THE ANATOMICAL RECORD 252:102–116 (1998)

Tongue Flicking in Agamid Lizards: Morphology, Kinematics, and Muscle Activity Patterns

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ABSTRACT

We wanted to examine whether a relation between foraging strategy, morphology, the mechanics of tongue protrusion, and prey chemical detection and discrimination exists in agamid lizards. Tongue-flick behavior was observed in two species of this family: *Uromastix acanthinurus* and *Plocederma stellio*. Potential prey chemical discrimination by means of tongue flicking was examined by using applicator tests. Tongue flicks were subsequently recorded by high-speed video in combination with the electrical activity of a number of jaw and hyolingual muscles. The kinematics of jaws and tongue and the muscle activity patterns were quantified. To investigate if the observed differences in tongue-flick behavior (mainly in the frequency of use) are translated into corresponding differences in tongue morphology, the tongues of both species were examined by light and scanning electron microscopy. The species differed mainly in the surface morphology of the foretongue and in the abundance and distribution of taste buds on the tongue and oral cavity. These differences can be related to behavioural observations; whereas *U. acanthinurus* readily uses tongue flicks to detect and discriminate between food items, *P. stellio* does not. However, differences in tongue-flick mechanics (kinematics, electromyograms) between both species were minor. Based on the data gathered in this study and from previously published data, an evolutionary transformation series leading to the complex tongue-flick cycles as observed in snakes is proposed. The required morphological and mechanical changes that accompany such an evolutionary sequence are discussed. Anat. Rec. 252:102–116, 1998.

Key words: tongue flicking; morphology; kinematics; EMG; chemical prey discrimination; *Plocederma stellio*; *Uromastix acanthinurus*

The tongue of lizards is used for diverse functions such as lingual prey prehension in iguanian lizards (Schwenk and Throckmorton, 1989; Herrel et al., 1995), prey transport and swallowing in most lizards (Delheusy and Bels, 1992; Herrel et al., 1996, 1997), defensive display in some scincids (e.g., shingleback lizards, Gans et al., 1985), spectacle cleaning in geckoes (Simon, 1983), and chemical sampling from the external environment by means of tongue flicks or tongue touches (for overviews, see Schwenk, 1993; Cooper, 1994b,c, 1995a). Tongue extrusions, such as flicks or touches, can be used in the detection of conspecifics (Cooper and Vitt, 1984; Simon, 1985), kin recognition (Werner et al., 1987), sex recognition and courtship (Cooper and Vitt, 1984; Cooper et al., 1986), general exploration (Bissinger and Simon, 1979; Simon et al., 1981), predator detection (Thoen et al., 1986; Van Damme et al., 1990), and food detection and discrimination (see Schwenk, 1993; Cooper 1994b,c, 1995a). However, tongue

Grant sponsor: IWT; Grant number: 943039; Grant sponsor: FKFO; Grant number: G.0221.96.

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Received 23 December 1997; Accepted 28 April 1998

flicking in foraging and feeding behaviour differs dramatically among major lizard taxa and may be affected by foraging ecology (sit and wait vs. active foragers; see Cooper 1989, 1990a,b, 1997).

A tongue flick as such can be defined as "the movements of the tongue from its appearance outside the mouth until its complete withdrawal" (Gove, 1979). Based on tongue movements, three types of tongue flicks are recognised: simple downward extensions (SDEs) that show no oscillation phase between the protrusion and retraction, single oscillations (SOCs), and multiple oscillations (MOCs) where the tongue performs more than one oscillation before retraction (see Ulinski, 1972). In iguanians only the first type (SDE) is present (Gove, 1979; Goosse and Bels, 1992).

Based on tongue morphology (Camp, 1923; Schwenk, 1988), squamates have been subdivided into two large suprafamilial taxa: Iguania and Scleroglossa (Estes et al., 1988). Iguania possess a short fleshy tongue that is used for both prey capture and food transport. In contrast, Scleroglossans show an elongated, usually strongly bifurcate tongue that is not or seldom used during prey capture (but see Urbani and Bels, 1995; personal observation). Accordingly, it has been suggested that most Iguania do not tongue flick live prey and probably cannot discriminate between chemical stimuli from prey and other sources (see Cooper, 1989, 1994a). Nevertheless, herbivorous iguanids (e.g., *Dipsosaurus dorsalis*) are known to locate and identify food by tongue flicking (Krekorian, 1989; Cooper and Alberts 1990, 1991).

Although numerous studies have investigated the occurrence of tongue-flick behaviour in various lizard species (for reviews, see Simon, 1983; Cooper, 1994b,c; Schwenk, 1993, 1995), the mechanistic background of the tongue flick itself remains obscure. Only for *Lacerta viridis* (Goosse and Bels, 1992) and *Anguis fragilis* (Toubeau et al., 1994) have kinematical data been gathered. However, the knowledge of functional characteristics such as movement and motor patterns is critical when discussing the origin and evolution of this behavior.

The aims of the present study were (1) to examine the occurrence of tongue-flick behavior in relation to food detection and discrimination in both herbivorous (*Uromastix acanthinurus*) and insectivorous agamid lizards (*Plocederma stellio*), (2) to investigate the morphology of the hyolingual apparatus and the tongue surface in detail, (3) to compare the kinematic characteristics of the tongue-flick cycle in both species, and (4) to investigate the underlying motor patterns that govern tongue flicks and compare these between both species.

MATERIALS AND METHODS

Specimens

Two adult specimens (snout–vent length; SVL: 120 ± 30 mm, mass: 42 ± 3 g) of the species *Plocederma stellio* and two *Uromastix acanthinurus* (SVL: 127 ± 20 mm, mass: 140 ± 10 g) were used in the electromyographic (EMG) experiments; an additional five *P. stellio* and five *U. acanthinurus* were used to investigate food chemical discrimination capabilities. Two *P. stellio* and two *U. acanthinurus* were killed for microscopic investigation. The specimens of *P. stellio* used in this study were collected in Israel and provided to us by Dr. E. Kochva; the two *U. acanthinurus* specimen used for the EMG experiments and the two specimens used for microscopical investigation were obtained from a commercial dealer; the other five specimens were on temporary loan from the Antwerp Zoo. The animals were kept in a glass vivarium on a 12-hr light/dark cycle. The *P. stellio* specimens were offered water and food consisting of crickets, grasshoppers, and mealworms ad libitum. The *U. acanthinurus* were offered endive, salad, tomato, banana, apple, and a variety of other vegetables and fruits. The environmental temperature varied from 28°C at daytime to 20°C at night; an incandescent bulb provided the animals with a basking place at a higher temperature (35–40°C).

An additional four animals of the species *P. stellio* and two specimens of *U. acanthinurus* (Royal Belgian Museum for Central Africa) were dissected and stained to characterize all jaw and hyolingual muscles (Bock and Shear, 1972). Drawings were made of all stages of the dissection by using a Wild M5 dissecting microscope, provided with a camera lucida.

For light microscopy the heads of one specimen of each species were prepared for paraffin histology by using standard techniques (Humason, 1979). Serial 8–10-µm sections (both transverse and longitudinal) were made and stained with Masson's trichrome. In addition, two animals of each species were killed by an overdose of Ketamin hydrochloride (Imalgene 500 Parke-Davis, Zaventen, Belgium, 50 mg/ml; 1 g/kg body mass). For scanning electron microscopy the tongues and lower and upper jaws were extensively rinsed in water and fixed in 2.5% glutaraldehyde in 0.1 M Na-cacodylate buffer (pH 7.2) for 24 hr. After rinsing in buffer, the tissue samples were dehydrated in an increasing ethanol series, critical-point dried, mounted on aluminium stubs, and sputter coated with gold. Observations were made by using a Philips SEM-515 scanning electron microscope at 15–20 kV.

Electromyographic and Video Recordings

The animals used in the EMG experiments were anaesthetized by an intramuscular injection of Ketalar (*P. stellio*: 200 mg/kg body mass, *U. acanthinurus*: 100 mg/kg body mass) before electrode implantation. Bipolar 25-cm-long electrodes were prepared from teflon-insulated 0.065-mm Ni-Cr wire (Gans and Gorniak, 1980). The insulation was scraped away at the tip, thus exposing 1 mm of electrode wire. The electrodes were implanted percutaneously into each muscle belly by using hypodermic needles with 2 mm of the electrode bent back as it emerged from the needle barrel. Electrodes were placed in several jaw closers for both species: *Plocederma stellio*: the musculus pterygoideus (lateral and medial parts), the musculus adductor mandibulae externus (medial part), and the musculus adductor mandibulae posterior; *Uromastix acanthinurus*: the musculus pterygoideus (medial and externus parts) and the musculus adductor mandibulae externus (superficial and profundus parts). Electrodes were also placed in the jaw opener (the musculus depressor mandibulae, both species) and into several hyolingual muscles: the musculus genioglossus (both species), the musculus hyoglossus (both species), the ring muscle (*P. stellio*), the musculus sternohyoideus (*P. stellio*), and the musculus omohyoideus (*U. acanthinurus*). Electrode placement was confirmed by lateral and dorsoventral X-rays in both species and by dissection in one *P. stellio* specimen.

