FEEDING KINEMATICS OF *PHELSUMA MADAGASCARIENSIS* (REPTILIA: GEKKONIDAE): TESTING DIFFERENCES BETWEEN IGUANIA AND SCLEROGLOSSA

VERONIQUE DELHEUSY[1] AND VINCENT L. BELS[2,*]

[1]*Institut de Zoology, University of Liège, Quai Van Beneden 22, B-4020 Liège, Belgium* and [2]*Hautes Ecoles Provinciales de Charleroi et du Hainaut Occidental and Centre Agronomique de Recherches Appliquées du Hainaut, Rue Paul Pastur 11, B-7800 Ath, Belgium*

*Author for correspondence and present address: Centre Agronomique de Recherches Appliquées du Hainaut, rue de l'Agriculture 301, B-7800 Ath, Belgique (e-mail: vincent.bels@umh.ac.be)

Summary

The kinematics of feeding in the gekkotan lizard *Phelsuma madagascariensis* (Scleroglossa) was investigated using high-speed cinematography (200–300 frames s^{-1}) and X-ray films (64 frames s^{-1}). Qualitative kinematic analysis of the head and jaw displacement of the prey to (capture) and within (reduction, transport, swallowing, licking) the buccal cavity are compared for two types of prey (crickets and mealworms) in 30 feeding sequences from four individuals. Maximal displacement of structures and timing of events are compared statistically to assess the differences among the phases and the prey using analysis of variance. *P. madagascariensis* uses its jaws only to capture the two types of prey item, and the capture jaw cycle is divided into fast-opening (FO), fast-closing (FC) and slow-closing (SC) stages only. As in iguanians and other scleroglossans, the reduction and transport cycles always involve a slow opening (SOI and SOII) stage before the FO stage, followed by FC and SC stages: this last stage was not easily identified in all feeding phase. Transport of the prey was followed by a large number of licking cycles. Our data show (i) that the capture profile in gekkotans is similar to that observed for other

scleroglossans and different from that described for iguanians (e.g. the absence of an SO stage); (ii) that the kinematics of jaw and related hyo-lingual cycles of intraoral manipulation (reduction and transport) are similar in lizards with a very different hyo-lingual system (Iguania, Gekkota and Scincomorpha), suggesting a basic mechanism of feeding cycles in squamates, transformed in varanids and snakes; and (iii) that prey type affects the kinematics of capture and manipulation, although the high level of variation among lizards suggests a possible individual modulation of feeding mechanism. A principal components analysis was performed to compare capture and transport cycles in this study of *P. madagascariensis* (Gekkota) and a previous study of *Oplurus cuvieri* (Iguania). This analysis separated the capture cycle of each species, but the transport cycles were not completely separated. These results demonstrate the complexity of the modulation and evolution of feeding process in squamates.

Key words: feeding, kinematics, evolution, squamate, Gekkonidae, *Phelsuma madagascariensis*.

Introduction

The last 10 years have seen intensive study of the use of the diversified jaw apparatus and hyo-lingual system in very different behaviours including feeding, drinking, chemoreception and display in Squamata (Bels et al., 1994). With the exception of varanids (Smith, 1986), the tongue plays a key role during all feeding phases, from capture to swallowing (Bels and Goosse, 1989; Delheusy and Bels, 1992; Delheusy et al., 1994; Herrel et al., 1995, 1996). Capture and chemosensory evolutionary transformations of the tongue are intimately integrated (Schwenk, 1993a,b, 1994; Cooper, 1995a; Toubeau et al., 1995; Kardong et al., 1997), and the phylogenetic dichotomy based on lingual/jaw prehension between Iguania and Scleroglossa is strongly related to the evolution of vomerolfaction (Schwenk, 1993a, 1994). Lingual

prehension in Iguania constrained chemosensory evolution, whereas the loss of prehensile ability in Scleroglossa probably allowed the evolution of chemoreception by liberating the tongue from its capture function (Schwenk, 1993a). Lingual prehension described in Iguania has often been considered as the primitive mode of prey capture in Squamata (Schwenk, 1988; Schwenk and Bell, 1988; Schwenk and Throckmorton, 1989), although this problem remains to be resolved (Bels and Goosse, 1990; Bels, 1997; V. L. Bels and K. Kardong, in preparation). Several scleroglossan species such as *Gerrhonotus*, *Lacerta* and *Varanus* capture all kinds of preys using only their jaw apparatus (Frazzetta, 1983; Smith, 1986; Goosse and Bels, 1992a), whereas the scincomorphan *Zonosaurus laticaudatus* (Cordilydae) uses the tongue to pin a

