.	CV
IGUANIDAE																
<i>Dipsosaurus dorsalis</i> (2) (32 g)	10	25°	4	14	12	238	67	28	12	56	15	26	9	0.31	0.04	14
<i>Iguana iguana</i> (1) (2000 g)	4	42°	10	25	4	543	138	25	4	155	0	0	2	0.20	0.09	42
<i>Phrynosoma platyrhinos</i> (1) (22 g)	5	32°	1	4	3	231	92	40	3	49	12	25	3	0.50	0.03	6
<i>Sauromalus obesus</i> (3) (200 g)	10	38°	7	18	11	516	158	31	11	180	19	10	7	0.17	0.05	31
AGAMIDAE																
<i>Pogona barbata</i> (1) ³ (500 g)	6	28°	4	15	—	—	—	—	5	102	14	14	2	0.44	0.01	2
<i>Phrynocephalus helioscopus</i> (2) (5 g)	8	33°	8	25	11	187	85	45	11	67	9	13	6	0.54	0.06	11
<i>Uromastyx aegyptius</i> (4) (1200 g)	8	23°	2	—	13	410	139	34	13	157	20	13	6	0.21	0.10	48

¹fps measured (*Dipsosaurus*, *Phrynosoma*, *Phrynocephalus*); 64 fps assumed (*Sauromalus*, *Pogona*); 32 fps assumed (*Iguana*, *Uromastyx*)

²Maximum tongue protrusion distance expressed as a function of head size, T/J (see Fig. 1)

³Formerly *Amphibolurus barbatus* (see Storr, 1982)

⁴Hand-held food

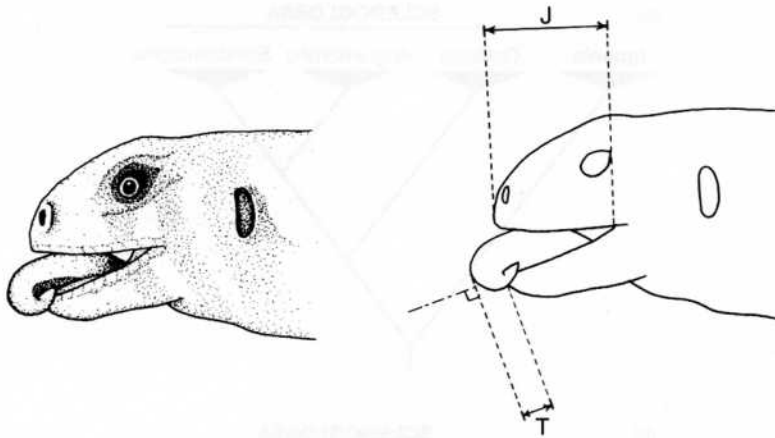


FIG. 1. Tongue protrusion during lingual ingestion in an iguanian lizard (*Dipsosaurus dorsalis*, Iguanidae). Note the curling of the tongue tip and presentation of the tongue's dorsal surface anteriorly, toward the food item. Tongue protrusion distance is expressed as a function of head size, T/J . T = distance tongue protruded beyond tip of mandible; J = upper jaw length measured from its distal end to point of intersection of upper and lower labial scale rows. Drawing made from cine film tracing.

Use of the tongue to ingest liquids (lapping) characterizes all squamates, including scleroglossans (Gove, 1979, pers. obs.), and is probably a primitive tetrapod behaviour. However, in our observations of feeding in squamates (including every supra-familial taxon shown in Fig. 2 and representatives of most families within each taxon) we have observed use of the tongue in prey capture (lingual ingestion) only in species of Iguania. In all other taxa, the jaws are the means of prey prehension, including capture of very small prey. Outgroup analysis suggests that lingual prey prehension is primitive for squamates (Schwenk, 1988). *Sphenodon punctatus*, the only living non-squamate lepidosaur, uses the tongue for ingestion of small prey (Farlow, 1975; Gorniak *et al.*, 1982). The kinematic pattern of lingual feeding in *Sphenodon* is nearly identical to that shown here for iguanian squamates (compare Fig. 4 in Gorniak *et al.*, 1982: 334 with Plates I and II in this paper). Furthermore, lingual ingestion characterizes many birds (Ziswiler & Farner, 1972), many mammals (Doran & Baggett, 1971), terrestrial turtles (pers. obs.; D. Bramble, pers. comm.), and two of three orders of Lissamphibia (e.g. Larsen & Guthrie, 1975; Lombard & Wake, 1976, 1977; Gans & Gorniak, 1982a, b) (crocodilians have a secondarily reduced, non-protrusible tongue; see Schwenk, 1988). Given the near identity of lingual ingestion in the sister group of Squamata and its ubiquitous occurrence in other tetrapods, lingual ingestion is certainly the plesiomorphic state for squamates. Therefore, exclusive use of the jaws for ingestion is a derived feature of Scleroglossa. As such, jaw feeding represents the *loss* of tongue use during the initial (ingestion) stage of feeding. Figure 3 summarizes the phylogenetic distribution and polarity of lingual versus jaw feeding among lepidosaurian reptiles.