Electrical signals were amplified 2,000 times with Gould Bioelectric and Universal preamplifiers (Gould Instru-

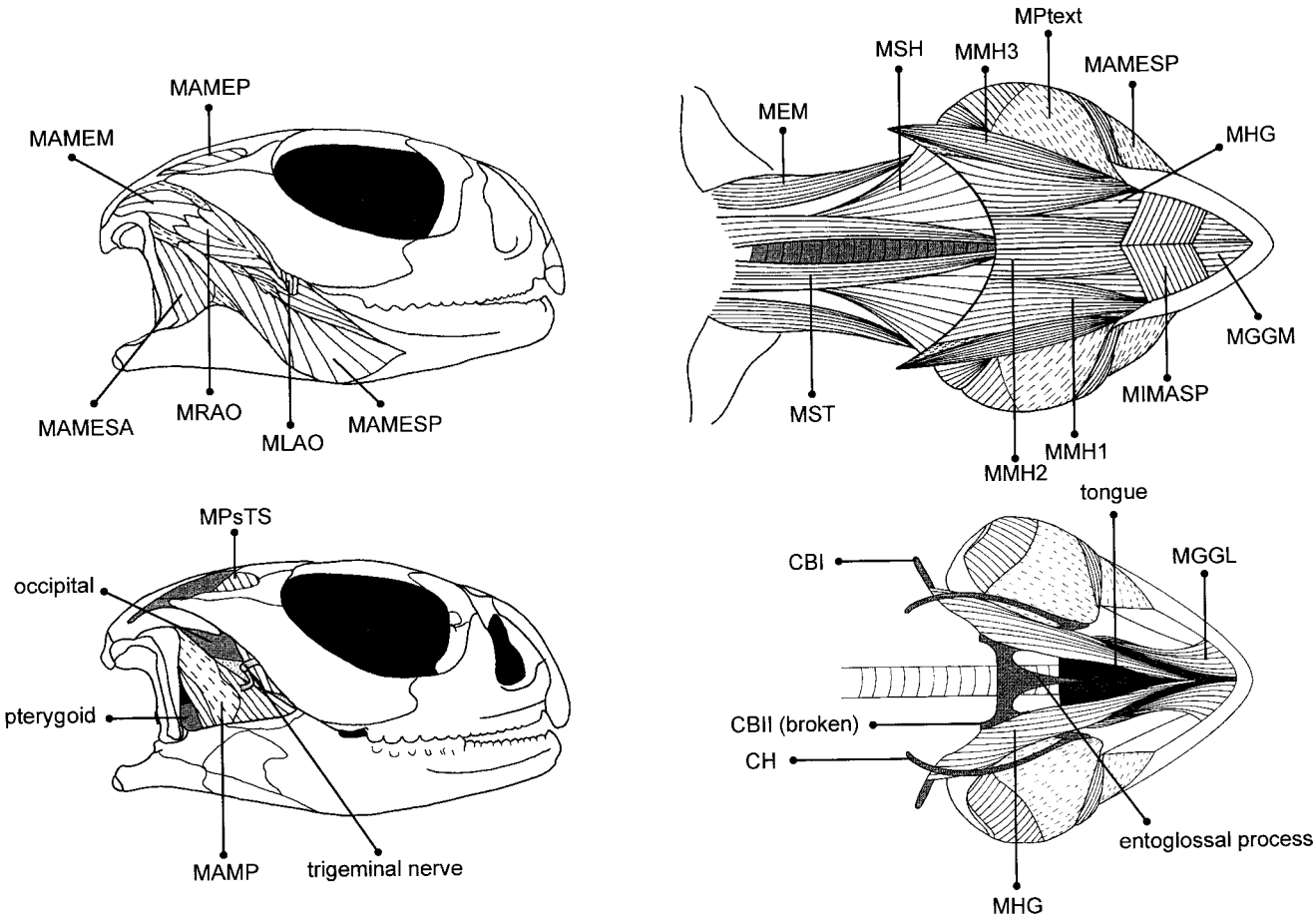

Fig. 1. *Uromastix acanthinurus*. Jaw and hyolingual musculature. Upper left: Lateral view after removal of the skin, the m. pterygoideus externus, the quadratojugal ligament, and the m. depressor mandibulae. Lower left: Deeper lateral view, after the additional removal of the complete m. adductor mandibulae externus. Upper right: Superficial ventral view of the hyolingual muscles after removal of the skin, part of the m. intermandibularis anterior, the m. constrictor colli, and the m. omohyoideus. Lower right: Deeper dissection; after removal of the hyoid retractor and protractor muscles, the m. genioglossus medialis and the m. branchiohyoideus. CBI, ceratobranchiale I; CBII, ceratobranchiale II; CH, ceratohyale; MAMEM, m. adductor mandibulae externus medialis; MAMEP, m. adductor mandibulae externus profundus; MAMESA, MAMESP, mm. adductor mandibulae externus superficialis anterior and posterior; MAMP, m. adductor mandibulae posterior; MEM, m. episternocleidomastoideus; MGGL, MGGM, mm. genioglossus medialis and lateralis; MHG, m. hyoglossus; MIMASP, m. intermandibularis anterior superficialis posterior; MLAO, m. levator anguli oris; MMH1, MMH2, MMH3, mm. mandibulohyoideus 1, 2, and 3; MPsTS, m. pseudotemporalis superficialis; MPtext, m. pterygoideus externus; MRAO, m. retractor anguli oris; MSH, m. sternohyoideus; MST, m. sternothyroideus.

ment Systems, Inc., Valley View, OH) (range = 100 Hz to 10 kHz) and Honeywell Accudata 117 DC amplifiers and were recorded on a Honeywell 96 FM 14 channel tape recorder (Honeywell Inc., Denver, CO) (medium bandpass) at a speed of 19.05 cm/sec.

Tongue flicks were simultaneously recorded by using a NAC-1000 high-speed video system set at 500 frames per second using video lights (TRI-LITE, Cool Light Co. Inc., Hollywood, CA). The animals were filmed in a plexiglass cage (50 cm × 15 cm × 10 cm). The output of a Tectronix wave pattern generator (square wave) was recorded on the FM tape recorder and sent to a LED (light emitting diode) kept in the visual field. This allowed synchronisation of the electromyographic and kinematic records.

Video Data and Electromyographical Analysis

Clearly visible external markers (colour spots) were digitized by using the NAC1000 X–Y Coordinator (Fig. 1). Horizontal (x) and vertical (y) coordinates were recorded for each digitized point at intervals of two frames. Aspects calculated were changes in gape profile (distance: 2–4, angle: 2–3–4), displacement of the upper and the lower jaws (y coordinate of points 2 and 4, respectively), cranial elevation (angle subtended by the line interconnecting points 2–3 and the horizontal), lower jaw depression (angle subtended by the line interconnecting points 3–4 and the horizontal), and tongue protrusion (x coordinate of point 5, x coordinate of point 4).

The recorded EMG signals were digitized at 10 kHz by using a Keithley DAS series 500 12-bit A-D converter (Keithley Instruments, Inc., Cleveland, OH). After digitization, the signals were integrated by following the procedure of Beach et al. (1982; 100 data = 10 msec/bin), and the number of spikes and the average amplitude per interval were calculated. The exact duration of muscular activity and the onset of each muscle relative to the m. depressor

mandibulae (MDM) were then measured. Several muscles had more than one activity burst. Different bursts were defined on the basis of abrupt amplitude differences. The EMG variables were then related to the kinematic data.

Prey Chemical Discrimination Tests

The responses of the lizards to chemical stimuli from prey and control substances presented on the cotton swabs of wooden applicators (25 cm) were recorded. In the experiments each lizard responded to each stimulus once in a randomized block design (see Cooper et al., 1996). The lizards responded to all stimuli in counterbalanced sequence to avoid sequential bias. The responses of the lizards to cricket surface chemicals, squashed endive, cologne (Caractère, Daniel Hechter, Paris, France), fish, and distilled water were recorded.

Cologne and fish (for a discussion on the validity of these stimuli, see Dial and Schwenk, 1996) were used as a pungency control to examine the effects of a (highly volatile) stimulus lacking relevance to feeding behaviour. Distilled water served as an odourless control for the reactions to the swab and the experimental setting. Before testing, the cotton tip of an applicator was first dipped in distilled water and then dipped in cologne, rolled over the cricket integument, rolled over fish, or rolled over squashed endive. Excess water was blotted with tissue paper.

The experiments were conducted when the lizards were sufficiently active and alert (between 11.00 and 17.00 hr). Temperatures varied between 35°C and 40°C during testing. During a trial the experimenter approached a lizard's cage slowly and positioned a swab 1–2 cm anterior to the lizard's snout. The number of tongue flicks was recorded for 60 sec after the first tongue flick unless the lizard bit the swab. In that case the trial was terminated. If a lizard did not tongue flick within 40 sec, the swab was brought gently into contact with its snout for about 1 sec. If the lizard did not tongue flick in the next 20 sec, the trial was terminated. Each lizard was tested for all stimuli on the same day. The intertrial interval was at least 1 hr. Lizards were not fed for 3 days before testing.