mealworm larva to the substratum before catching it using the jaws. Lingual prehension reported in *Tiliqua scincoides* (Scincidae) for this kind of food is similar to that described for iguanians (Bels et al., 1994; Urbani and Bels, 1995; Kiene et al., 1996, 1999).

Among scleroglossans, the morphological and functional properties of the tongue (and associated hyoid apparatus) are highly diverse (Gove, 1979; Schwenk, 1988, 1993a; Iwasaki, 1990; Cooper, 1995b; Goosse and Bels, 1992b). Our current database for this monophyletic sister-group of Iguania includes only a few species from the Scincomorpha (e.g. Lacertidae, Cordylidae, Teiidae and Scincidae) and Anguimorpha (e.g. Varanidae) with a rather deeply bifid tongue used predominantly for chemoreception. Apart from the preliminary study of *Eublepharis macularius* (Delheusy et al., 1995), no quantitative analyses of the feeding behaviour of Gekkota have been presented, although their phylogenetic position (Fig. 1) and behavioural ecology are of particular interest in a comprehensive analysis of the evolution of feeding behaviour in squamates. Gekkota stem first from the scleroglossan lineage, showing evident phylogenetic dichotomy with Iguania (Estes et al., 1988), and are unique among Scleroglossa because of their extensive use of olfaction (Schwenk, 1993b; Dial and Schwenk, 1996). The majority of gekkonids are nocturnal, and several authors have emphasized that the properties of their tongue (e.g. extensibility) could be related not only to chemoreception (as is found in the majority of scleroglossans) but also to spectacle-wiping or facial tongue-wiping (Greer, 1985; Schwenk, 1993b).

The primary purpose of this study is to provide a quantitative analysis of the kinematic properties of the feeding behaviour of *Phelsuma madagascariensis*, a diurnal arboreal gekkonid derived from a nocturnal ancestor. This species is a good candidate for comparing feeding behaviour between Gekkota and other Scleroglossa because it presents all the typical characteristics of gekkonids (Russell, 1977). We focused on two main questions. (i) What are the kinematics of the different phases of feeding? (ii) How do prey characteristics influence the kinematics of feeding? Our data allow a preliminary evaluation of the effects of morphological specialization of the tongue on the kinematics of feeding in lizards. For this purpose, we compare the feeding kinematics of *P. madagascariensis* (Gekkota) with data obtained previously in the iguanian *Oplurus madagascariensis* (Delheusy and Bels, 1992). Finally, the results are contrasted with the evolutionary models of feeding in tetrapods (Bramble and Wake, 1985; Reilly and Lauder, 1990) and with functional features proposed as plesiomorphic for all Amniota by Lauder and Gillis (1997).

Materials and methods
Animals

Four adult male *Phelsuma madagascariensis* (Gray) (108±4 mm upper jaw–vent length; mean ± S.D.) were filmed at 200 and 300 frames s^{-1} with Eastman Ektachrome high-speed 7250 Tungsten 16 mm film and a Photosonic 1 PL camera. The
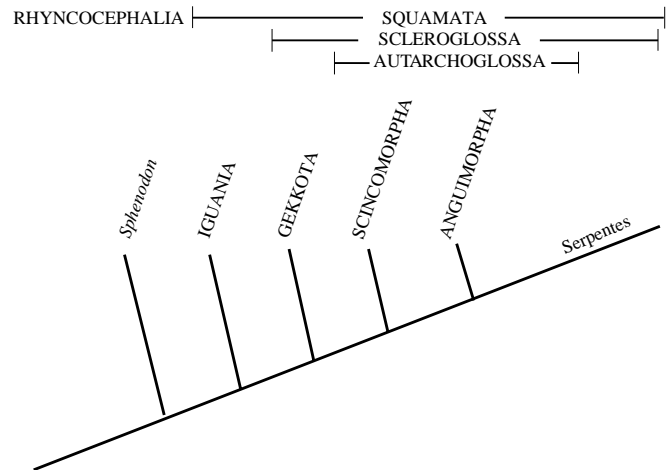

