KINEMATICS OF INTRAORAL TRANSPORT AND SWALLOWING IN THE HERBIVOROUS LIZARD *UROMASTIX ACANTHINURUS*

ANTHONY HERREL* AND FRITS DE VREE

Department of Biology, University of Antwerp (UIA), Universiteitsplein 1, B-2610 Antwerp, Belgium

*e-mail: aherrel@uia.ua.ac.be

Summary

The kinematics of intraoral transport and swallowing in lizards of the species *Uromastix acanthinurus* (Chamaeleonidae, Leiolepidinae) were investigated using cineradiography (50 frames s^{-1}). Additional recordings were also made using high-speed (500 frames s^{-1}) and conventional video systems (25 frames s^{-1}). Small metal markers were inserted into different parts of the upper and lower jaw and the tongue. Cineradiographic images were digitised, and displacements of the body, head, upper and lower jaw and the tongue were quantified. Twenty additional variables depicting displacements and the timing of events were calculated. Multivariate analyses of variance indicated significant differences between feeding stages. Remarkably, only very few food-type-dependent differences were observed during intraoral transport, and no such differences could be demonstrated during swallowing. Using previously published data for the closely related insectivorous lizard *Plocederma stellio*, the effect of dietary specialisation in *U. acanthinurus* on the kinematic variables while eating locusts was examined. Species differed in a number of gape- and tongue-related variables. These differences may be related to differences in tongue structure between the species. Clearly, *U. acanthinurus* possesses a specialised gut and dental structure that allows them efficiently to cut pieces from whole leaves. However, a decrease in modulatory capacity seems to be a consequence of dietary specialisation in *Uromastix acanthinurus*.

Key words: kinematics, feeding behavior, lizard, *Uromastix acanthinurus*, herbivory.

Introduction

The origin of the amniote feeding mechanism can be considered as a key event in the evolution of the vertebrate skull. However, it has been proposed that many functional attributes of the feeding mechanism of amniotes are plesiomorphies retained from anamniote ancestors (Lauder and Gillis, 1996), which is reflected in a generally 'stereotyped' feeding mechanism (e.g. Bramble and Wake, 1985; Reilly and Lauder, 1990; Lauder and Reilly, 1994). However, the quantitative data required to test such hypotheses are still rare in both amniote and anamniote groups. Additionally, several recent studies did not find the supposed stereotypy in the feeding patterns of fish and other anamniotes (Wainwright and Lauder, 1986; Wainwright et al., 1989).

An insight into the ability of organisms to modulate the pattern of neuromuscular and kinematic events as a response to changes in feeding conditions is thus critical to test evolutionary hypotheses. However, the trophic ecology of species can place direct limitations on the modulatory capacities of organisms. Organisms with a narrow diet may be limited in their ability to modulate specific components of their feeding mechanism, which in turn results in a decrease in potential trophic breadth (Liem, 1980; Lauder, 1983; Ralston and Wainwright, 1997). Organisms that exploit extremely limited and demanding (i.e. requiring a specialised feeding system) diets such as eggs or plants may become constrained in their ability to ingest other food items. In the African egg-eating snakes of the genus *Dasypeltis*, this has led to an almost complete reduction of teeth on the palato-maxillary arches, precluding other food items such as rodents or birds from their diet (Gans, 1974).

In mammals, the adoption of a herbivorous lifestyle had important consequences for the morphological (Maynard Smith and Savage, 1959; for overviews, see Hiiemae and Crompton, 1985; Russell and Thomason, 1993), physiological (Sibly, 1981; Demment and Van Soest, 1985; Maloiy and Clemens, 1990) and functional (De Vree and Gans, 1976; Weijs, 1994) properties of the mouth and gut processing systems. Whereas the feeding mechanics of herbivorous mammals are well studied, only a limited amount of information is available regarding the feeding mechanics of herbivorous lizards (Throckmorton, 1976, 1978, 1980). However, being basal amniotes, lizards are key study organisms in the understanding of the evolution of mammalian feeding systems. In addition, a detailed analysis of feeding in herbivorous lizards might shed some light on the long-standing debate concerning the absence of a radiation of herbivorous

lizards (Szarski, 1962; Ostrom, 1963; Sokol, 1967; Pough, 1973; Iverson, 1980, 1982). In particular, a quantitative analysis of the feeding kinematics, which can be used to characterise the feeding system in plant-eating lizards and can be compared with published data for insectivorous species, might provide new insights into the absence of such a radiation.

In the present study, the quantitative properties of jaw and tongue movements in the herbivorous lizard *Uromastix acanthinurus* were studied. Species of the genus *Uromastix* are especially interesting (1) because they are considered to be 'true' herbivores, consuming predominantly plant material throughout their active season (Dubuis et al., 1971; Grenot, 1976; Al-Ogily and Hussain, 1983; Bouskila, 1986, 1987); (2) because quantitative kinematic data are available for the closely related (see Frost and Etheridge, 1989; Joger, 1991) generalised insectivorous lizard *Plocederma stellio* (Herrel et al., 1996), and (3) because previous studies on this genus have demonstrated several dietary specialisations in dentition (Cooper et al., 1970; Cooper and Poole, 1973; Robinson, 1976; Throckmorton, 1979) and gut structure (El Toubi and Bishai, 1959; Iverson, 1980, 1982). Although limited kinematic data are available for these lizards (*U. aegyptius*, see Throckmorton, 1976, 1980), they do not allow a statistical analysis of a large number of jaw- and tongue-related kinematic variables.

Materials and methods

Specimens

Four adult specimens (snout–vent length: 162±2 mm; mass 141±10 g; means ± s.d.) of the species *Uromastix acanthinurus* Bell (Chamaeleonidae, Leiolepidinae; see Frost and Etheridge, 1989) were used in the experiments. The specimens were obtained from a commercial dealer. The animals were kept in a glass vivarium on a 12 h:12 h L:D cycle and were offered water and food consisting of endive, salad, tomato, banana and various other fruits and vegetables *ad libitum*. The environmental temperature varied from 35 °C during the day to 25 °C at night; an incandescent bulb provided the animals with a basking place at a higher temperature (45 °C). An additional two animals were dissected and stained (Bock and Shear, 1972) to characterise all jaw and hyolingual muscles. Drawings were made of all stages of the dissection using a Wild M3Z dissecting microscope, provided with a *camera lucida*.

Cineradiographic and video recordings

Cineradiography was accomplished using a Siemens Tridoros-Optimatic 880 X-ray apparatus equipped with a Sirecon-2 image intensifier. Feeding bouts were recorded laterally using an Arriflex 16 mm ST camera equipped with a 70 mm lens at a film speed of 50 frames s^{-1}. Before cineradiography, small metal markers were inserted subcutaneously on the upper and lower jaws, at the base and the top of the quadrate, in the tongue, on the frontal and parietal bones and dorsally in the neck just below the skin using a hypodermic needle (Fig. 1). During implantation of these radio-opaque markers, animals were anesthetised with an intramuscular injection of Ketalar (100 mg kg^{-1} body mass). Placement of the markers was checked using dorsoventral and lateral X-ray photographs before and after the recording sessions. During the cineradiographic recordings, the insect prey were injected with barium sulphate to aid the visualisation of their position.

Additional recordings of the feeding process were made using high-speed (NAC-1000 system, 500 frames s^{-1}) and conventional (Panasonic camera and zoom lens, 50 frames s^{-1}) video systems. Video torches (2.4 kW; Tri-Lite, Cool Light Co. Inc., Hollywood, USA) provided the necessary illumination. In both the cineradiographic and the video recording sessions, the animals were filmed in an acrylic cage (100 cm×30 cm×30 cm) while feeding on endive, and during one recording session while feeding on locusts *Locusta migratoria* (L.) (2.0–3.0 cm).