Responsiveness to chemical stimuli was measured by the tongue-flick attack score by using repeated measure designs (see Burghardt, 1967; Cooper and Burghardt, 1990). Nonparametric tests were used due to the extreme nonnormality (large number of zero values). Data were analyzed by the Friedman analysis of variance and/or sign tests ($P = 0.05$; Sokal and Rolff, 1995; Zar, 1996).

RESULTS

Morphology

Gross morphology of the feeding apparatus. The skull of *Plocederma stellio* and *Uromastix* has been adequately described by El Toubi (1945, 1947) and Jollie (1960). The hyoid apparatus (Figs. 1 & 2) has a distinctly tapered entoglossal process (Fig. 2c), one pair of ceratohyals, and two pairs of ceratobranchials (see Fürbringer, 1922; Richter, 1933; Gnanamuthu, 1937; Sondhi, 1958; Tilak, 1964; Smith, 1988). The ceratohyal (CH) is similar in both species and consists of three parts. The proximal part articulates with the basihyoid (Fig. 2d), runs anteriorly, and is connected to the posteriorly directed intermediate part by means of a cartilaginous jointlike structure. The distal part is short in both species and is connected to the base of the quadrate. The first ceratobranchial (CBI; Fig. 2d), situated at the posterolateral side of the basihyoid, is also similar in both species. However, the second ceratobranchial (CBII) is very different in both species. In *P. stellio*, the CBIIs, which touch each other along the midline of the trachea, are long and taper gradually along their length. In *U. acanthinurus*, the CBII is short and ends in a flat cartilaginous part. In addition, in *U. acanthinurus*, the CBIIs are situated on both sides of the trachea and do not touch. In contrast to *U. acanthinurus*, where only the entoglossal process (Fig. 2c, 2e, & 2f) and the most distal parts of the hyoidarches are cartilaginous, in *P. stellio* only the CBIs are ossified.

The jaw and hyolingual muscles in agamids have been described by several researchers (Sanders, 1872; De Vis, 1884; Gandolfi, 1908; Lakjer, 1926; Gnanamuthu, 1937; Haas, 1973; Gomes, 1974; Schwenk, 1988; Smith, 1988; for *P. stellio* more specifically, see also Herrel et al., 1995, 1997). The jaw adductors in agamid lizards can be described as consisting of three major groups: the m. adductor mandibulae externus, the m. adductor mandibulae internus, and the m. adductor mandibulae posterior (see Fig. 1). A full, detailed description of the jaw musculature in both species will be published elsewhere.

The fleshy tongue of *Plocederma stellio* is composed of intrinsic and extrinsic muscles. The tongue musculature in agamid lizards has been described in detail elsewhere (Gandolfi, 1908; Gnanamuthu, 1937; Smith, 1988). The most important differences in intrinsic tongue musculature between both species examined are (1) the absence of a true ring muscle surrounding the entoglossal process (Fig. 2e & 2f) and (2) the absence of vertical septa in *Uromastix* (see also Smith, 1988).

The extrinsic lingual musculature (Fig. 1) originates on the mandible or the hyoid and consists of distinct genioglossus and hyoglossus muscles (Fig. 2) and is similar in both species. The genioglossus (MGG) originates on the anteromedial part of the mandible and runs posteriorly to insert on the tongue (Fig. 2a & 2c). Near its insertion it separates into medial, lateral, and internal parts. The hyoglossus (MHG) originates on the first ceratobranchial and runs into the tongue, dorsally to the MGG. Anterior of the basihyoid, the MHG is recognisable as a distinct muscle bundle (Fig. 2e).

Several hyoid muscles lie ventral to the tongue. The mandibulohyoideus (MMH) consists of three portions that originate on the medial side of the mandible and insert on the ceratohyal and the first ceratobranchial. The sternohyoideus (MSH) and sternothyroideus (MST) muscles both originate on or near the episternum and run anteriorly to insert on the basihyal and first ceratobranchial. The omohyoideus muscle (MOH) originates on the anterior edge of the interclavicula and suprascapula and its fibres run anteroventrally to insert on the first ceratobranchial.

Morphology of the tongue and oral cavity: Occurrence and distribution of taste buds. In the following description of tongue surface morphology, we adopt the terminology of Schwenk (1985) and Rabinowitz and Tandler (1986). The tongue of the examined lizards can be subdivided into three distinct areas (Fig. 3): the tongue tip, the foretongue, and the hindtongue; each is characterized by a specific surface topology (Table 1). The tongue tip is the bifurcated anterior end of the tongue with a small area

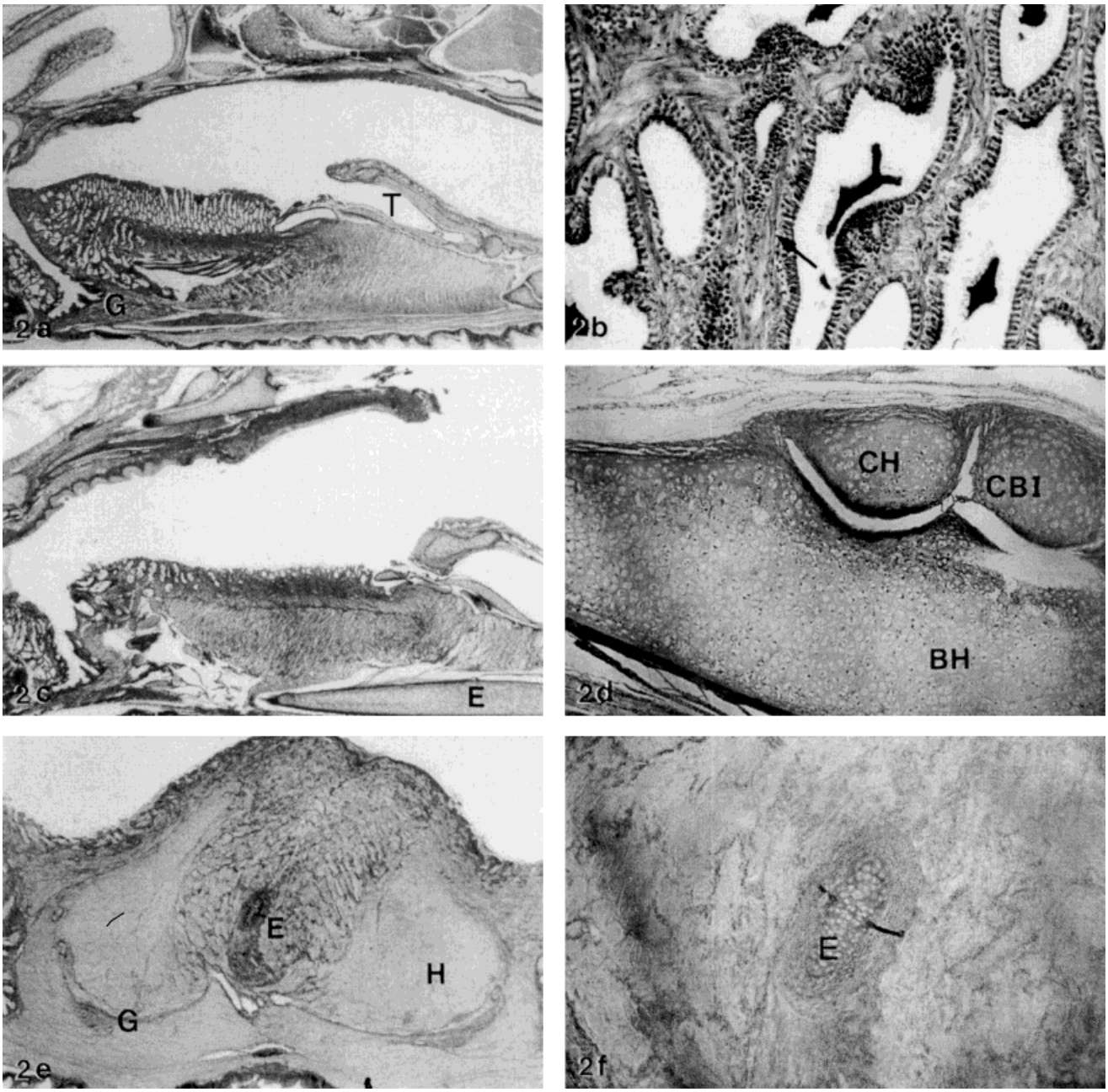

Fig. 2. Light microscopic view of transverse and sagittal sections in different areas of the heads of *P. stellio* and *U. acanthinurus*. **a:** Medial sagittal section of the head of *P. stellio*. ×8. Numerous secretory cells are present on the foretongue. **b:** Detail of an illustrating muscle fibre (arrow) running into the dorsal papillae. ×250. **c:** Sagittal section illustrating the arrangement of the tongue, entoglossal process, and intrinsic tongue muscles in *P. stellio*. ×16. **d:** Sagittal section through the hyoid apparatus of *P. stellio* illustrating the joint between the basihyoid, the ceratohyal, and first ceratobranchial. ×100. **e:** Transverse section through the hindtongue in *U. acanthinurus* illustrating the arrangement of the hyoglosus and genioglossus muscles. ×16. **f:** Detail of e at higher magnification (×100) showing the entoglossal process. Note the large amount of connective tissue surrounding the entoglossal process. BH, basihyoid; CBI, ceratobranchiale I; CH, ceratohyale; E, entoglossal process; G, m. genioglossus; H, m. hyoglossus; T, trachea.