Putative exceptions

There are several possible exceptions to the phylogenetic patterns noted above. First, the dichotomy of lingual versus jaw ingestion applies only to relatively small food items. As such,

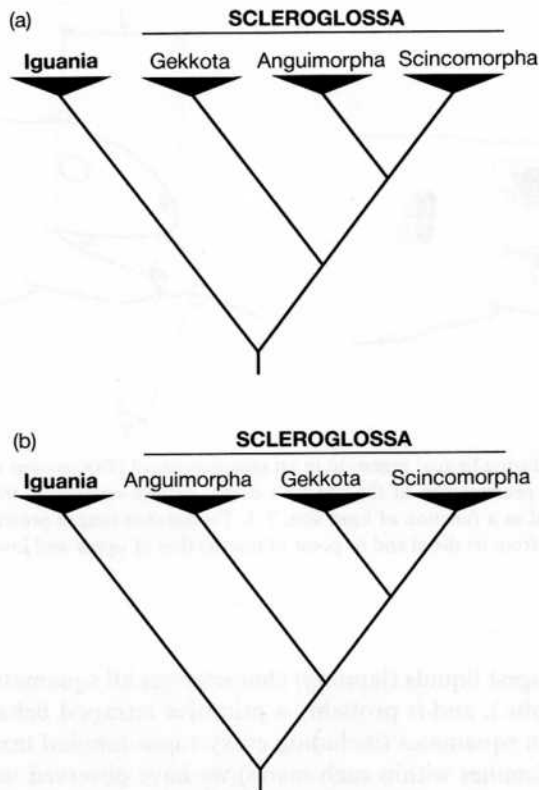


FIG. 2. Phylogenetic hypotheses of supra-familial relationships within Squamata. (a) From Estes *et al.* (1988). (b) From Schwenk (1988), based only on lingual characters. The cladograms agree strongly in their identification of a basal bifurcation dividing squamates into two lineages, Iguania and Scleroglossa. Lingual prey prehension is confined to Iguania. Scleroglossans use the jaws for ingestion.

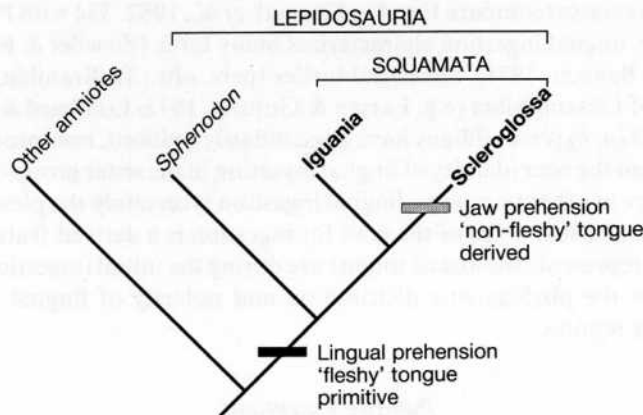


FIG. 3. Summary of phylogenetic conclusions. Lingual prehension in lepidosaurs is correlated with the presence of a 'fleshy', papillose tongue and is the primitive mode of ingestion. Jaw prehension is a derived feature of scleroglossans. It is correlated with a modified foretongue and represents the *loss* of lingual prehension.