Cineradiographic and video analysis

Only feeding sequences in which the animal remained at right angles to the axis of the camera were analysed. Cineradiographic films were projected frame by frame onto a HIPAD-digitiser with a Vanguard projector. The position of each marker (see Fig. 1) was digitised, and the horizontal (x) and vertical (y) coordinates of each were recorded for each frame. High-speed and conventional video recordings were analysed by digitising seven clearly visible external markers (coloured spots, as in Herrel et al., 1996) using the NAC x,y coordinator. Horizontal (x) and vertical (y) coordinates were recorded for each digitised point at intervals of two frames for high-speed recordings.

Variables calculated for cineradiographic (X-ray) recordings were (with respect to the numbered markers on Fig. 1): changes in gape profile (distance 1–4; angle subtended by the two lines 1–2 and 3–4), vertical displacement of the upper and the lower jaw (y coordinate of points 1 and 4), cranial elevation (angle subtended by line 1–2 and the horizontal), lower jaw depression (angle subtended by line 3–4 and the horizontal) and streptostylic angle (angle subtended by the two lines 9–10 and 6–5; a decrease in this angle indicates an anteriad rotation of the quadrate). On the cineradiographic recordings, the displacement of the tongue was also calculated from the x and y coordinates of both tongue markers relative to the anterior marker on the lower jaw (Fig. 1).

Twelve complete endive feeding bouts were recorded. From these, 31 intraoral transport and 15 swallowing bites were selected. In two feeding sequences, one animal accepted locusts. From these, 11 intraoral transport and 12 swallowing bites were selected. The other three animals refused to eat locusts.

On the basis of the kinematic plots of the movements of jaws and tongue, the following variables were determined: (1) the durations of the slow opening (SO) phases (DSOI and DSOII) when present (if not, the duration of the whole SO phase was recorded), the duration of the fast opening phase (DFO), the duration of the fast closing phase (DFC), the duration of the slow closing/power stroke or stationary phase (DSC/PS,
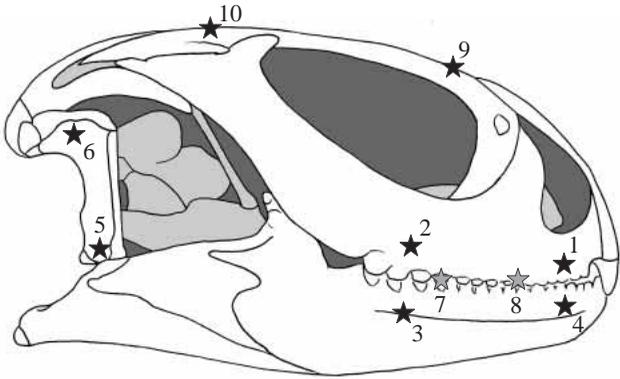
Fig. 1. Positions of lead markers inserted into the skull of *Uromastix acanthinurus* and used to calculate different kinematic variables. 1, anterior marker of the upper jaw; 2, posterior marker of the upper jaw; 3, posterior marker of the lower jaw; 4, anterior marker of the lower jaw; 5, lower marker of the quadratum; 6, upper marker of the quadratum; 7, posterior tongue marker; 8, anterior tongue marker; 9, marker placed on the frontal bone; 10, marker placed on the parietal bone.

DSTAT) and the duration of the total cycle (DTC); (2) the maximal values of the gape distance (GD), gape angle (GA), lower jaw depression (MDLJ), cranial elevation (MEUJ), horizontal (MHDTO) and vertical (MVDTO) tongue displacement, and streptostylic angle (STREPTO; the difference between the initial angle at the beginning of the cycle and the maximal angle at the end of the FO phase); (3) the time to maximal gape angle (TGA), the time to the most anterior (TMHDTO) and to the most dorsal (TMVDTO) tongue positions, the times to maximal depression of the lower jaw (TMDLJ) and elevation of the neurocranium (TMEUJ); and (4) the duration of horizontal and vertical tongue retraction (THTR, TVTR). The different phases within a jaw cycle were determined on the basis of the changes in angular velocity of the gape cycle in conjunction with the changes in tongue movement. When sequences were partially analysed, frame 1 was arbitrarily chosen as the beginning of the slow opening of the mouth.

Several analyses were performed on the kinematic data (1) to explore the similarities between feeding stages (intraoral transport, swallowing), (2) to evaluate the effect of food type on the kinematic variables and (3) to compare feeding in *U. acanthinurus* with data published for the closely related insectivorous lizard *P. stellio* (Herrel et al., 1996). For these analyses, the Statistica (StatSoft Inc.) statistical package was used.

The data, containing both endive and locust intraoral transport and swallowing bites, were submitted to a multivariate analysis of variance (MANOVA). As significant interaction effects were detected, the original data set was subdivided into separate intraoral transport and swallowing data sets. A MANOVA was performed on these coupled to univariate *F*-tests (see Table 1) to determine which variables were significantly different for endive and locust cycles. For

all univariate *F*-tests performed, the significance level was corrected using a sequential Bonferroni correction (see Rice, 1989).

Next, a data set consisting of locust intraoral transport and swallowing cycles from *U. acanthinurus* and *P. stellio* (data from Herrel et al., 1996) was constructed and submitted to a two-way MANOVA to investigate the species effect and the interactions between species and feeding stage on the kinematic characteristics of the feeding cycle. Because of significant interaction effects, a single data set per cycle type was then constructed to evaluate the effect of species separately on the kinematic variables. On these data sets, a MANOVA was performed to evaluate the differences observed for different species. If significant effects were detected, univariate *F*-tests were carried out to determine which variables were significantly different.

All analyses were performed on data sets consisting of 15 kinematic variables representing all aspects of the feeding cycle [GA, MHDTO, DSO, DFO, DFC, DSC/PS, DTC, THTR, TVTR, TMEUJ, TMDLJ, TMHDTO, TMVDTO, TGA and STREPTO (for *Uromastix* only); for an explanation of the abbreviations used see above and Table 1].

Results

In the following description of feeding cycles, the terminology of Bramble and Wake (1985) is used. Since *Uromastix acanthinurus* is a herbivorous lizard (three of the four lizards refused to eat insects), the following descriptions of feeding stages are based on endive feeding sequences. Differences between endive and locust cycles will be discussed separately.

A feeding sequence consists of three distinct stages: food prehension, intraoral transport and swallowing (De Vree and Gans, 1989; Herrel et al., 1996). During intraoral transport, five phases can be recognised within one cycle: slow opening (SO), sometimes separable into phases I and II (SOI, SOII); fast opening (FO); fast closing (FC); and a slow closing/power stroke phase (SC/PS). During swallowing, no SOI and SOII phases are discernible. In addition, because the food item is no longer situated between the teeth, no SC/PS phase is present. However, a stationary phase, during which no jaw or tongue movements occur, is present during swallowing.

In *U. acanthinurus*, the difference between the two SO phases is often hard to delineate on the basis of the jaw movements only. However, when examining tongue movements, these phases are generally clearer. During the second part of the SO phase, the speed of the anteriad tongue movement decreases markedly (see Fig. 2). Nevertheless, in a relatively large number of the intraoral transport cycles examined, no subdivision of the SO phase was possible (endive intraoral transport, 37 %; locust intraoral transport, 56.5 %).