immediately posterior to the bifurcation (Schwenk, 1985). The bifurcation is more prominent in *U. acanthinurus* than in *P. stellio* (compare Fig. 3b with 3e). The anteriormost part is characterized by a smooth surface and absence of taste buds in both species (Fig. 3b & 3e). The adjacent, more posteriorly situated part of the tongue tip bears groups of anteriorly flattened, short, and closely packed cylindriform papillae. The surface of such a group appears smooth at low magnification and often carries taste buds. At the posterior part of the tongue tip, the structure of the tongue surface gradually changes (through a small area bearing plicae in *U. acanthinurus*) into a

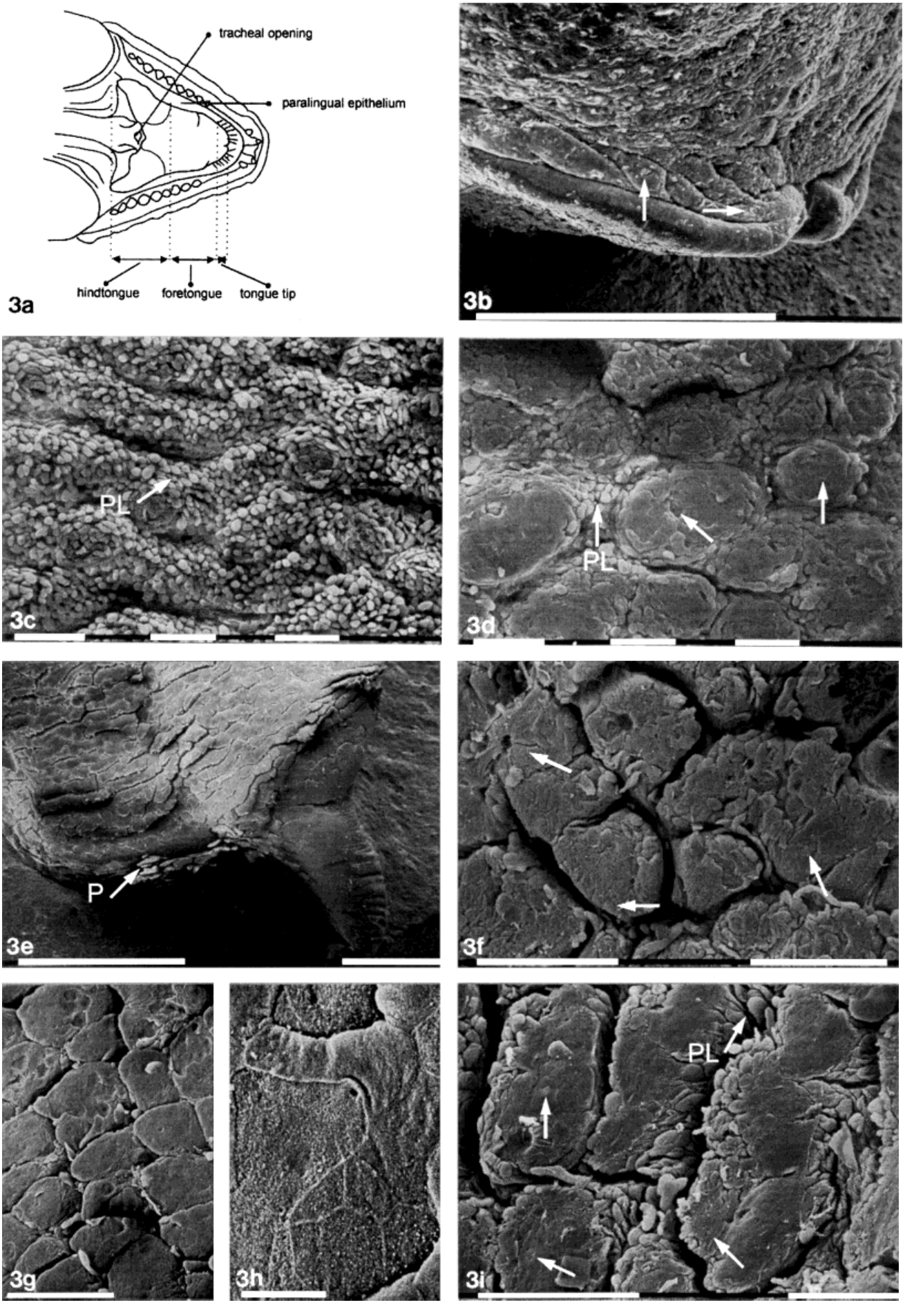
tracheal opening
paralingual epithelium
hindtongue
foretongue
tongue tip
3a
3b
PL
3c
PL
3d
P
3e
3f
3g
3h
PL
3i

Fig. 3.

TABLE 1. Summary of Lingual and Oral Morphology and the Presence and Abundance of Taste Buds

Species	Region	No. taste buds[a]	Structure
Plocederma stellio	Tongue tip	+ (posterior part)	Smooth epithelium
	Foretongue		
	Lateral	+	Transversely oriented rows of plume cells
	Medial	−	Plumose papillae
	Hindtongue	+	Densely packed plumose papillae
	Oral epithelium	+	
Uromastix acanthinurus	Tongue tip	+ (posterior part)	Smooth epithelium
	Foretongue		
	Lateral	++	Dense papillae with prominent microstructure
	Medial	−	Papillae with loose plume cells at the edges
	Hindtongue	+	Densely packed cylindriform papillae
	Oral epithelium	++	

[a]No. taste buds indicates presence and abundance of taste buds as follows: −, absent; +, present; ++, abundant.

typical foretongue structure, with an increase in the number of filamentous cylindrical and/or plumose papillae. These papillae are characterized by a large number of secretory cells and several muscle fibres running into them (Fig. 2b). Whereas the tongue tip of both species is rather similar, the foretongue structure of both species differs markedly. In *P. stellio*, the surface of the foretongue is composed of transversely oriented rows of plumose papillae (Fig. 3c) bearing apparently randomly disposed plume cells (see also Rabinowitz and Tandler, 1986). This area of the tongue is characterized by the absence of taste buds. In *U. acanthinurus*, the foretongue can be subdivided into two distinct areas. The medial part is composed of densely packed triangular papillae, characterized by a surface with a prominent microstructure (Fig. 3g & 3h). The lateral part consists of rectangular papillae; at the edge of such a papilla, free-standing plume cells are observed (Fig. 3f). Whereas the medial part (Fig. 3g) is devoid of taste buds, the lateral part shows a limited number of taste buds anteriorly and a high density of taste buds (one or more per papilla) posteriorly (see arrows on Fig. 3f). The hindtongue in both species somewhat resembles the posterior part of the tongue tip and is composed of typical papillae consisting of groups of concentrically arranged cylindrical cells, generally bearing microvilli or microridges (Fig. 3d & 3i). Papillae are interspersed with plumose cells and usually carry one taste bud (Fig. 3d & 3i).

The oral epithelium was also examined for the presence of taste buds (see Fig. 4). In *P. stellio*, only on the tissue fold just medial to the teeth of the lower jaw were any taste buds observed (Fig. 4c). The surface of this tissue fold is composed of flattened cylindriform epithelial cells. Taste buds are abundant in the anterior part, present in the middle part, and absent from the posterior part. No taste buds were observed on the epithelium on the dorsal side of the oral cavity. In *U. acanthinurus*, taste buds were not only present along the entire medial dental tissue fold but also abundant on various parts of the dorsal side of the oral cavity (see Fig. 4a, 4b, & 4d).

Prey chemical discrimination and observations of tongue-flick behavior.

Plocederma stellio. In *P. stellio*, tongue-flick behavior is only occasionally observed and usually consists of tongue touches. In one of the recorded sequences, the lizard attempted to capture a prey item but lost it. The prey item fell to the bottom of the cage and showed no further movements. After a few seconds, the lizard approached the prey again, tongue flicked, and subsequently captured the prey. In all other recorded sequences, the lizards approached the live prey, tongue flicked, and captured the prey item. Nevertheless, only six tongue flicks were observed in the more than 50 feeding sequences recorded. These observations are supported by the prey chemical discrimination tests. None of the five animals tested tongue flicked an applicator (Table 2).