iguanians, as well as scleroglossans, use the jaws to seize large prey. This switch was observed by Gorniak *et al.* (1982) in *Sphenodon*. They found that the tongue was used for prehension of crickets and neonate mice, but the jaws were used for adult mice. The salient point, however, is that scleroglossan squamates use the jaws for prehension of all prey items, including very small ones. Furthermore, we note that jaw prehension of large prey items by iguanians may involve initial tongue contact. We have observed that iguanid and agamid lizards biting a finger will first strike with the tongue, as if to draw the finger into the lizard's mouth. Herbivorous species of both families often bite off fixed pieces of leaf with the jaws. However, our films reveal that usually the leaf is first contacted by the tongue and drawn into the lizard's mouth. These preliminary observations suggest that iguanians may continue to use a lingual prehension mode even when apparently using the jaws to ingest food. Thus, there may be no 'switch' in mode of prehension, only a continuum of behaviour modulated according to prey mass or size (see **Discussion**).

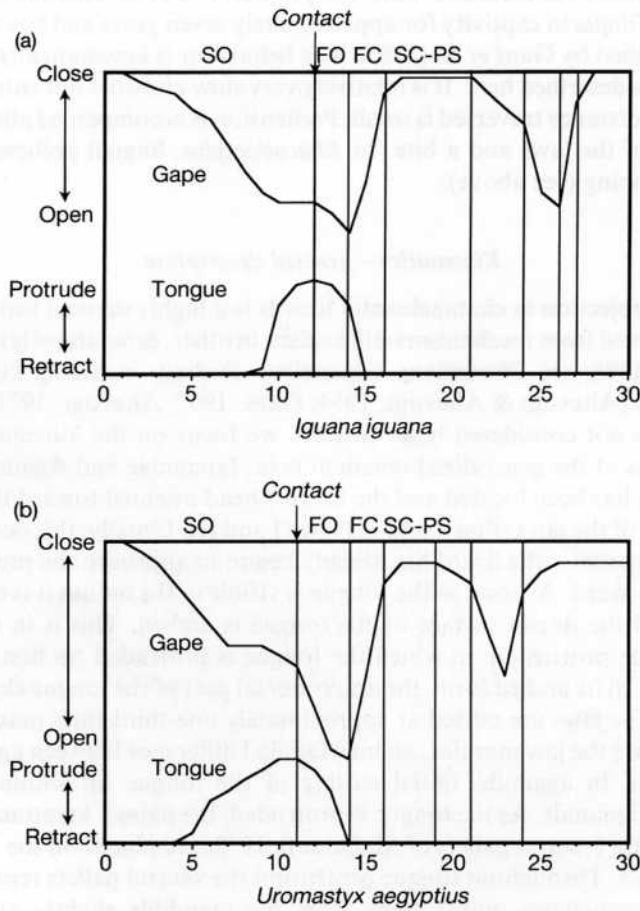


FIG. 4. Kinematic profiles of jaw and tongue movements during ingestion and one transport cycle in iguanian lizards. Note that only extra-oral tongue protrusion is shown. (a) *Iguana iguana* (Iguanidae). (b) *Uromastix aegyptius* (Agamidae). Contact = tongue-prey contact; FC = fast close; FO = fast open; SC-PS = slow close-power stroke; SO = slow open. Cine film frame numbers are shown along the horizontal axis. Films were taken at 48 and 32 fps, respectively.

Additional studies of individuals from species that feed on prey spanning a wide range of mass are being undertaken to test this hypothesis.

Secondly, some anecdotal field observations of *Sphenodon* and iguanian lizards have noted jaw prehension of small prey items (e.g. Walls, 1981; Vitt & Lacher, 1981). We point out that in most cases lingual prehension occurs in a fraction of a second (see below) and is not easily observed, even in the laboratory. Particularly in small and medium-sized species, film analysis is necessary to confirm lingual involvement.