Fig. 1. Summary of the phylogenetic relationships among living squamates based on the phylogenetic tree for this group of Reptilia (Schwenk, 1988, 1993a). The Gekkota are the first to emerge from the Scleroglossa.

lizards were filmed under two 1000 W tungsten photoflood lights. Each lizard was isolated in a vivarium for 2 or 3 weeks before filming. Vivaria measured 100 cm×50 cm×50 cm. An incandescent bulb and two True-Lite tubes provided the animal with a temperature ranging from 22 °C (night) to 30 °C (day). The relative humidity was maintained near 60 %. Natural spots on the lizards were used for digitizing.

Kinematics
High-speed cinematography

Eighty-two truly lateral cycles were digitized (6–10 cycles per invidual) for intrabuccal manipulation (reduction, transport, licking). For capture, it was not possible to measure this large number of cycles because the lizard often rotated its head and the prey obscured the jaws. Only 10 truly lateral capture cycles were obtained in this study. Filming with a mirror was not successful because the lizard interacted aggressively with its reflection. For this reason, only a general comparison of the kinematic profiles of capture is made between scleroglossans and iguanians. Two kinds of food were provided to the lizards: (i) live adult crickets (*Acheta domesticus*) of approximately equal length (24 mm); and (ii) live mealworms (*Tenebrio molitor*) measuring approximately 20 mm. The prey items differed not only in size but also in shape, width, mass, hardness and behaviour.

High-speed cineradiography

Additional data were obtained from two other individuals of *P. madagascariensis* (upper jaw–vent length 110 and 114 mm) feeding on live crickets (length approximately 24 mm), filmed in the Laboratory of Comparative Anatomy of the Museum of Natural History of Paris (France) using a Massiot-Philips cinefluoroscopic apparatus (50 kV, 2 mA). These data display intra-buccal kinematic profiles of tongue displacements during reduction and transport. A lead marker (diameter 0.55 mm) was

inserted gently into the mid-tongue of lizards using a hypodermic needle under general anaesthesia (Ethrane). A solution of barium sulphate (20 %) was gently injected into the thorax of the prey to follow its movements within the buccal cavity. Thirty jaw and tongue cycles (10 reduction cycles and 20 transport cycles involving swallowing) were filmed for each individual.

Analysis

All cinematographic feeding cycles were projected onto a graphics tablet (AGMEE, ULg) using a NAC motion analyser, and the data were digitized using a Copam AT microcomputer. Data files were constructed using a set of computer programs developed by V. Bels and P. Theate. Frame 1 (time zero) was chosen to occur at the commencement of the opening of the jaws. Jaw displacement was calculated by computing the displacements of the anteriormost tip of the upper jaw and the lower jaw. The lower jaw angle was the angle of the lower jaw tip relative to point AO and point H on the body (Fig. 2). The upper jaw angle was the angle of the upper jaw tip relative to point AO and point H on the body. The gape angle referred to the angle between the mandibular symphysis, the angulus oris (AO) and the tip of the upper jaw. Horizontal and vertical displacements of the food were illustrated by calculating the difference between the x and y coordinates of a point painted on the middle of the thorax of the prey and the x and y coordinates of the tip of the lower jaw. For X-ray films, these distances corresponded to the difference between the x and y coordinates of the tip of the lower jaw and the centre of a drop of barium sulphate introduced behind the head of the insect. The displacements of the head corresponded to the x and y coordinates of point H. The points used for digitising are illustrated in Fig. 2.
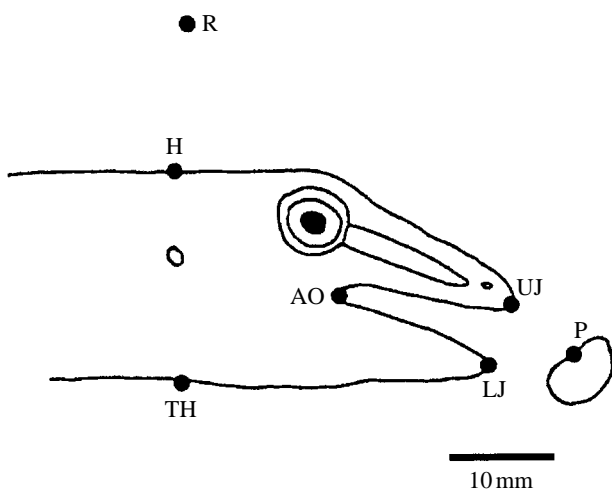