Uromastix acanthinurus. Uromastix acanthinurus readily used tongue flicks when placed in a new environment or when brought in contact with other lizards. The lizards also invariably tongue flicked food introduced into the cage before eating it. Prey chemical discrimination tests indeed showed clear responses to prey chemicals (Table 2). Animals attacked only after tongue flicks, during

Fig. 3. Scanning electron micrographs of the tongue tip, the foretongue, and hindtongue in both species. **a:** Schematic representation of the tongue (*U. acanthinurus*) illustrating the subdivision of the tongue into three distinct areas. **b:** Tongue tip in *P. stellio* showing only a minor bifurcation, covered with smooth epithelium and carrying several taste buds (arrows). **c:** Typical foretongue structure in *P. stellio* showing transversely oriented rows of plumose cells (PL and arrow). **d:** Typical hindtongue structure in *P. stellio*, with closely packed cylindriform papillae with relatively few taste buds (arrows) and free-standing plume cells at the edge. **e:** Tongue tip in *U. acanthinurus*. Note the more prominent bifurcation; taste buds are present just posterior to the plicae (P and arrow) at the posterior edge of the bifurcation. **f:** Lateral part of the foretongue in *U. acanthinurus* showing several taste buds (arrows). **g:** Medial part of the foretongue in *U. acanthinurus* with seemingly smooth papillae. **h:** Detail of g showing the presence of a very distinct microstructure. **i:** Hindtongue in *U. acanthinurus* bearing papillae with usually not more than one taste bud associated (arrows) and with loose plumelike cells (PL and arrow) at the periphery. Scale bars 1 mm in b,e, 0.1 mm in c,d,f,g,i, 0.01 mm in h.

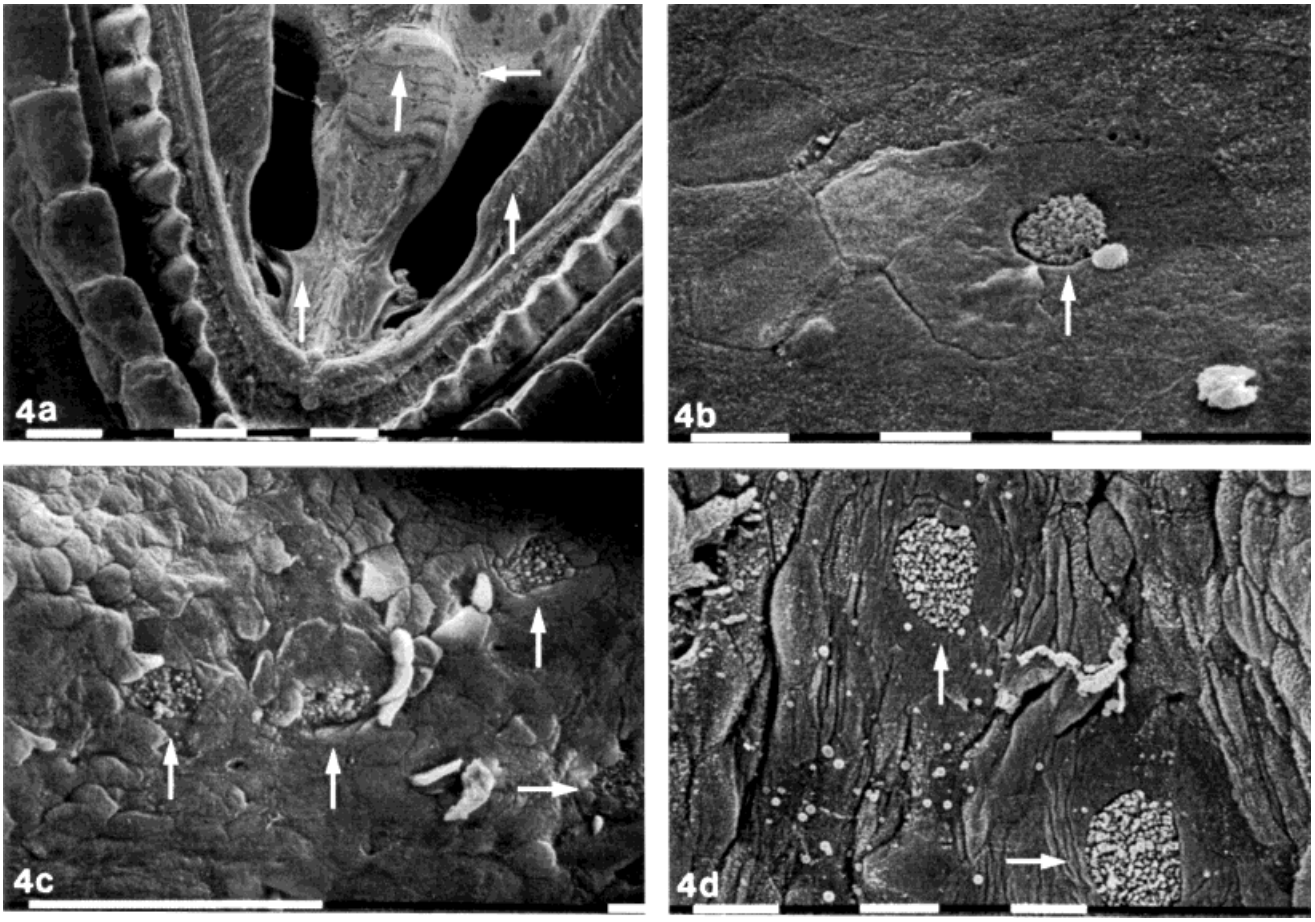

Fig. 4. Scanning electron micrographs illustrating the occurrence and distribution of extralingual taste buds. **a:** Ventral view of the anterior mouth roof in *U. acanthinurus* at low magnification; arrows indicate areas with large numbers of taste buds. **b:** Detail of a showing a taste bud (arrow) and prominent microstructure. **c:** Paralingual epithelium in *P. stellio* showing several taste buds (arrows), indicating the high number present. **d:** Anterior paralingual epithelium in *U. acanthinurus* illustrating the presence of taste buds (arrows). Scale bars = 1 mm in a, 0.01 mm in b,d, 0.1 mm in c.

TABLE 2. Prey Chemical Descrimination in *Plocederma stellio* (PS) and *Uromastix acanthinurus* (UA)[a]

Stimulus	Response	PS1	UA1	PS2	UA2	PS3	UA3	PS4	UA4	PS5	UA5
Control	# TF	0	14	0	1	0	0	0	0	0	0
	TTA	0	0	0	0	0	0	0	0	0	0
Cologne	# TF	0	0	0	0	0	0	0	0	0	0
	TTA	0	0	0	0	0	0	0	0	0	0
Fish	# TF	0	0	0	0	0	0	0	0	0	2
	TTA	0	0	0	0	0	0	0	0	0	0
Cricket	# TF	0	0	0	3	0	0	0	3	0	0
	TTA	0	0	0	40	0	0	0	0	0	0
Endive	# TF	0	2	0	2	0	0	0	1	0	1
	TTA	0	50	0	0	0	0	0	0	0	0

[a]Table entries are number of tongue flicks (# TF) and time to attack (TTA).

which the swab was touched (i.e., tongue touches). Animals tongue flicked the control swab an average of three times (±6.2); stimulus control swabs were flicked even less (0 and 0.4 ± 0.9). Controls did not differ significantly from one another ($\chi^2 = 2$, df = 2; $P > 0.05$). Swabs bearing food stimuli were flicked more (cricket: 5.2 ± 10.0, endive: 5.6 ± 10.3), but responses to cricket surface chemicals did not differ from those of the control ($\chi^2 = 0.33$, df = 1; $P > 0.05$). However, swabs bearing endive chemicals elicited significantly more tongue flicks ($\chi^2 = 4$, df = 1; $P < 0.05$) than did control swabs. However, as one of the animals attacked a swab bearing cricket chemicals, this can be considered as a clear tongue-flick-mediated recognition of food stimuli.