Feeding in *U. acanthinurus* usually consists of several short feeding sequences where the animals bite off small pieces from larger leaves. After a piece has been swallowed, a new sequence starts. Although the average number of sequences is

Table 1. *Results of univariate analyses performed on different data sets*

	U. acanthinurus, endive: intraoral transport × swallowing (d.f. 1, 44) (*N*=4)	*U. acanthinurus*, locust: intraoral transport × swallowing (d.f. 1, 21) (*N*=1)	*U. acanthinurus*, intraoral transport: endive × locust (d.f. 1, 40) (*N*=4)	Intraoral transport, locust: *U. acanthinurus* × *P. stellio* (d.f. 1,128) (*N*=3)	Swallowing, locust: *U. acanthinurus* × *P. stellio* (d.f. 1, 33) (*N*=2)
GD	62.38**	170.52**	42.57**	123.70**	75.26**
GA	47.94**	66.68**	9.56	9.27*	0.32
MEUJ	3.58	8.95	3.21	0.02	4.13
MDLJ	1.93	10.21	0.10	16.55**	8.67
MHDTO	13.33**	4.04	1.84	28.17**	2.36
MVDTO	13.86**	2.55	1.70	14.90**	0.06
DSO	18.65**	4.84	3.11	1.56	0.53
DFO	22.28**	5.82	9.20	4.34	4.26
DFC	2.70	0.72	2.38	8.70*	15.30**
DSC/PS or DSTAT	3.48	3.09	1.44	20.15**	0.08
DTC	–	–	–	8.14	5.39
TGA	13.20**	4.17	4.89	2.3	2.73
TMEUJ	12.38*	4.17	6.72	2.67	2.78
TMDLJ	12.80**	3.87	5.38	2.16	2.14
TMHDTO	17.61**	6.59	1.76	4.25	3.24
TMVDTO	19.34**	6.58	2.82	11.54*	4.40
THTR	0.69	0.10	9.56	2.54	17.24**
TVTR	3.90	0.22	4.93	0.10	2.72
STREPTO	0.04	60.89**	0.93	–	–

Table entries are *F*-values.

*Significant at the *P*<0.05 level after sequential Bonferroni correction; **significant at the *P*<0.01 level after sequential Bonferroni correction; *N*=number of animals from which data were used in the analysis.

DFC, duration of the fast closing phase; DFO, duration of the fast opening phase; DSC/PS, duration of the slow closing/power stroke phase; DSO, duration of the slow opening phase; DSTAT, duration of the stationary phase; DTC, duration of the total cycle; GA, gape angle; GD, gape distance; MDLJ, maximal displacement of the lower jaw; MEUJ, maximal elevation of the neurocranium; MHDTO, maximal horizontal displacement of the tongue; MVDTO, maximal vertical displacement of the tongue; STREPTO, maximal streptostylic angle; TGA, time to maximal gape; THTR, duration of tongue retraction in the horizontal plane (*x*-coordinate); TMDLJ, time to maximal depression of the lower jaw; TMEUJ, time to maximal elevation of the upper jaw; TMHDTO, time to maximal horizontal displacement of the tongue; TMVDTO, time to maximal vertical displacement of the tongue, TVTR, duration of tongue retraction in the vertical plane (*y*-coordinate).

approximately 10, up to 20 consecutive sequences are sometimes observed. Depending mainly on the size of the food item, dorso-ventral and antero-posterior head movements may play an important role. When eating large food items such as whole leaves, the animals literally tear off pieces by bending their neck ventrolaterally. When eating large locusts (>4.0 cm), the animals use vigorous lateral head shaking just after capture, presumably to try to kill the prey item.

A MANOVA performed on a data set consisting of endive intraoral transport and swallowing cycles indicated significant differences between these two feeding stages (Rao's *r*=6.08, d.f.=18, 27; *P*<0.001). Univariate *F*-tests (Table 1) indicated significant differences in most variables (see Table 2), except the maximal displacements of the upper and lower jaw, the duration of the FC and SC/PS phases, the duration of tongue retraction (both horizontal and vertical) and the maximal streptostylic angle. Similarly, a MANOVA on locust intraoral transport and swallowing cycles showed clear stage effects also to be present (Rao's *r*=29.60, d.f.=18, 4; *P*<0.01; see also Table

3). Subsequent univariate *F*-tests indicate significant stage-dependent differences in gape distance, gape angle and streptostylic angle (Table 1). All these variables are significantly larger for intraoral transport cycles (Table 3).

Feeding stages

Food prehension

Only a qualitative description of prehension cycles will be presented here. A detailed kinematic and electromyographic analysis will be published elsewhere. Food items are invariably examined by tongue-flicking when introduced into the cage. Once a food item is considered edible, the food prehension stage starts. When capturing locusts, the animals often failed to bring the prey into the mouth the first time, and usually several attempts were required to capture a locust successfully. When eating endive, however, animals usually successfully brought the leaf into their mouth on the first or second attempt. During prehension cycles, whole-body movements sometimes contributed, depending on the distance between the animal and

the food item. When whole body-movements occur, they usually involve a rotation of the anterior part of the body over the front limbs at the shoulder joint, without displacement of the hind legs.

Prey capture is initiated by a slow jaw opening phase during which the tongue is slightly protruded. During this first phase of jaw opening, no tongue clearance (*sensu* Kraklau, 1991) is observed. Upon protrusion, the tongue bulges and the tongue tip is curved ventrally so that the dorsal side of the tongue is exposed anteriorly (see also Schwenk and Throckmorton, 1989; Herrel et al., 1995). By the end of the slow opening phase, the tongue is completely protruded from the mouth and contacts the food. After food contact, the tongue and adhering food item are retracted and the jaws are opened quickly, mainly by an elevation of the upper jaw. Once the tongue has been retracted within the jaw margins, the jaws are closed quickly. Once the jaws touch the food item, the closing speed decreases, and the slow closing/power stroke phase starts. This last phase is often absent during prehension cycles in *U. acanthinurus*.

Intraoral transport

Intraoral transport bites in *U. acanthinurus* are similar to those for other chamaeleonids (Schwenk and Throckmorton, 1989; Kraklau, 1991; Herrel et al., 1996) and last an average of 575 ms (Table 2). A cycle is initiated by an SO phase during which the jaws are slowly parted. During most intraoral transport cycles, the SO phase can be subdivided into two separate phases (Fig. 2). During the SOI phase, the lower jaw

Table 2. *Summary kinematics of endive-feeding in* Uromastix acanthinurus

	Intraoral transport	Swallowing
GD (mm)	11.28±1.43	7.77±1.38
GA (degrees)	26.48±5.47	15.07±4.71
MEUJ (mm)	1.81±2.93	0.36±0.38
MDLJ (mm)	7.63±2.52	6.37±3.51
MHDTO (mm)	3.60±1.16	5.09±1.55
MVDTO (mm)	3.68±1.46	5.50±1.75
DSOI (ms)	211.72±108.43	–
DSOII (ms)	119.31±45.19	–
DSO (ms)	321.29±137.59	574.67±262.24
DFO (ms)	54.19±15.66	33.33±9.76
DFC (ms)	69.68±14.49	61.33±19.22
DSC/PS or DSTAT (ms)	129.68±51.09	100.00±49.57
DTC (ms)	574.84±156.80	769.33±267.25
TGA (ms)	377.42±136.01	596.00±274.46
TMEUJ (ms)	363.87±137.93	562.67±246.21
TMDLJ (ms)	380.65±137.94	598.67±277.90
TMHDTO (ms)	281.29±137.79	530.67±267.46
TMVDTO (ms)	274.84±136.92	532.00±261.62
THTR (ms)	134.19±59.60	120.00±40.71
TVTR (ms)	146.45±58.28	114.67±30.67
STREPTO (degrees)	12.46±16.73	11.53±5.73

Values are means ± S.D. (*N*=31 for intraoral transport; *N*=15 for swallowing).