Finally, two scleroglossans have been noted to use the tongue in some form of lingual ingestion. Gans, de Vree & Carrier (1985) observed initial tongue contact with the food item (a snail) in *Trachydosaurus rugosus* (Scincidae). The snail was drawn by the tongue a short distance across the ground to the mouth before initial biting. The snail was never lifted by the tongue. Bauer (1985) noted that a large gekkonid, *Rhacodactylus chahoua*, used its tongue to scoop pieces of soft banana into its mouth. However, he also observed that the jaws and not the tongue were used to ingest crickets. We believe that both cases above are exceptional. One of us (KS) has kept *Trachydosaurus* and closely related *Tiliqua* in captivity for approximately seven years and has observed behaviour similar to that described by Gans *et al.* (1985). The behaviour is kinematically distinct from 'true' lingual prehension as described here. It is relatively very slow and does not entail lifting of the prey into the mouth. The distance traversed is small. Prehension is accompanied almost simultaneously by close approach of the jaws and a bite. In *Rhacodactylus*, lingual prehension of soft food is clearly a form of lapping (see above).

Kinematics—general description

Ballistic tongue projection in chamaeleontid lizards is a highly derived form of lingual feeding thought to have evolved from mechanisms still evident in other, generalized iguanians (Schwenk & Bell, 1988; Smith, 1988; see **Discussion**). Chameleon feeding, including kinematics, has been described previously (Altevogt & Altevogt, 1954; Gans, 1967; Altevogt, 1977; Bell, 1984; Bels & Baltus, 1987) and is not considered here. Instead, we focus on the kinematics of lingual prey prehension in species of the generalized iguanian taxa, Iguanidae and Agamidae.

When a food item has been located and the lizard's head oriented toward the prey, ingestion is initiated by opening of the jaws (Figs 4 and 5; Plates I and II). Usually, this occurs when the lizard is stationary, but sometimes the lizard has already begun to approach the prey. As the jaws part, the tongue moves forward. As soon as the tongue is visible in the mouth it is evident that its tip is curled ventrally and the dorsal surface of the tongue is arched. This is in marked contrast to chemosensory tongue protrusion, in which the tongue is protruded tip first, dorsal surface flat (Schwenk, *In prep.*). In its arched form, the anterodorsal part of the tongue clears the jaw margins first. At this point, the jaws are parted at approximately one-third their maximum gape.

As the tongue clears the jaw margins, an interfamilial difference between agamids and iguanids is apparent (Fig. 6). In agamids, initial curling of the tongue tip within the mouth is less pronounced than in iguanids. As the tongue is protruded, the paired, keratinized pads underlying the notched tongue tip (ventral pallets of McDowell, 1972) are placed on the tip of the mandible, ventral surfaces down. Throughout tongue protrusion the ventral pallets remain in this position, although they are sometimes pulled away from the mandible slightly at maximum tongue protrusion (see Plate IVc). However, all tongue protrusion and deformation occurs with the tip more or less fixed in this position, the ventral pallets positioned with their ventral surfaces directed ventrally or posteroventrally. In contrast, iguanids immediately curl the tongue tip so the ventral