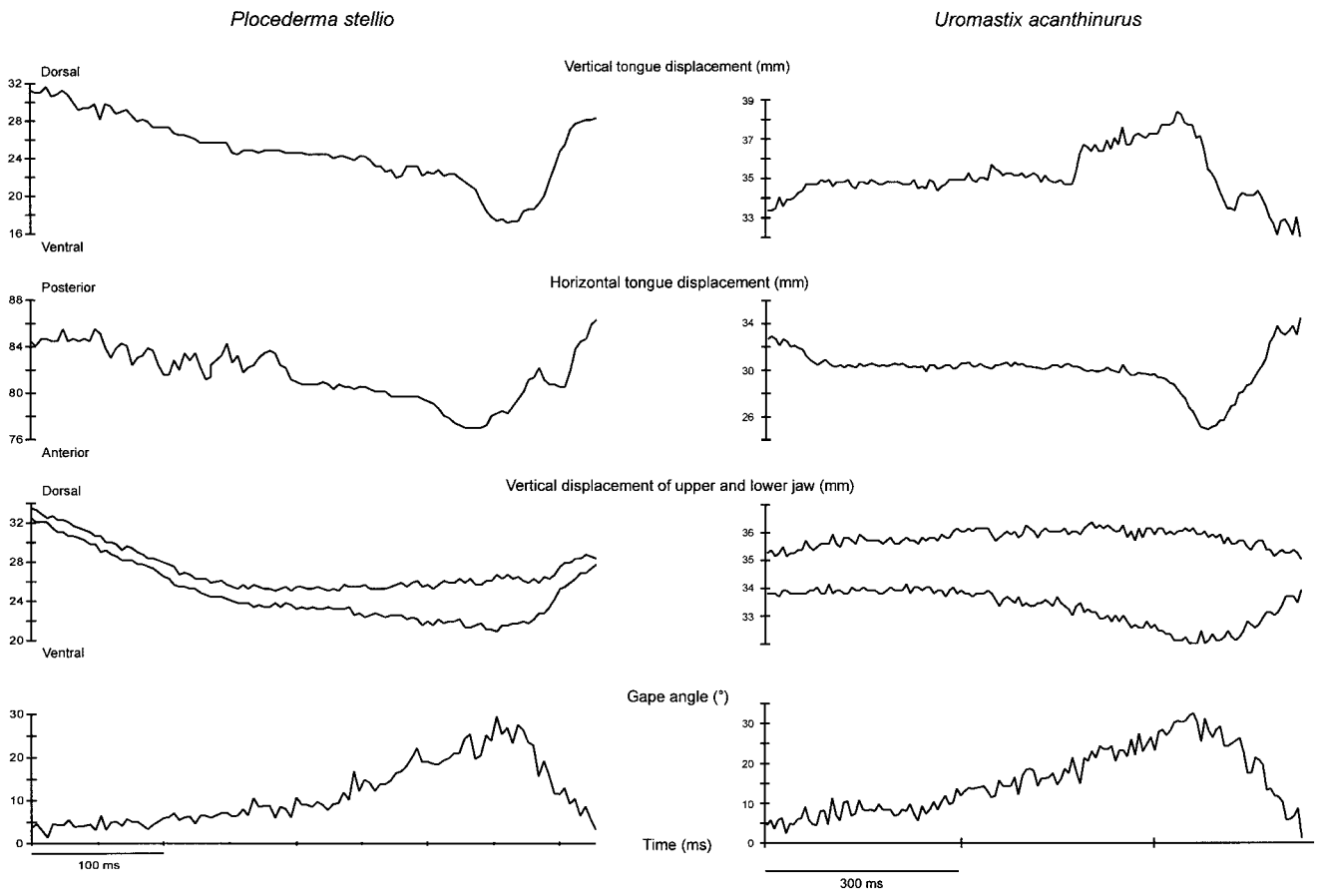

Fig. 5. Kinematic profiles (based on high-speed video recordings, 500 frames sec^{-1}) of tongue and jaw movements during tongue flicking. On the left, the vertical and horizontal displacements of the tongue, the vertical displacement of the upper and lower jaws, and the changes in gape angle are represented for one tongue-flick cycle in *P. stellio*. On the right, the vertical and horizontal displacements of the tongue, the tongue protrusion relative to the lower jaw, the vertical displacements of upper and lower jaws, and the changes in gape distance are represented for one tongue-flick cycle in *U. acanthinurus*. Note the difference in time scale between the two series of profiles.

Kinematics

The tongue flicks seen in both lizards are always of the most simple type: the SDEs. In *P. stellio*, tongue flicks usually involve touching the prey or the substrate with the tongue (tongue touch). In *U. acanthinurus*, both tongue touches and tongue flicks, where the tongue does not touch the prey or substrate, are observed.

Tongue touches in both species usually involve whole head movements, but tongue flicks usually consist of simple tongue extrusions without head movements (Fig. 5). The jaw movements during a tongue flick consist of an opening and a closing phase that cannot be subdivided any further into separate slow and fast phases. The opening phase lasts an average of 446 ± 234 msec in *U. acanthinurus* and 258 ± 59 msec in *P. stellio*. Jaw opening is mainly achieved by a depression of the lower jaw in both species (Fig. 5, Table 3). The maximal gape angle is rather similar in both species (27° in *U. acanthinurus* vs. 24° in *P. stellio*). Jaw closing lasts only half as long as jaw opening in both species (Table 3).

Tongue movements start as soon as the jaws are slightly parted and consist of an anterior and downward displacement of the tongue. The maximal extrusion of the tongue, both horizontal and vertical, is achieved around a maximal gape in both species. The tongue protraction phase lasts about twice as long as tongue retraction in *P. stellio* and about three times as long in *U. acanthinurus* (Table 3).

Electromyography

The first muscles that become active during a tongue-flick cycle in both species (Fig. 6) are the MGG and the MHG. In *P. stellio*, the ring muscle becomes active simultaneously with the onset of activity in the MGG and the MHG (Fig. 6, Table 4). The activity level of these muscles gradually increases to reach a maximum at maximal gape. In *P. stellio*, the hyoid protractor becomes active later on and shows only low-level activity that ends at maximal gape. The jaw opener in both species occasionally shows a short activity peak of low intensity just before and ending at maximal gape (Fig. 6, Table 4). This activity may coincide with an activity in the deeper parts of the external adductor in *U. acanthinurus* (Fig. 6). At maximal gape, the hyoid retractor becomes active and simultaneously the MHG shows a second activity burst. The jaw closers (medial and deep parts of the external adductor; the m. pterygoideus and the posterior adductor) occasionally

TABLE 3. Tongue-Flick Kinematics of *Uromastix acanthinurus* and *Plocederma stellio*[a]

	U. acanthinurus		*P. stellio*	
	Mean	S.D.	Mean	S.D.
OPEN (msec)	446	234	258	59
CLOSE (msec)	204	56	102	19
TC (msec)	649	269	361	49
TTP (msec)	331	243	104	22
TTR (msec)	113	33	69	16
GP (degrees)	27	1	24	4
LJD (mm)	3.8	1.2	7.3	3.1
CREL (mm)	2.1	1.2	1.2	0.6
TPRDX (mm)	14.6	3.8	7.3	2.6
TPRDY (mm)	10.9	4.2	9.7	2.8
TMG (msec)	446	234	258	59
TMDLJ (msec)	1.6	3.2	2.4	10.3
TMEUJ (msec)	−11	11	6	6
TMHDT (msec)	21	23	−2.4	17.6
TMVDT (msec)	−37	36	24.8	26.9

[a]TMDLJ, TMEUJ, TMHDT and TMVDT are expressed relative to maximal gape; TMG is expressed relative to the beginning of the cycle. (n = 5 for *P. stellio;* n = 15 for *U. acanthinurus*). CLOSE, duration of the closing phase; CR, maximal elevation of the neurocranium; GP, maximal gape; LJD, maximal depression of the lower jaw; OPEN, duration of the opening phase; TC, duration of the total cycle; TMDLJ, time to the maximal depression of the lower jaw; TMEUJ, time to the maximal elevation of the neurocranium; TMG, time to maximal gape; TMHDT, time to maximal horizontal displacement of the tongue; TMVDT, time to maximal vertical displacement of the tongue; TPRDX, maximal extension of the tongue in the horizontal plane; TPRDY, maximal extension of the tongue in the vertical plane; TTP, duration of tongue protraction; TTR, duration of tongue retraction.

show a short activity peak of low intensity just after maximal gape (Fig. 6, Table 4).

DISCUSSION

Behavioral Implications

The agamid lizards used in this study used tongue touches, but their frequency of use differed drastically. Whereas the herbivorous species (*Uromastix acanthinurus*) tongue flicks readily and is able to discriminate between food and other stimuli, the insectivorous one (*Plocederma stellio*) hardly ever tongue flicks and no food chemical discrimination could be demonstrated. Nevertheless, our observations based on video recordings suggest that these animals are able to and in reality sometimes do use tongue flicks to judge possible food items. Differences between both situations may be due to the absence of visual stimuli in applicator tests (see Chiszar et al., 1988; Ford and Burghardt, 1993). It is likely that in these lizards, gustation and vomerolfaction are triggered by visual rather than olfactory cues. Although applicator tests provide useful information on the frequency of use, caution is required when making statements about the absence of such behaviours based solely on such methods.

The traditional hypothesis states that a strong relationship exists between the foraging mode and the ability to discriminate prey by chemical stimuli (Cooper, 1995a, 1997). Active foragers more than do ambush foragers would use chemical senses to detect food. This would suggest that ambush foraging lizards lack the ability to detect food and discriminate between food items. Because most lizards belonging to the Iguania are ambush foragers (Vitt and Price, 1982), these lizards, with the exception of the herbivorous lizard *Dipsosaurus dorsalis* (Krekorian, 1989; Cooper and Alberts, 1990, 1991), are supposed to be incapable of food detection and discrimination by means of chemical sampling (Cooper, 1989, 1994a,b). Moreover, no tongue-flick mediated food detection and discrimination could be demonstrated in agamid lizards (Cooper, 1994a). In the present study, it is shown that agamids do tongue flick and that at least the herbivorous species *U. acanthinurus* uses this behavior to detect and discriminate between food items. Because herbivorous lizards have to search actively for their food, lingual chemical sampling may be an important sensory mode in these animals (Cooper and Alberts, 1990; Cooper 1995a).