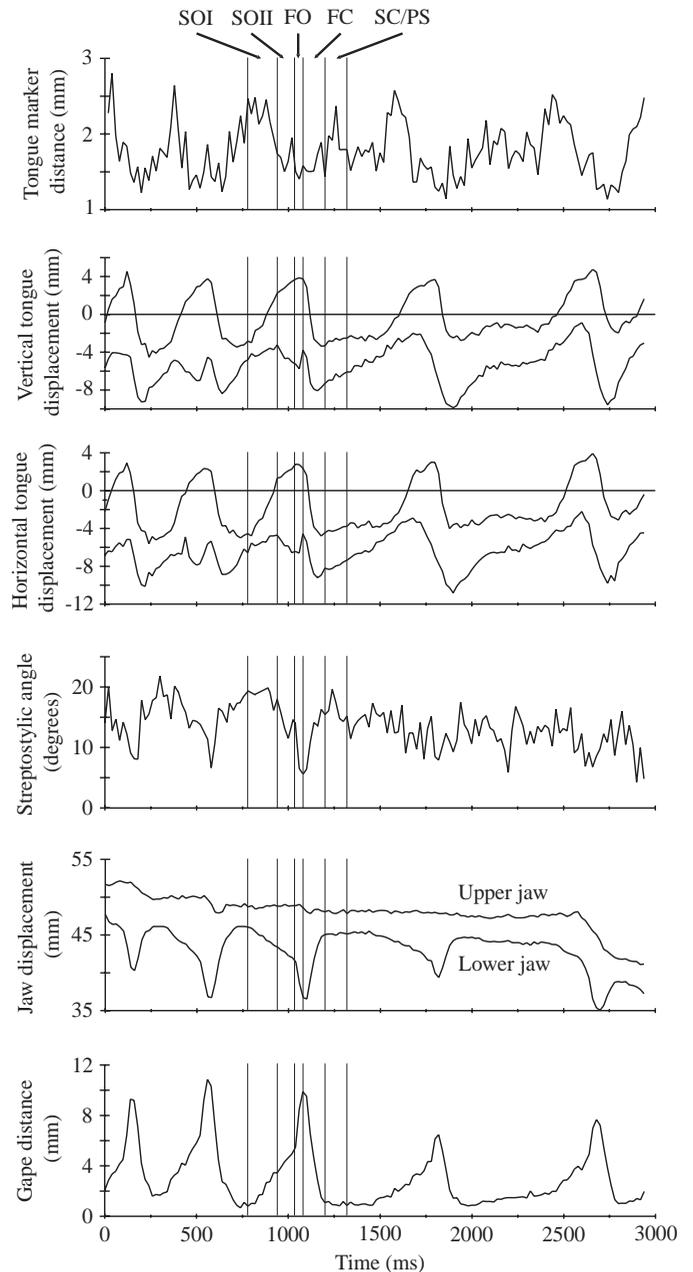See Table 1 and Materials and methods for definitions of abbreviations.

Fig. 2. Kinematic profiles (based on cineradiography, 50 frames s⁻¹) of the distance between the two tongue markers, the vertical displacement of the tongue (the two lines indicating the two markers in the tongue), the horizontal displacement of the tongue (again, the two lines indicating the two markers in the tongue), the streptostylic angle, the displacements of the upper (upper line) and lower jaw (lower line) and the gape distance during intraoral transport (first three cycles) and swallowing (last two cycles) in *Uromastix acanthinurus* while eating endive. Note that a decrease in streptostylic angle indicates an anteriad rotation of the quadrate at the quadrato-squamosal joint. FC, fast closing phase; FO, fast opening phase; SC/PS, slow closing/power stroke phase; SOI, first part of the slow opening phase; SOII, second part of the slow opening phase.

is depressed, the quadrate slowly rotates anteriorly at the quadrato-squamosal joint and the tongue is protracted. No bulging occurs during this first phase. The SOII phase, however, is generally characterised by a marked decrease in opening speed and by tongue bulging. The quadrate continues its slow anteriad rotation. This second phase results in a firm tongue–food contact by pulling the tongue against the food item. The first part of the slow opening phase typically lasts much longer than the second part (see Table 2). The subsequent FO phase is initiated by rapid lower jaw depression (7.63 mm on average) and anteriad quadrate rotation. Cranial elevation (1.81 mm; see Table 2) is not as pronounced as during prey capture, but is present during most intraoral transport bites.

At maximal gape (26.48 °; 11.28 mm on average, see Table 2), when the tongue has almost reached its posteriormost position, the jaws are closed rapidly (elevation of the lower and depression of the upper jaw) in the FC phase. The FC phase is further characterised by a fast posteriad rotation of the quadrate at the quadrato-squamosal joint. Simultaneously, the tongue is retracted. During retraction, the tongue is extended, as indicated by an increase in the distance between both tongue markers (Fig. 2). Once the jaws touch the food, the crushing/shearing starts (=SC/PS phase). During shearing, the quadrate remains immobile, and the tongue usually returns to its resting position or slowly begins to move anteriad again.

Despite the large variation in the absolute timing, the maximal vertical tongue displacement is reached well before maximal gape (Table 1). The dorsal vertical-most position of the tongue is invariably reached before the horizontal-most position. Tongue retraction is much faster than tongue protraction in both horizontal and vertical planes. The average anteriad rotation of the quadrate (STREPTO, see Table 2) during an endive intraoral transport cycle is 12.46 °.

Swallowing

Once the food has been transported to the back of the oral cavity, swallowing starts. Clear differences are present in jaw and tongue movements when comparing intraoral transport and swallowing cycles. A swallowing cycle is characterised by a decrease in the importance of the FO phase, an increase in the duration of the SO phase and more pronounced tongue movements (Fig. 2; Table 2). Swallowing is initiated by a slow depression of the lower jaw. Simultaneously, the tongue is protracted beyond the food item and subsequently retracted. During tongue retraction, the posterior edge of the tongue pushes the food further down the oesophagus. Maximal jaw opening is reduced in comparison with intraoral transport cycles (7.77 mm; 15.07 °). Tongue protrusion is closely associated with jaw opening, and the time to maximal tongue displacement is more closely associated with the time to maximal gape (Table 2) compared with intraoral transport cycles. Although not significantly different, tongue retraction tends to be faster than during intraoral transport and takes approximately four times less time than tongue protrusion (Table 2). The quadrate displacements are similar to those observed during intraoral transport phases.

Prey type

A MANOVA performed on a data set containing both endive and locust intraoral transport and swallowing bites indicates significant stage (Rao's r=16.23, d.f.=18, 48; P<0.001), food-type (Rao's r=7.17, d.f.=18, 48; P<0.01) and interaction (Rao's r=3.18, d.f.=18, 48; P<0.01) effects. Because interaction effects are significant, a MANOVA was subsequently performed on a data set containing both endive and locust intraoral transport cycles. This analysis indicates significant prey type effects (Rao's r=5.33, d.f. 18, 23; P<0.01). However, subsequent univariate F-tests show that, after Bonferroni correction, only gape distance remains significantly different between food types (Table 1). Still, both the duration and timing variables show a clear tendency towards a longer duration while feeding on locusts (compare Tables 2, 3; Figs 2, 3). Additionally, the streptostylic angle shows a tendency towards increased values for locust intraoral transport cycles. A MANOVA performed on a data set containing only swallowing cycles for both food types indicates no significant effects (Rao's r=2.92, d.f.=18, 8; P>0.05).