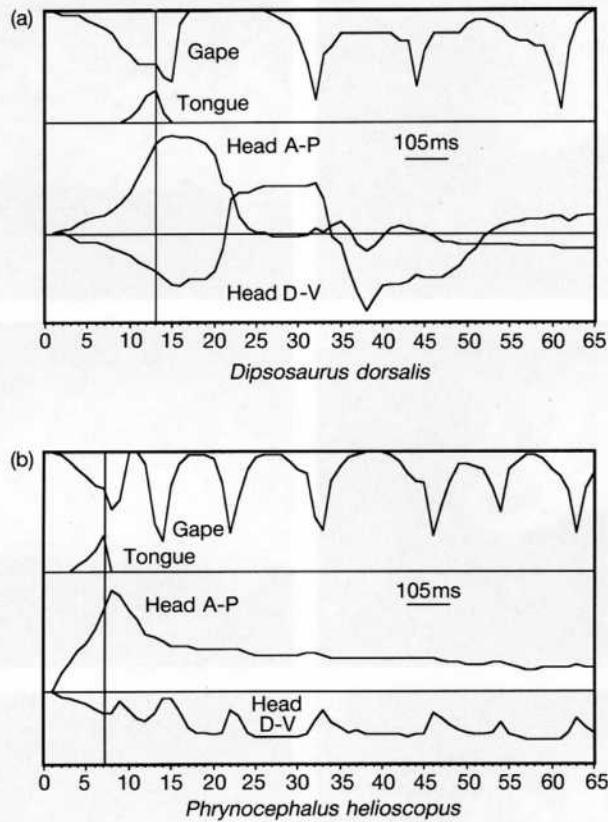


FIG. 5. Kinematic profiles of jaw, tongue and head movements during ingestion and transport in iguanian lizards. Jaw and tongue movements as in Fig. 4. For anteroposterior head movements, anterior is up. For dorsoventral movements, dorsal is up. The horizontal lines indicate the starting or zero point. The vertical line indicates the frame in which tongue-prey contact occurred during the initial (ingestion) cycle. All subsequent gape cycles are transport cycles. Cine frame numbers are shown along the horizontal axis. Note that in both (a) and (b), head movements are shown at half scale relative to jaw and tongue movements. (a) *Dipsosaurus dorsalis* (Iguanidae). (b) *Phrynocephalus helioscopus* (Agamidae).

pallets are tucked beneath the tongue, ventral surfaces up (Fig. 6; Plate III). Curling of the tongue tip into this conformation occurs while the tongue is still in the mouth. The tongue tip remains in this orientation throughout protrusion, but is not fixed in space as it is in agamids. None the less, the tip of the tongue does not usually move far from the end of the mandible.

Apart from the difference outlined above, lingual ingestion proceeds similarly in species of both families. The tongue continues to be protruded beyond the mandible at a fairly constant rate while the jaws increase their gape (Figs 4 and 5). As this occurs, the lizard moves its head forward and usually downward towards the prey. Anterior head movement is principally a result of whole-animal locomotion. At approximately one-half to two-thirds maximum gape, jaw movement pauses and tongue movement slows as maximum protrusion is achieved. Head movement, however, continues toward the prey. Tongue-prey contact occurs at maximum tongue extension during the pause in gape increase (Figs 4 and 5). Even after prey contact, the head continues to