The proposed diphyletic behavioral specialization of the tongue (Schwenk and Throckmorton, 1989), whereby its use is restricted to prey capture and drinking in iguanians and to drinking and chemoreception in scleroglossans, is thus not supported by our data. The tongue structure of iguanid lizards apparently does not impose a limitation on simple tongue extrusion capability as observed during SDE. However, whether this behavior is used to transfer chemicals to the vomeronasal organ (VNO) is uncertain. The exact mechanism by which chemicals are detected by squamates in general remains obscure; usually, it is assumed that upon tongue protrusion volatile molecules in the air and nonvolatiles on substrates adhere to its moist surface. When the tongue is retracted, the molecules pass into the vomeronasal ducts and are transferred to the VNOs, where they may stimulate the epithelial receptor cells (Halpern and Kubie, 1980; Gillingham and Clark, 1981; Graves and Halpern, 1989; Young, 1990). Although such vomerolfaction is theoretically possible in this family, the simple downward extensions as observed in these lizards are presumably not suited for chemical collection for the VNO, which may be required for chemosensory searching (scanning of a larger volume of air; see also Gove, 1979; Goosse and Bels, 1992) as observed in scleroglossan lizards (see Cooper, 1994a).

Morphological Correlates

On a morphological level, differences between both agamids are mainly situated in the tongue surface topography and the abundance and distribution of taste buds. The surface topology of the tongue tip and the hindtongue is rather similar in both species. Differences are mainly situated in the foretongue structure. In *Plocederma stellio,* the whole foretongue is composed of transverse rows of plumoselike papillae carrying microvilli and bears numerous secretory cells (Fig. 2). Near the edges of the tongue, the apparent random disposition of plume cells changes into a more papillary organization. In contrast, in *Uromastix acanthinurus,* the central part of the foretongue shows

Fig. 6. Overleaf. Representative original electromyograms of a number of jaw and hyolingual muscles during tongue flicking in the lizards *P. stellio* (left) and *U. acanthinurus* (right). Vertical lines indicate the occurrence of maximal mouth opening. MAMEM, m. adductor mandibulae externus medialis; MAMEP, m. adductor mandibulae externus profundus; MDM, m. depressor mandibulae; MGG, m. genioglossus; MHG, m. hyoglossus; MMH1, m. mandibulohyoideus 1; MPt, m. pterygoideus; MRing, ring muscle; MSH, m. sternohyoideus.

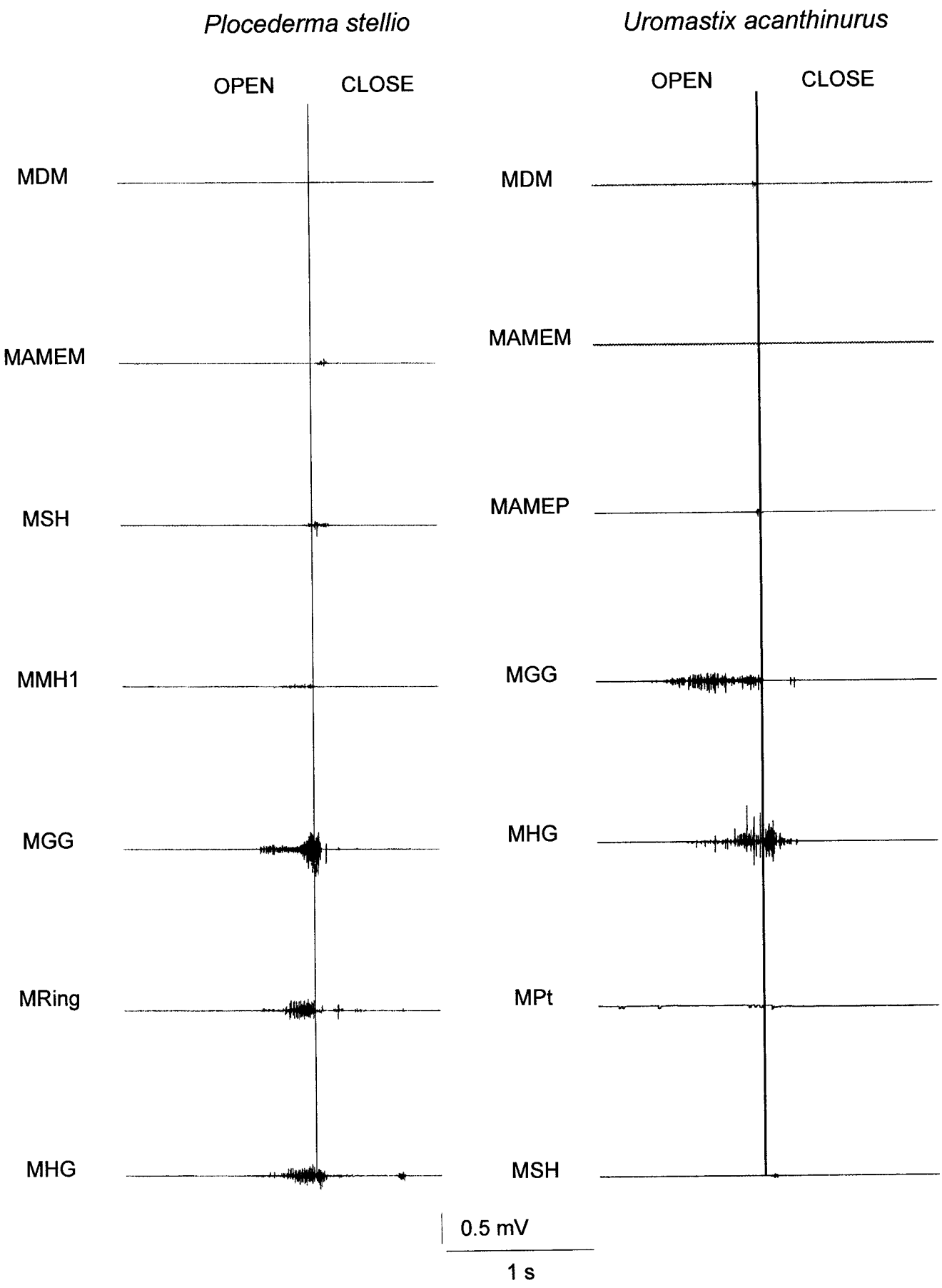
Plocederma stellio
Uromastix acanthinurus
OPEN
CLOSE
OPEN
CLOSE
MDM
MAMEM
MSH
MMH1
MGG
MRing
MHG
MDM
MAMEM
MAMEP
MGG
MHG
MPt
MSH
0.5 mV
1 s

Fig. 6.

TABLE 4. Muscle Activities During Tongue Flicking in *Plocederma stellio* and *Uromastix acanthinurus*[a]

	Burst presence (%)	Onset ± S.D. (msec)	Duration ± S.D. (msec)
P. stellio			
MDM	80	260 ± 0	103 ± 42
Preburst	60	144 ± 201	160 ± 163
MAMEM	80	305 ± 101	70 ± 46
Preburst	60	147 ± 147	153 ± 42
MAMP	100	720 ± 141	208 ± 66
MPtlat		Not active	
MPtmed	50	460 ± 0	80 ± 0
MSH	100	330 ± 0	140 ± 0
MGG	100	4 ± 184	514 ± 85
MRing	100	0 ± 0	410 ± 0
MHG	100	157 ± 159	410 ± 90
U. acanthinurus			
Preburst	23	69.06 ± 53.44	68.75 ± 59.38
R. MDM	23	492.81 ± 41.56	95.00 ± 73.75
L. MDM	14	506.88 ± 0.00	51.25 ± 0.00
R. MPtext		Not active	
L. MPtext		Not active	
Preburst	14	0.00 ± 0.00	40.63 ± 0.00
R. MPtmed	29	651.25 ± 107.50	78.13 ± 15.63
Postburst	14	690.63 ± 0.00	67.50 ± 0.00
L. MAMEP		Not active	
R. MAMESP		Not active	
L. MAMESP		Not active	
Preburst	46	28.91 ± 28.07	115.39 ± 63.40
R. MGG	100	169.35 ± 85.56	316.05 ± 74.40
Postburst	77	583.57 ± 148.08	84.33 ± 46.19
Preburst	100	188.40 ± 143.49	386.88 ± 154.13
R. MHG	100	593.56 ± 129.54	129.65 ± 52.83
Postburst	57	678.29 ± 69.65	66.72 ± 20.02
Preburst	67	73.91 ± 128.01	67.19 ± 55.53
R. MSH	100	330.73 ± 84.79	296.35 ± 65.89
L. MOH	86	671.04 ± 130.12	38.54 ± 11.29
Postburst	29	669.07 ± 15.93	92.82 ± 14.69

[a]Onset variables were measured from the beginning of the cycle (first sign of muscle activity) to the onset of the muscle burst. Different bursts in the same muscle within one tongue flick are referred to as pre-, main, and postbursts. The main burst is the first activity burst in which muscles are fully active; sometimes this burst is preceded by an activity burst of low intensity (pre) and followed by a burst of either high or low intensity (post). *P. stellio:* n = 5 for the MGG (m. genioglossus), the MAMP (m. adductor mandibulae posterior), the MDM (m. depressor mandibulae), and the MAMEM (m. adductor mandibulae externus medialis); n = 4 for the MPTIat (m. pterygoideus lateralis); n = 3 for the MHG (m. hyoglossus); n = 2 for the MPtmed (m. pterygoideus medialis); n = 1 for the MSH (m. sternohyoideus), the MRing (ring muscle). *U. acanthinurus:* n = 15 for the R.MGG and the R.MDM; n = 8 for the L.MDM, the LMAMEP (m. adductor mandibulae externus profundus), the RMHG, the R.MPtmed, the L.MOH (m. omohyoideus); n = 7 for the R. and L.MPtext (m. pterygoideus externus), the R. and L.MAMESP (m. adductor mandibulae externus superficialis posterior), and the R.MSH.

a completely different papillary surface. In this species, the central area of the foretongue is composed of rather smooth papillae, but with extensive microstructure when examined at higher magnification. In addition, taste buds are more abundant in *Uromastix* and occur in rather high densities on the mouth roof and paralingual epithelium. The distribution of taste buds on the tongue is rather similar in both species, except for the central part of the foretongue, where they are absent in *P. stellio* but present at the lateral parts of the foretongue in *Uromastix*.