Species effects

Using the locust feeding data collected here and data from Herrel et al. (1996) for the closely related lizard *P. stellio*, a

Table 3. *Summary kinematics of locust feeding in* Uromastix acanthinurus

	Intraoral transport	Swallowing
GD (mm)	14.67±1.63	7.76±0.81
GA (degrees)	33.12±7.74	13.24±3.22
MEUJ (mm)	3.84±4.00	0.38±0.27
MDLJ (mm)	8.58±3.22	5.05±1.97
MHDTO (mm)	4.17±1.26	5.40±1.64
MVDTO (mm)	3.04±1.26	3.98±1.55
DSOI (ms)	226.00±81.68	–
DSOII (ms)	184.00±89.84	–
DSO (ms)	403.64±118.26	618.33±302.77
DFO (ms)	74.55±26.97	51.67±18.01
DFC (ms)	78.18±18.88	71.67±18.01
DSC/PS or DSTAT (ms)	150.91±48.47	263.33±206.76
DTC (ms)	707.27±107.80	1005.00±482.13
TGA (ms)	478.18±109.35	690.00±327.25
TMEUJ (ms)	481.82±100.98	690.00±323.45
TMDLJ (ms)	485.45±95.95	686.67±326.12
TMHDTO (ms)	341.81±103.71	595.00±311.02
TMVDTO (ms)	354.55±130.57	605.00±298.25
THTR (ms)	203.64±75.27	195.00±51.96
TVTR (ms)	190.91±53.19	216.67±176.60
STREPTO (degrees)	17.39±3.11	8.733±2.16

Values are means ± S.D. (*N*=11 for intraoral transport; *N*=12 for swallowing).

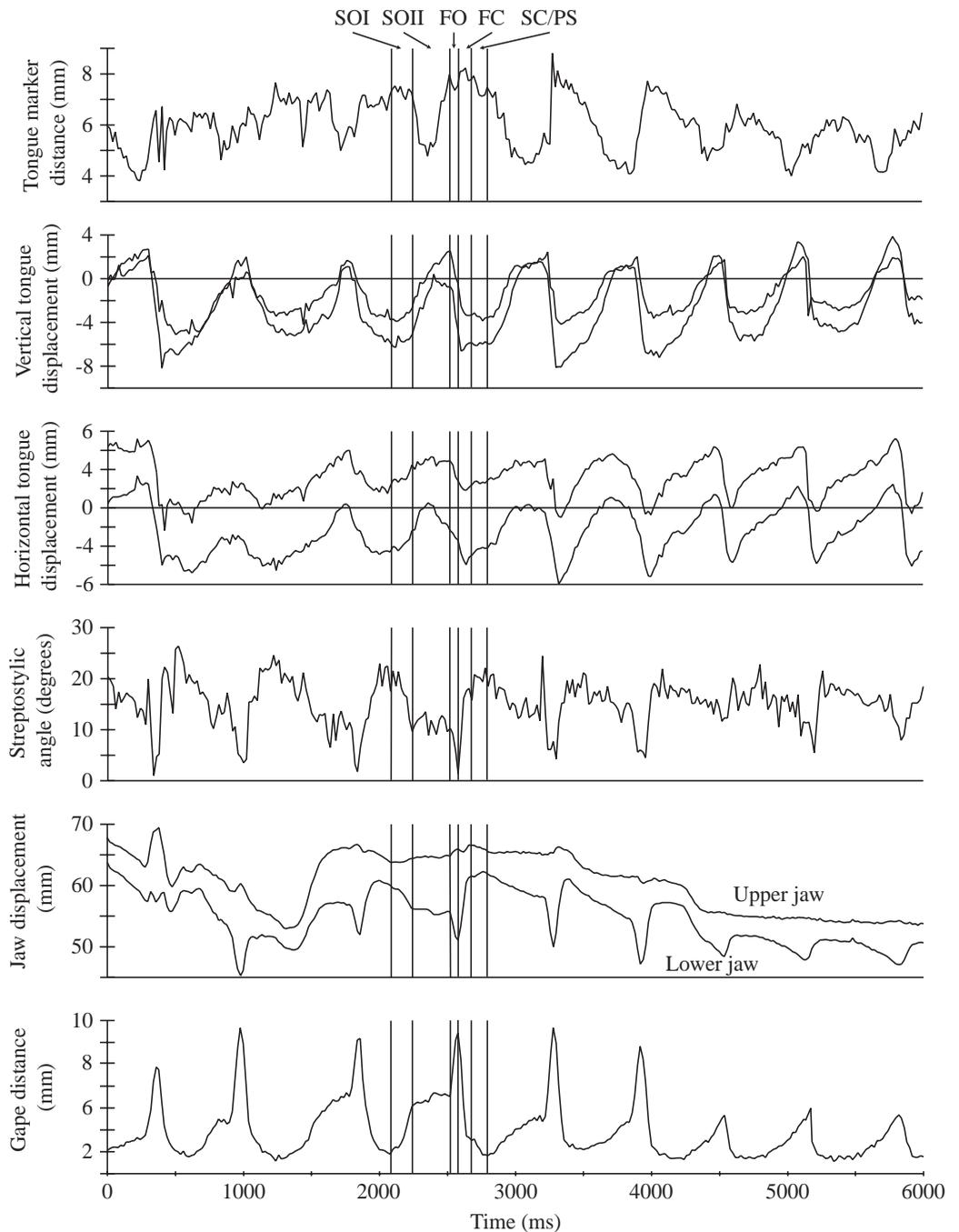See Table 1 and Materials and methods for definitions of abbreviations.

Fig. 3. Kinematic profiles (based on cineradiography, 50 frames s^{-1}) of the distance between the two tongue markers, the vertical displacement of the tongue (the two lines indicating the two markers in the tongue), the horizontal displacement of the tongue (again, the two lines indicating the two markers in the tongue), the streptostylic angle, the displacements of upper (upper line) and lower jaw (lower line) and the gape distance during intraoral transport (first six cycles) and swallowing (last two cycles) in *Uromastix acanthinurus* while eating a 2.0 cm long locust. Note that a decrease in streptostylic angle indicates an anteriad rotation of the quadrate at the quadrato-squamosal joint. Abbreviations are as in Fig. 2.

data set composed of both intraoral transport and swallowing cycles was constructed. A MANOVA performed on this data set indicated significant species (Rao's r=21.50, d.f.=18, 144; P<0.01), stage (Rao's r=28.39, d.f.=18, 144; P<0.01) and interaction (Rao's r=4.88, d.f.=18, 144; P<0.01) effects. Because of significant interaction effects, the data were subdivided into separate intraoral transport and swallowing data sets. MANOVAs performed on these data sets clearly show species-dependent effects for both the intraoral transport (Rao's r=31.26, d.f.=18, 111; P<0.01) and the swallowing (Rao's r=12.19, d.f.=18, 16; P<0.01) data.

Intraoral transport cycles differ in several jaw and tongue displacement, as well as timing, variables (see Table 1). Gape distance, gape angle, lower jaw depression and horizontal tongue displacement are significantly larger in *U. acanthinurus*. The duration of the SC/PS phase, the duration of the FC phase and the maximal vertical displacement of the tongue are all significantly larger in *P. stellio*. Swallowing cycles show fewer significant differences (Table 1). Whereas the gape distance is larger, the duration of the FC phase and the duration of horizontal tongue retraction are smaller in *U. acanthinurus* (compare Table 4 of Herrel et al., 1996, with Table 3 in this study).

Discussion

General feeding kinematics

As observed in other lizard species (e.g. Delheusy and Bels, 1992; Delheusy et al., 1995; Urbani and Bels, 1995; Herrel et al., 1996), a feeding sequence in *U. acanthinurus* can be subdivided into three stages: food prehension, intraoral transport and swallowing. Indeed, quantitative analyses show significant differences between feeding stages for both vegetable and insect food items. Differences between feeding stages are consistently found in the maximal gape angle/distance achieved in *U. acanthinurus* (see also Throckmorton, 1980) as well as in other iguanian (Delheusy and Bels, 1992; Herrel et al., 1996) and scleroglossan (Goosse and Bels, 1992; Urbani and Bels, 1995; Delheusy et al., 1995) lizards. Still, in *U. acanthinurus*, differences between stages are more pronounced while eating endive (see Table 1).