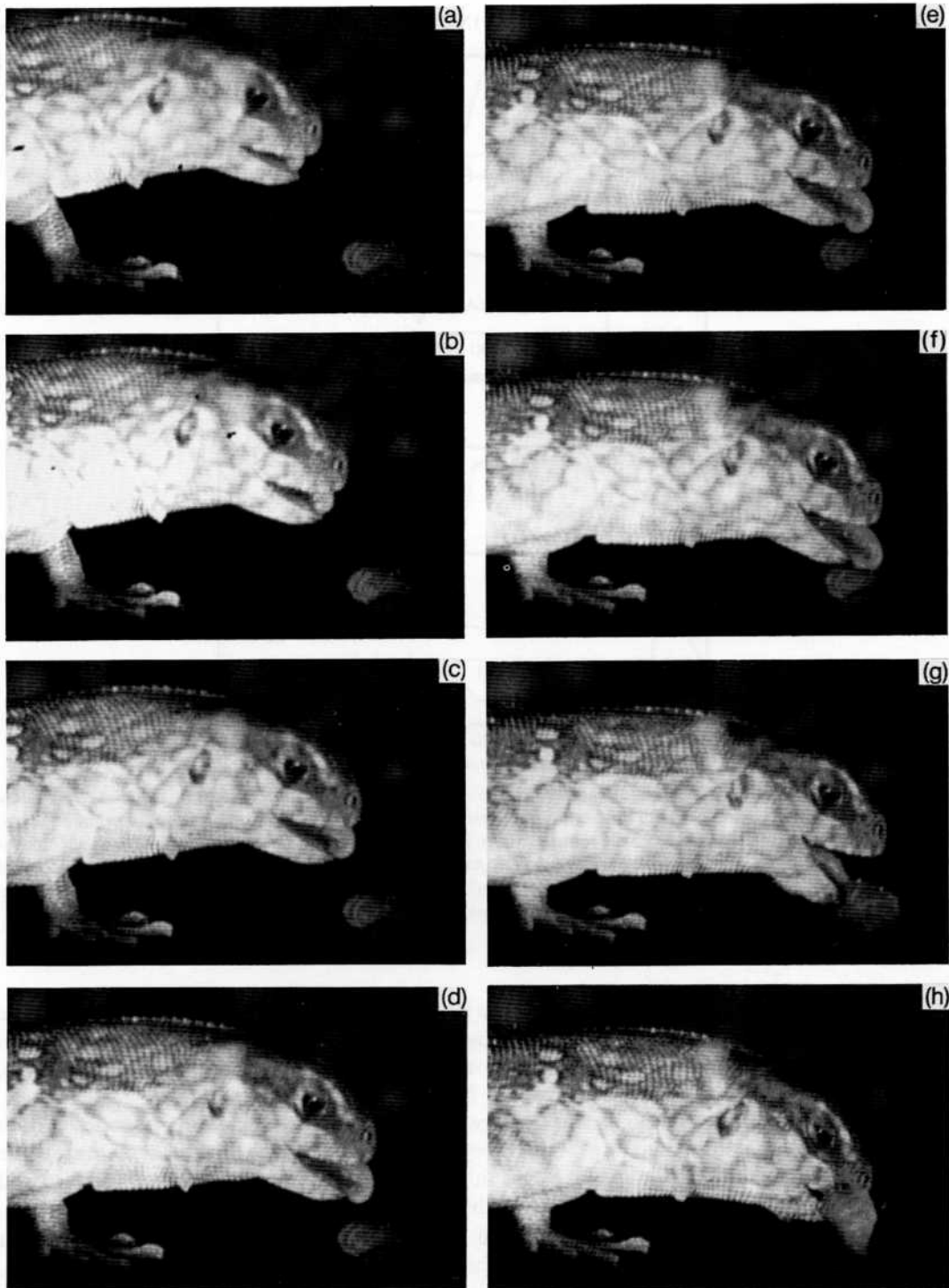


PLATE I. (a-h) Lingual ingestion in an iguanid lizard, *Dipsosaurus dorsalis*, from consecutive 16 mm cine frames. Note that the tongue tip is already curled ventrally as the tongue is initially protruded. Tongue-prey contact occurs on the anterior third of the tongue's dorsal surface. See text for further explanation.