Fig. 2. Points used for digitizing from high-speed films (200 and 300 frames s^{-1}). AO, angulus oris; H, head; LJ, lower jaw; P, prey; R, reference point on the grid behind the lizard; TH, throat, UJ, upper jaw. The kinematic variables were calculated as the distances between the coordinates of these points. Graphs and computed variables are given for truly lateral sequences only.

Comparison of feeding phases and effect of prey item on kinematics in Phelsuma madagascariensis

The mean and standard deviation of all variables were calculated for each prey item within each feeding phase obtained from cinematographic films. All analyses were performed on a data set representing the amplitude and timing of the feeding cycles. Abbreviations are as follows: maximal gape, GA (degrees); maximal depression of the lower jaws, LJA (degrees); maximal elevation of the upper jaws, UJA (degrees); time of maximal gape angle, MGA (s); time of maximal depression of the lower jaws, MLJA (s); time of maximal elevation of the upper jaws, MUJA (s); duration of slow opening, SO (s and percentage of cycle duration), divided into stages SOI and SOII (when present); duration of fast opening, FO (s and percentage of cycle duration); duration of fast closing, FC (s and percentage of cycle duration) and total duration of the gape cycle, TC (s). Three additional variables were measured for licking cycles: duration (s) of jaw opening (OPENING), duration (s) of the jaw 'plateau' involving tongue movements out of the buccal cavity (PLAT) and duration (s) of jaw closing (CLOSING).

First, we compared the capture of crickets with intra-buccal processing (reduction and transport) by using a two-way analysis of variance (ANOVA) to examine the effects of phase (fixed effect) and individual (random effect) and their interaction. During capture, lizards catch food recognized by different sensory inputs (e.g. visual and olfactory), while inputs from the food into the buccal cavity (i.e. tactile, gustative, proprioceptive) may regulate the mechanism of food processing. Crossed factors were selected because each level of one factor is the same across the level of the other factors. Phases were crossed with individuals because each level of phase (capture and intra-oral processing) was the same for all individuals. The *F*-ratios for the main effects were calculated as follows: for phase, phase mean square was divided by phase × individual interaction mean square; for individual, individual mean square was divided by error (Sokal and Rohlf, 1995). For variables for which the two-way ANOVA showed a significant difference between phases, a *post-hoc* multiple-comparison Newman–Keuls test was performed to determine which phases were different from the others.

Second, an initial three-way multiple analysis of variance was performed on the three phases of intra-oral prey processing (reduction, transport and licking) for two prey items (mealworms and crickets) because the sensory inputs of each type of prey were very different during this processing. In this analysis, phases were crossed with individuals because each level of phase was the same for all individuals. Type of prey was crossed with individual because each level of prey type (cricket and mealworm) was the same for each individual. Finally, prey was crossed with phase and with individual because each prey type was the same for all phases and all individuals. First-order interactions were tested over the second-order interaction (Sokal and Rohlf, 1995).

Third, a second three-way multiple analysis of variance was performed to compare reduction and transport to investigate

the effects of prey type alone on the two main phases of intra-oral processing. The *F*-ratios for the main effects were calculated as follows: for phase, phase mean square was divided by phase × individual interaction mean square; for prey, prey mean square was divided by prey × individual interaction mean square; for individual, individual mean square was divided by error, and first-order interactions were tested over the second-order interaction. For variables where the three-way ANOVA showed a significant difference between phases, a *post-hoc* multiple-comparison Newman–Keuls test was performed to determine which phases (reduction, transport and licking) were significantly different from each other.