In general, the movements of the jaws and hyolingual apparatus show strong similarities with those published for other lizard species and support the models of Bramble and Wake (1985) and Reilly and Lauder (1990) (but see Herrel et al., 1996). However, some aspects of the jaw and tongue cycles do seem to differ from the predictions of the model of Bramble and Wake (1985). Whereas the duration of the SO phase should increase with increasing prey size and mass (as was observed for other iguanian lizards; see Herrel et al., 1996; J. Cleuren, personal communication), this does not seem to be the case in *U. acanthinurus* (see also Throckmorton, 1980). In particular, the prediction that the second part of the SO phase should increase in importance for heavier prey remains generally unsupported by the present data. Despite locusts being much heavier and larger than endive, the SOII phase still occurs less frequently (in only 43.5 % of the examined cycles) and the duration of the SO phase does not differ compared with endive intraoral transport cycles. For the closely related *P. stellio* (Herrel et al., 1996), the data did support this prediction of the Bramble and Wake (1985) model. Since there are indications that the tongue in *U. acanthinurus* might be less suited to transport insect food items (see below), the functional demands on the tongue during the SOII phase might have changed for *U. acanthinurus*.

When examining the literature on lizard feeding, a general discrepancy seems to exist. Whereas the SOII phase is clearly discernible during most intraoral transport cycles in some iguanians (Schwenk and Throckmorton, 1989; Herrel et al., 1996) and scleroglossans (Goosse and Bels, 1992; Delheusy et al., 1995; Urbani and Bels, 1995), it is not recognisable in others (Delheusy and Bels, 1992; So et al., 1992). Because tongue movements are crucial to delineate the SOII phase, the absence of information on tongue movements in a large number of studies may be problematic. Since the data in some studies do not always support the predictions of the model of Bramble and Wake (1985), the occurrence of the SOII phase and the variability of the SO phase in general need to be quantified further by examining cineradiographic records of intraoral transport in lizards.

Within feeding stages, remarkably few food-type-dependent differences are observed in *U. acanthinurus*. During intraoral transport, the average maximal gape distance is the only significantly different variable, being larger during locust intraoral transport (see Tables 2, 3). Other variables showing a non-significant tendency to differ between food items are the duration of the FO phase and the horizontal tongue retraction time (both tending to be larger for locust intraoral transport). These differences are hardly surprising because grasshoppers are bulky food items in comparison with endive, requiring a larger gape and a somewhat longer jaw opening time. Similarly, owing to the larger size of locusts, tongue retraction times tend to be larger because more effort and/or time are required to pull the prey backwards within the oral cavity. During the subsequent swallowing stage, no significant differences were found between food items. This is predictable since prey items have been reduced previously. Together, these data support previous observations on the conserved character of swallowing cycles (see also Herrel et al., 1996).

Nevertheless, it is rather surprising that so few food-type-dependent differences are observed in *U. acanthinurus* given the large differences in texture, toughness, size, shape and mobility of the food items offered. In insectivorous lizards, changes in food type result in changes in both tongue- and jaw-related kinematic variables (Urbani and Bels, 1995; Herrel et al., 1996) and in number of intraoral transport cycles observed (Bels and Baltus, 1988). Although only two food types were tested in the present study, the data available for the related species *U. aegyptius*, eating several other food types (sweet potato, dog food), also show strong similarities in the average maximal gape and the duration of kinematic phases (see Table 2 in Throckmorton, 1980).

Since locust feeding cycles differ very little from endive feeding cycles in *U. acanthinurus*, a comparison of the kinematic variables with those collected for the closely related *P. stellio* feeding on similarly sized locusts (see Herrel et al., 1996) allows an assessment of the impact of the dietary specialisation in *U. acanthinurus* on its feeding kinematics. Clear species-dependent differences are observed within both the intraoral transport and swallowing stages. Whereas in *U. acanthinurus* during intraoral transport, maximal excursions of the lower jaw and the average horizontal displacement of the tongue are larger, in *P. stellio* the duration of the closing phases and the maximal vertical and horizontal tongue displacement are larger. What might be the origin of these differences between these species? One possible explanation is that the tongue in *U. acanthinurus* might have decreased adhesive properties and thus be less suited for transporting insects. This observation is supported by the larger number of attempts generally required to capture locusts in this species. Clear differences in the tongue-surface topology of both species have been identified (Herrel et al., 1998c). Whereas the medial foretongue surface in *P. stellio* is composed of plumose papillae and numerous secretory cells, in *U. acanthinurus* the tongue surface is composed of dense papillae with extensive microstructure. The larger mouth opening in *U. acanthinurus*

causes less friction between the prey and the mouth upon retraction, thus decreasing the chances of losing the prey.

In *P. stellio*, the fitting of the tongue to the prey is more pronounced, as indicated by the larger TMVDTO and MVDTO values and the more frequent absence of an SOII phase in *U. acanthinurus*. The durations of the closing phases are also significantly longer in *P. stellio*. Apparently, thorough prey reduction is a key element in the feeding cycle of *P. stellio*. Clearly, it is of prime importance for insectivorous lizards (1) to ensure tight prey contact to avoid prey loss upon tongue retraction, and (2) to utilise fast immobilisation/killing of the prey, again to avoid its potential loss and escape. Given these differences between species, it seems that, at first sight, herbivorous lizards such as *U. acanthinurus* do not 'recognise' the importance of a fast reduction of insect prey. However, this might not be completely true; although they apparently do not modulate the feeding cycle itself, they do tend to increase the number of intraoral transport cycles before ingestion of the prey (10±4 endive, *versus* 16±5 locust intraoral transport bites are generally observed; means ± S.D. $N=25$ for endive; $N=15$ for locust), despite their much larger potential bite force (see Herrel et al., 1998a,b). Presumably, the animals are able to kill the prey quickly as a result of their larger bite force but, because the prey is rather large, more cycles are needed to reduce the prey adequately before swallowing. When eating vegetable food items, small pieces can be cropped very easily because of the specialised dentition of *U. acanthinurus*, which allows an accurate shearing bite (Throckmorton, 1979). Still, a decrease in modulatory capacities seems to have occurred in *U. acanthinurus* as a result of its specialised herbivorous diet, as predicted for trophic specialists (Ralston and Wainwright, 1997).

Cranial kinesis

One major difference in feeding kinematics between *U. acanthinurus* and *P. stellio* is the mobility of the quadrate in the former species. It is of course tempting to try to relate the presence of streptostyly in *U. acanthinurus* to its herbivorous diet because, in mammals and numerous extinct reptiles, relative jaw movements are key features associated with a herbivorous diet. Previously, it has been suggested that quadrate mobility in *Uromastix* functions to facilitate cropping and that the retraction of the lower jaw acts to hold the food in position as the teeth shear through it (Throckmorton, 1976). However, this hypothesis is not supported by the data gathered in the present study. Three lines of evidence indicate this: (1) the most important agent playing a role in the holding and transport of food items is clearly the tongue, (2) no quadrate movement is observed during the SC/PS phase, during which the actual shearing of the food takes place, and (3) no significant differences are observed in quadrate mobility during endive intraoral transport and swallowing (during which no shearing takes place).