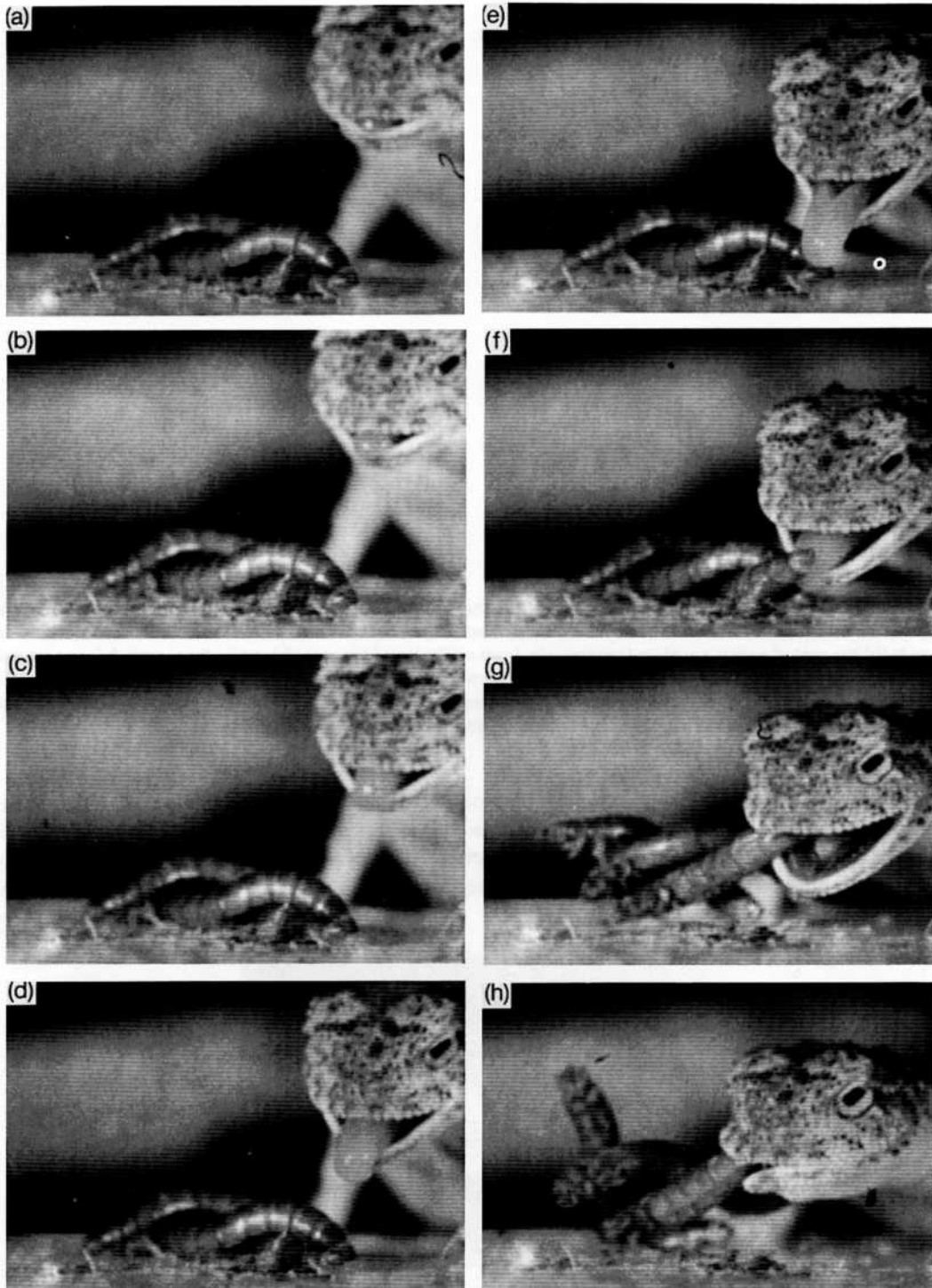


PLATE II. (a-h) Lingual ingestion in an agamid lizard, *Phrynocephalus helioscopus*, from consecutive 16 mm cine frames. Note that the tongue tip is less curled at protrusion than in *Dipsosaurus* (Plate I), but that the pattern of ingestion is essentially similar. Also note that in (g) the tongue tip is evident after retraction, lying between raised epithelial ridges containing the sublingual salivary glands.

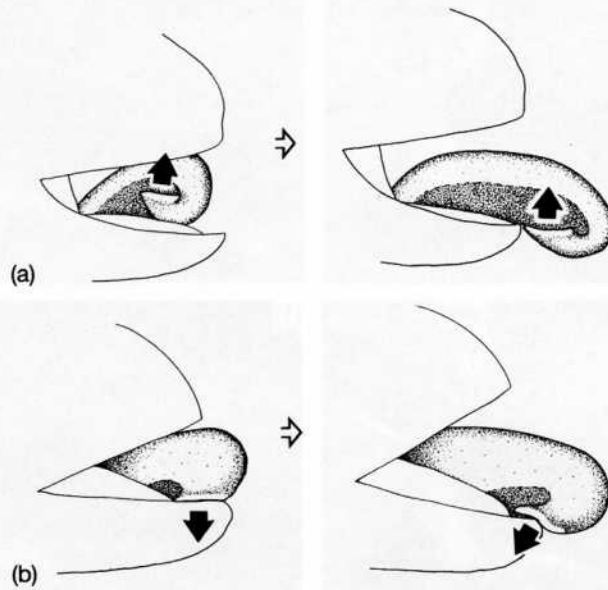


FIG. 6. Interfamilial difference in conformation of the tongue during lingual ingestion in lizards. In iguanids (a) the tongue is curled within the mouth so that the ventral pallets come to lie with their ventral surfaces directed dorsally. In agamids (b) the ventral pallets are placed ventral side down on the tip of the mandible while the tongue deforms around them. The black arrows indicate the orientation of the ventral pallet surfaces. Note that when the tongue is at rest in the mouth the ventral pallets lie over the swellings of the sublingual glands in the floor of the mouth, ventral surfaces down (see McDowell, 1972). Drawn from cine film tracings, not to scale. (a) *Iguana iguana*. (b) *Uromastyx aegyptius*.

move forward and downward, pressing the food item against the substratum. At this time, deformation of the tongue is sometimes observed. It is not known whether this deformation is active or passive, however, it seems to result in better fitting of the tongue surface to the food item. Contact and prehension occur on the anterior one-third of the tongue's dorsal surface (Plates I and II).