The vegetable diet of *U. acanthinurus* clearly has implications on its tongue structure. Not only does the tongue tip show a stronger bifurcation, which in lizards seems to be related to a greater dependence on the use of tongue-mediated chemoreception (see Bissinger and Simon, 1979; Cooper, 1996), but the number of taste buds is also greatly increased. In addition, the surface topology of the central part of the foretongue, which is used during prey capture and transport (see Delheusy et al., 1994; Herrel et al., 1995, 1996), is different in both species. Apparently, the transport of vegetable matter requires a predominantly rough tongue surface (adhesion between tongue and food is mediated mainly through interlocking of the tongue surface with the prey; see Fahrenbach and Knutson, 1975; Sperry and Wassersug, 1976), whereas the transport of insects requires both interlocking and wet adhesion through the secretion of mucous substances. Based on the presence of numerous taste buds and the absence of complex tongue flicks (involving an oscillation phase; see Gove, 1979), it is proposed that in *U. acanthinurus*, *P. stellio*, and presumably also in other iguanians lingual chemical sampling is mediated predominantly through gustation and much less through vomerolfaction (see also Schwenk, 1985).

Tongue-Flick Mechanics

Remarkably, the jaw and hyolingual movement and motor patterns are very similar in both species despite the previously cited behavioral and morphological differences. Given our data, we propose that a tongue flick in agamids consist of both hydrostatic elongation and whole tongue movements (activity in MGG and the ring muscle is observed during a tongue flick). Although no bulging of the tongue occurs upon protrusion, the MHG, which causes bulging as observed during prey capture (Herrel et al., 1995), is active. Nevertheless, during tongue flicking its activity is lower than that of the MGG and muscle ring (compare Fig. 7 in Herrel et al., 1995 with Fig. 6 in the present study), which may explain the absence of bulging. Jaw opening is mainly achieved by tongue protrusion, as indicated by the low levels of activity in the MDM and the strong correlation between maximal gape and maximal tongue protrusion (see Table 3). Because gape angles remain very small and no prey is situated between the jaws, little force is required to close the jaws and accordingly activity levels in the jaw closers are low.

Based on the kinematical and EMG data of this and other studies, speculations about the origin and evolution of tongue flicking are possible. Because tongue flicking is characterised by an extraoral lingual extrusion, the following have been proposed to lie at the basis of this behavior: lingual prey capture and drinking (both showing an extraoral lingual component). Previously, several researchers (Gove, 1979; Goosse and Bels, 1992) argued in favour of drinking rather than prey capture as the mechanistic precursor of tongue flicking. The results gathered in the present study support this hypothesis. Not only is a slow open phase absent during tongue flicking (see also Goosse and Bels, 1992), but the EMG patterns differ considerably between both behaviors in the species examined (compare EMGs in Herrel et al., 1995, with those of the present study). Moreover, in contrast to what is commonly believed

(see Schwenk and Throckmorton, 1989), lingual prey capture may not be a plesiomorphic character for lizards (see Herrel et al., 1995, 1996). Therefore, it can hardly underlie a behavior observed in nearly all scleroglossan lizard families (Cooper, 1995a). Alternatively, it is proposed in our study that the extraoral lingual behavior associated with late swallowing (sometimes termed labial licking; Cooper, 1989) may provide a suitable basis for the evolution of tongue flicking. Both the movement and motor patterns associated with this behavior are similar to those observed during tongue flicking (compare the EMGs and movement profiles from the present study with those in Herrel et al., 1996, 1997).

Presumably, tongue flicking originated from a behaviour whereby the tongue was protruded and chemicals were collected. Although this was a purely gustatorial situation in the primitive stage, the opening of the vomeronasal ducts paved the way for an additional vomerolfactory component. Such chemical assessment allows a rapid and continuous sampling of the environment. Nonetheless, tongue touches in lizards with relatively short tongues such as agamids are potentially dangerous because the head is often directed toward the substratum. Tongue flicks without substrate contact eliminate this drawback, but lingual sampling without substrate contact is probably less effective and thus an additional component is built into the behavior: an oscillation phase. These oscillation phases are essential because the rate of diffusion of chemical molecules into the seromucous coating of the tongue is directly related to the velocity gradient of the air layers surrounding the tongue (Schwenk, 1996). Tongue oscillations increase the velocity gradient and thus enhance diffusion of molecules. In its most complex and derived state (as observed in colubrid snakes; see Ulinsky, 1972; Gove, 1979), tongue flicking involves multiple oscillation phases. These complex behaviors evolved most likely by a sequential addition of oscillation phases from an SDE to an SOC to MOCs. The submultiple oscillation tongue flicks (as observed in lacertid lizard; Goosse and Bels, 1992) are presumably a special case of MOC tongue flicks.

The incorporation of one or more oscillations in a tongue-flick cycle requires a special muscular arrangement. Demands for tongue extensibility are completely different from those for tongue protrusiveness. Elongation in muscular hydrostats such as tongues is achieved by reducing the diameter of the tongue (Kier and Smith, 1985). Ideally suited for this purpose are the transverse muscles surrounding the longitudinal hyoglossal bundles in the tongues of scleroglossan lizards (Smith, 1984, 1986). However, to produce bending in a muscular hydrostat, the longitudinal muscles should be situated at the periphery of the tongue (Kier and Smith, 1985; Smith and Kier, 1989), as has been observed in the anterior part of snake tongues (Smith and Kier, 1989).

The structural rearrangement of the lingual musculature enabling the inclusion of oscillations in a tongue-flick cycle can be summarized as follows. Departing from the primitive state as observed in iguanians, where tongue movements are the result of both an elongation and whole tongue movement through sliding on the entoglossal process (Smith, 1988; Herrel et al., 1995; present study), muscular rearrangements include the expansion of the transverse musculature around the longitudinal muscle bundles of the MHG, resulting in a greater elongation capacity (Smith, 1984, 1986; Smith and Kier, 1989). In the most advanced squamates, which are capable of performing a wide array of different tongue flicks including numerous oscillations, the anterior part of the tongue is modified and the arrangement of longitudinal and transverse musculature inversed (Smith and Kier, 1989).

Evolutionary Pathways

Based on our results, an evolutionary transformation pathway is proposed. Starting from a primitive gustatory condition (no contact between the vomeronasal organ and the oral cavity) as observed for *Sphenodon punctatus*, the opening of the vomeronasal ducts in the oral cavity creates the possibility for vomerolfaction. In this stage, similar to what is observed in extant insectivorous iguanans, tongue extrusions still occur mainly in the functions of drinking and prey capture. The next intermediate and still strongly gustatory state would be like the one observed in herbivorous iguanians, where tongue extrusions are common and the dependence on vomerolfaction is already greater, but still little or no modification of the motor and movement patterns are noted. To allow for "true" tongue flicks (including an oscillation phase; see Gove, 1979; Goosse and Bels, 1992) as observed in scleroglossans, where chemicals are transferred to the VNO and vomerolfaction has become an important mode of chemical sampling, the tongue structure and accompanying motor patterns have to be modified. Changes in tongue structure would involve a backward displacement of the insertion site of the genioglossus muscle, a stronger bifurcation of the tongue tip, and an elongation of the tongue. Associated with tongue elongation and bifurcation is an increase in tongue surface area and thus an increase in the potential sampling area. In addition to an elongation of the tongue tip, the relative area of the tongue covered with a smooth epithelial structure increases. However, the extensibility of the whole tongue decreases (Cooper, 1995b).

In its most derived state, gustation is greatly reduced (absence of lingual taste buds but note that taste buds are still present on the oral epithelia; see Schwenk, 1984, 1985; Toubeau et al., 1994) and vomerolfaction is the predominant mode of chemical sampling (e.g., as in varanids and snakes).

ACKNOWLEDGMENTS

We thank Dr. P. Aerts for comments on an earlier version of the manuscript, Dr. R. Van Damme for help with the statistical analysis, Prof. Dr. D.W. Scheuermann for providing histological facilities, Dr. E. Kochva for providing us with the first specimens of *P. stellio*, Dr. D. Meirte (Royal Belgian Museum for Central Africa) for providing us with the preserved specimens of *U. acanthinurus*, The Antwerp Zoo for the loan of the *U. acanthinurus* specimen used in the prey chemical discrimination tests, and Mrs. J. Fret for the technical assistance. This study was supported by IWT grant 943039 to A.H. and FKFO grant G.0221.96 to F.D.V.

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