Other functions of streptostyly that have been proposed previously, such as allowing a firm grasp on large prey (De Vree and Gans, 1994), aiding in food transport (Throckmorton

and Clarcke, 1981; Smith, 1982) and giving increased grasping abilities by allowing both jaws to contact the prey simultaneously (Frazzetta, 1962), are not directly supported by the results presented here for *U. acanthinurus*. In *U. acanthinurus* and several other lizard species (Throckmorton, 1976; Throckmorton and Clarcke, 1981; Smith, 1982; De Vree and Gans, 1987; Herrel et al., 1998a,b), no meso- or metakinesis are observed, thus refuting Frazzetta's (1962) and Iordansky's (1990) hypothesis that amphikinesis is a general characteristic of most lizard families. Even if the results presented here do not indicate a functional alternative to the proposed hypotheses, they do indicate that streptostyly is closely correlated with maximal gape; the larger the gape, the larger the maximal streptostylic angle (compare gape and streptostylic angles during intraoral transport and swallowing in Tables 2, 3). Although some functional adavantages are probably associated with streptostyly (e.g. see Smith, 1980), streptostyly, in general, may be a plesiomorphic character for lizards related to the opening of the lower temporal arch (Iordansky, 1996).

Dietary correlates

Given the fact that lizards of the species *U. acanthinurus* are food specialists, feeding on a very demanding food type, what modifications of the feeding apparatus (both mouth and gut) are expected on theoretical grounds? Apart from modifications in gut structure allowing longer food retention, an increased surface area facilitating the uptake of nutrients and a suitable microhabitat for commensal micro-organisms and nematodes (for an overview, see Iverson, 1980, 1982; King, 1996), several modifications of the jaw apparatus are expected (for an overview, see King, 1996). First, modifications in tooth structure allowing accurate occlusion and an efficient shearing bite are expected and, indeed, are observed in *U. acanthinurus*. Second, a short snout and high skull, increasing the mechanical advantage of the jaw adductors at the front of the jaws, are again both expected and observed. Indeed, as a result of its specialised craniocervical apparatus, *U. acanthinurus* is capable of efficiently cutting small pieces from leaves (indicated by a low number of intraoral tranport bites), which is important in increasing its dietary efficiency (Bjorndal et al., 1990; Bjorndal and Bolten, 1992).

A comparison of the feeding kinematics in *U. acanthinurus* with those in the herbivorous scincid lizard *Corucia zebrata* (Herrel et al., 1999) clearly indicates that the former species is extremely specialised. A larger number of intraoral transport bites is observed in *Corucia zebrata* while eating the same food. Apparently, in lizards, no 'universal' changes in feeding mechanics in response to the demands of vegetable food are observed. For both species, the reduction of particle size is of prime importance, but the solutions employed to achieve this goal are clearly different. One drawback of a herbivorous diet (at least in *U. acanthinurus*) seems to be a reduction in the versatility of the feeding mechanics, which might eventually lead to a reduction of the potential dietary scope of these lizards.

References

Al-Ogily, S. M. and Hussain, A. (1983). Studies on the ecology of the spiny tailed lizard, *Uromastix aegyptius* (Forskal, 1775) in the Riyadh region, Saudi Arabia. *J. Coll. Sci. King Saud Univ.* **14**, 341–351.

Bels, V. and Baltus, I. (1988). The influence of food items on the feeding cycle in *Anolis equestris* (Reptilia: Iguanidae). *Copeia* **2**, 479–481.

Bjorndal, K. A. and Bolten, A. B. (1992). Body size and digestive efficiency in a herbivorous freshwater turtle: Advantages of a small bite size. *Physiol. Zool.* **65**, 1028–1039.

Bjorndal, K. A., Bolten, A. B. and Moore, J. E. (1990). Digestive fermentation in herbivores: effect of food particle size. *Physiol. Zool.* **63**, 710–721.

Bock, W. J. and Shear, C. R. (1972). A staining method for gross dissection. *Anat. Anz.* **130**, 222–227.

Bouskila, A. (1986). Habitat selection in the desert lizard *Uromastix aegyptius* and its relation to the autecological hypothesis. In *Environmental Quality and Ecosystem Stability*, vol. III A/B (ed. Z. Dubinsky and Y. Steinberger), pp. 119–128. Ramat Galan, Israel: Bar-Ilan University Press.

Bouskila, A. (1987). Feeding in the herbivorous lizard *Uromastix aegyptius* near Hazeva. *Israel J. Zool.* **33**, 122.

Bramble, D. and Wake, D. B. (1985). Feeding mechanisms of lower tetrapods. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. Bramble, K. Liem and D. Wake), pp. 230–261. Cambridge, MA: Harvard University Press.

Cooper, J. S. and Poole, D. F. G. (1973). The dentition and dental tissues of the agamid lizard, *Uromastyx*. *J. Zool., Lond.* **169**, 85–100.

Cooper, J. S., Poole, D. F. G. and Lawson, R. (1970). The dentition of agamid lizards with special reference to tooth replacement. *J. Zool., Lond.* **162**, 85–98.

Delheusy, V. and Bels, V. L. (1992). Kinematics of feeding behaviour in *Oplurus cuvieri* (Reptilia: Iguanidae). *J. Exp. Biol.* **170**, 155–186.

Delheusy, V., Brillet, C. and Bels, V. L. (1995). Etude cinématique de la prise de nourriture chez *Eublepharis macularius* (Reptilia, Gekkonidae) et comparaison au sein des geckos. *Amphibia-Reptilia* **16**, 185–201.

Demment, M. W. and Van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *Am. Nat.* **125**, 641–672.

De Vree, F. and Gans, C. (1976). Mastication in pygmy goats (*Carpa hircus*). *Ann. Soc. R. Zool. Belg.* **105**, 255–306.

De Vree, F. and Gans, C. (1987). Kinetic movements in the skull of adult *Trachydosaurus rugosus*. *Anat. Histol. Embryol.* **16**, 206–209.

De Vree, F. and Gans, C. (1989). Functional morphology of the feeding mechanisms in lower tetrapods. In *Fortschritte der Zoologie*, vol. 35 (ed. H. Splechtna and H. Hilgers), pp. 115–127. New York: Gustav Fischer Verlag.

De Vree, F. and Gans, C. (1994). Feeding in tetrapods. In *Advances in Comparative and Environmental Physiology*, vol. 18 (ed. V. L. Bels, M. Chardon and P. Vandewalle), pp. 93–113. Berlin: Springer.

Dubuis, A., Faurel, L., Grenot, C. and Vernet, R. (1971). Sur le régime alimentaire du lézard saharien *Uromastix acanthinurus* Bell. *C.R. Acad. Sci., Ser. D Sci. Nat.* **273**, 500–503.

El-Toubi, M. R. and Bishai, H. M. (1959). On the anatomy and histology of the alimenary tract of the lizard *Uromastix aegyptia* (Forskal). *Bull. Fac. Sci. Cairo Univ.* **34**, 13–50.

Frazzetta, T. H. (1962). A functional consideration of cranial kinesis in lizards. *J. Morph.* **111**, 287–319.

Frost, D. R. and Etheridge, R. (1989). Phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). *Misc. Publ. Mus. Nat. Hist. Univ. Kansas* **81**, 1–65.

Gans, C. (1974). *Biomechanics: An Approach to Vertebrate Biology*. Philadelphia: J. B. Lippincott. 261pp.

Goosse, V. and Bels, V. L. (1992). Kinematic and functional analysis of feeding behaviour in *Lacerta viridis* (Reptilia: Lacertidae). *Zool. Jb. Anat.* **122**, 187–202.

Grenot, C. (1976). Ecophysiologie du lézard saharien *Uromastix acanthinurus* Bell, 1825 (Agamidae herbivore). *Ecole Norm. Supér., Publ. Lab. Zool.* **7**, 1–323.