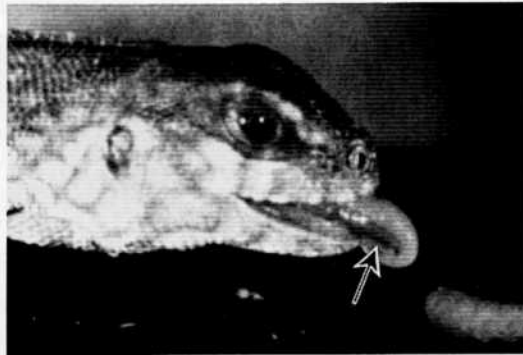


PLATE III. Tongue protrusion during ingestion in an iguanid lizard (*Dipsosaurus dorsalis*) showing the conformation of the tongue tip, with its ventral surface directed dorsally (arrow). Compare with Plate IV (a). See Fig. 6 and text for discussion of interfamilial difference in tongue tip conformation during protrusion.

Immediately after contact, a rapid gape increase and simultaneous tongue retraction are initiated (Figs 4 and 5). This occurs whether or not prehension of the food item is successful. As soon as the tongue and food item have cleared the jaw tips, the jaws are snapped closed. Jaw closure may or may not involve crushing of the food item, depending on the food item's size and/or position on the tongue during retraction. In any case, prehension is followed immediately by a

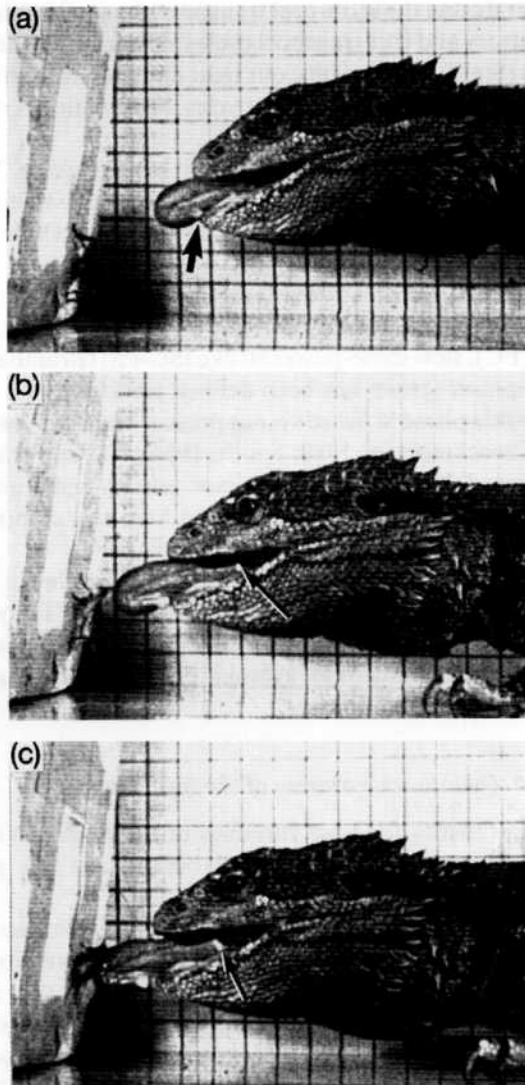


PLATE IV. Three consecutive 16 mm cine frames of lingual protrusion during ingestion in *Pogona barbata* (Agamidae) showing apparent hyoid protraction accompanying tongue protrusion. Thin arrows in (b) and (c) indicate putative anterior process of hyoid that emerges and moves anterodorsally with progressive tongue protraction. At tongue retraction, the anterior process moves rapidly posteroventrally with the tongue. Thick arrow in (a) indicates position of tongue tip, ventral surface down, on tip of mandible. At maximum protrusion (c) ventral pallets of tongue tip are pulled away from mandible, but remain directed posteroventrally. Compare with Plate III and Fig. 6.