Herrel, A., Aerts, P. and De Vree, F. (1998a). Static biting in lizards with a primitive skull: functional morphology of the temporal ligaments. *J. Zool., Lond.* **244**, 135–143.

Herrel, A., Aerts, P. and De Vree, F. (1998b). Ecomorphology of the lizard feeding apparatus: a modelling approach. *Neth. J. Zool.* **48**, 1–25.

Herrel, A., Cleuren, J. and De Vree, F. (1995). Prey capture in the lizard *Agama stellio*. *J. Morph.* **224**, 313–329.

Herrel, A., Cleuren, J. and De Vree, F. (1996). Kinematics of feeding in the lizard *Agama stellio*. *J. Exp. Biol.* **199**, 1727–1742.

Herrel, A., Timmermans, J.-P. and De Vree, F. (1998c). Tongue-flicking in agamid lizards: morphology, kinematics and muscle activity patterns. *Anat. Rec.* **252**, 102–116.

Herrel, A., Verstappen, M. and De Vree, F. (1999). Modulatory complexity of the feeding repertoire in scincid lizards. *J. Comp. Physiol.* (in press).

Hiiemae, K. M. and Crompton, A. W. (1985). Mastication, food transport and swallowing. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. Bramble, K. Liem and D. Wake), pp. 230–261. Cambridge: Harvard University Press.

Iordansky, N. N. (1990). Evolution of cranial kinesis in lower tetrapods. *Neth. J. Zool.* **40**, 32–54.

Iordansky, N. N. (1996). The temporal ligaments and their bearing on cranial kinesis in lizards. *J. Zool., Lond.* **239**, 167–175.

Iverson, J. B. (1980). Colic modifications in iguanine lizards. *J. Morph.* **163**, 79–93.

Iverson, J. B. (1982). Adaptations to herbivory in iguanine lizards. In *Iguanas of the World: Their Behavior, Ecology and Conservation* (ed. G. M. Burghardt and A. S. Rand), pp. 60–76. Park Ridge, NJ: Noyes.

Joger, U. (1991). A molecular phylogeny of agamid lizards. *Copeia* **1991**, 612–622.

King, G. (1996). *Reptiles and Herbivory*. London: Chapman & Hall, 160pp.

Kraklau, D. M. (1991). Kinematics of prey capture and chewing in the lizard *Agama agama*. *J. Morph.* **210**, 195–212.

Lauder, G. V. (1983). Functional and morphological bases of trophic specialisation in fishes. *Science* **219**, 1235–1237.

Lauder, G. V. and Gillis, G. B. (1996). Origin of the amniote feeding

mechanism: experimental analyses of outgroup clades. In *Amniote Origins* (ed. S. S. Sumida and K. L. M. Martin), pp. 169–206. Town: Publisher.

Lauder, G. V. and Reilly, S. M. (1994). Amphibian feeding behavior: comparative biomechanics and evolution. In *Advances in Comparative and Environmental Physiology*, vol. 18 (ed. V. L. Bels, M. Chardon and P. Vandewalle), pp. 163–195. Berlin: Springer.

Liem, K. F. (1980). Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am. Zool.* **20**, 295–314.

Maloiy, G. M. O. and Clemens, E. T. (1990). Aspects of digestion and *in vitro* fermentation in the caecum of some East-African herbivores. *J. Zool.* **224**, 293–300.

Maynard Smith, J. and Savage, R. J. G. (1959). The mechanics of mammalian jaws. *School Sci. Rev.* **141**, 289–301.

Ostrom, J. H. (1963). Further comments on herbivorous lizards. *Evolution* **17**, 368–369.

Pough, F. H. (1973). Lizard energetics and diet. *Ecology* **54**, 838–844.

Ralston, K. R. and Wainwright, P. C. (1997). Functional consequences of trophic specialisation in pufferfishes. *Funct. Ecol.* **11**, 43–52.

Reilly, S. M. and Lauder, G. V. (1990). The evolution of tetrapod prey transport behavior: kinematic homologies in feeding function. *Evolution* **44**, 1542–1557.

Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution* **43**, 223–225.

Robinson, P. L. (1976). How *Sphenodon* and *Uromastyx* grow their teeth and use them. In *Morphology and Biology of Reptiles* (ed. A. d'A. Bellairs and C. B. Cox). *Linn. Soc. Symp. Ser.* **3**, 43–46.

Russell, A. P. and Thomason, J. T. (1993). Mechanical analysis of the mammalian head skeleton. In *The Skull*, vol. 3 (ed. J. Hanken and B. K. Hall), pp. 345–383. Chicago: University of Chicago Press.

Schwenk, K. and Throckmorton, G. S. (1989). Functional and evolutionary morphology of lingual feeding in squamate reptiles: phylogenetics and kinematics. *J. Zool., Lond.* **219**, 153–175.

Sibly, R. M. (1981). Strategies of digestion and defecation. In *Physiological Ecology: an Evolutionary Approach to Resource Use* (ed. C. R. Townsend and P. Calow), pp. 109–144. Oxford: Blackwell Scientific Publications.

Smith, K. K. (1980). Mechanical significance of streptostyly in lizards. *Nature* **283**, 778–779.

Smith, K. K. (1982). An electromyographic study of the jaw adducting muscles in *Varanus exanthematicus* (Varanidae). *J. Morph.* **173**, 137–158.

So, K. K. J., Wainwright, P. C. and Bennett, A. F. (1992). Kinematics of prey processing in *Chamaeleo jacksonii*; conservation of function with morphological specialisation. *J. Zool., Lond.* **202**, 115–143.

Sokol, O. M. (1967). Herbivory in lizards. *Evolution* **21**, 192–194.

Szarski, H. (1962). Some remarks on herbivorous lizards. *Evolution* **16**, 529.

Throckmorton, G. S. (1976). Oral food processing in two herbivorous lizards, *Iguana iguana* (Iguanidae) and *Uromastix aegyptius* (Agamidae). *J. Morph.* **148**, 363–390.

Throckmorton, G. S. (1978). The action of the pterygoideus muscle during feeding in the lizard *Uromastix aegyptius* (Agamidae). *Anat. Rec.* **190**, 217–222.

Throckmorton, G. S. (1979). The effect of wear on the cheek teeth and associated dental tissues of the lizard *Uromastix aegyptius* (Agamidae). *J. Morph.* **160**, 195–208.

Throckmorton, G. S. (1980). The chewing cycle in the herbivorous lizard *Uromastix aegyptius* (Agamidae). *Arch. Oral Biol.* **25**, 225–233.

Throckmorton, G. S. and Clarcke, L. K. (1981). Intracranial joint movement in the agamid lizard *Amphibolurus barbatus*. *J. Exp. Zool.* **216**, 25–35.

Urbani, J. M. and Bels, V. L. (1995). Feeding behaviour in two scleroglossan lizards: *Lacerta viridis* (Lacertidae) and *Zonosaurus laticaudatus* (Cordylidae). *J. Zool., Lond.* **236**, 265–290.

Wainwright, P. C. and Lauder, G. V. (1986). Feeding biology of sunfishes: patterns of variation in the feeding mechanism. *Zool. J. Linn. Soc.* **88**, 217–288.

Wainwright, P. C., Sanford, C. P., Reilly, S. M. and Lauder, G. V. (1989). Evolution of motor patterns: aquatic feeding in salamanders and ray-finned fishes. *Brain Behav. Evol.* **34**, 329–341.

Weijs, W. (1994). Evolutionary approach of masticatory motor patterns in mammals. In *Advances in Comparative and Environmental Physiology*, vol. 18 (ed. V. L. Bels, M. Chardon and P. Vandewalle), pp. 282–314. Berlin: Springer.