Individual effect

Two groups of individuals were obtained from the *post-hoc* multiple comparison performed in the previous multiple ANOVA. Therefore, we used a two-way analysis to test the effect of two fixed factors (phase and prey type) in each group of lizards. In this analysis, the *F*-ratios for each of the fixed effects (phase and prey type) and the interaction (phase × prey type) term were tested over the error. Crossed factors were selected because each level of one factor (prey type) is the same across the level of the other factor (phase). For all the analyses, the significance levels were adjusted to $P \leq 0.007$ (comparison of seven variables), $P \leq 0.006$ (comparison of eight variables) and $P \leq 0.0045$ (comparison of 11 variables) using the sequential Bonferroni technique described by Rice (1989).

Comparison between P. madagascariensis and O. cuvieri

A kinematic comparison of capture and transport between *O. cuvieri* and *P. madagascariensis* was used as a preliminary comparison between differences in squamates based (i) on intra-oral transport and (ii) on modes of capture (lingual prehension in the iguanian *O. cuvieri*, Delheusy and Bels, 1992, and jaw prehension in the gekkotan *P. madagascariensis*, the present paper). In the iguanian *O. cuvieri*, the tongue is fleshy and the fore-tongue is covered with glandular papillae, and the relationships between the different types of papillae and intra-buccal manipulation and movements of food have been described on the basis of kinematics derived from cinematography and X-ray films (Delheusy and Bels, 1992; Delheusy et al., 1994). Although the tongue is broad, slightly notched and not forked like the tongue of iguanians, *P. madagascariensis* illustrates several functional characteristics different from those iguanians, including extensive protrusion and elongation, a slender fore-tongue and a surface with peg-like papillae and plicae. Data on *O. cuvieri* were obtained from Delheusy and Bels (1992). Kinematic variables were measured for capture and transport cycles of four individuals for each species. On the basis of seven common kinematic variables (GA, MGA, MLJA, TC, SO, FO and FC), differences between capture and transport cycles in both species for one prey type (cricket) were examined at a multivariate level by performing a principal components analysis (PCA). Principal components were extracted from the correlation matrix, their component loadings were studied, and projections of the cycles on the first two factors explaining the most variation were plotted.

Terminology

We followed previous workers in our use of terminology for describing each prey-processing cycle (Bramble and Wake, 1985; Hiiemae and Crompton, 1985; Reilly and Lauder, 1990; Delheusy and Bels, 1992; Lauder and Gillis, 1997). In *P. madagascariensis*, the slow opening stage (SO) began with the onset of mouth opening. Division of this stage into SOI and SOII was based on the gape angle. An increase in gape angle corresponded to SOI. During SOII, which always followed SOI, the gape angle did not change. The fast opening stage (FO) began with a sudden increase in the gape angle. The fast closing stage (FC) began with the first closure of the mouth. The closing of the mouth was identified as fast closing because it corresponded to the stage called fast closing in the model of Bramble and Wake (1985). We did not identify a slow closing power stroke (PS) stage because we did not measure clear variations in the gape velocity during the closing stage. The licking cycle presented a different pattern: opening, 'plateau' and closing. During the 'plateau' stage, the gape angle did not change.

Results

Feeding sequence

A typical feeding sequence in *P. madagascariensis* was divided into five phases: capture, reduction, transport, swallowing and licking. Capture was accompanied by a lunge phase involving horizontal displacements of the head towards the prey while the fore-limbs were fixed. Jaw prehension was always used to catch mealworms and crickets. After the initial acquisition of the prey, the head assumed a horizontal position with the prey held between the teeth, and the body was firmly attached to the substratum. With each reduction cycle, the thorax of the prey was pressed between the rows of teeth. The transport phase began with the food item having its long axis in line with the jaws and being moved further into the pharynx with each cycle. The transport phase was followed by swallowing. At the end of the complete feeding sequence, the lizard licked its jaws with its tongue. The tongue always contacted the scales of the head and moved in a large area from the anterior portion of the skull and the lower jaw to the eyes. Such licking tongue cycles were also observed after drinking.

Kinematics

Capture

To catch the prey, the lizard oriented its head towards the prey and achieved prey capture with forward body and jaw displacements (Fig. 3). Crickets were always caught by the thorax and mealworm larvae by the middle of the body (*N*=22 sequences). The mean gape angle for capturing crickets was 39.3 ° and that for mealworms was 30.2 ° (*N*=10 cycles). At almost 10 mm from the prey, the lizard stopped and rapidly
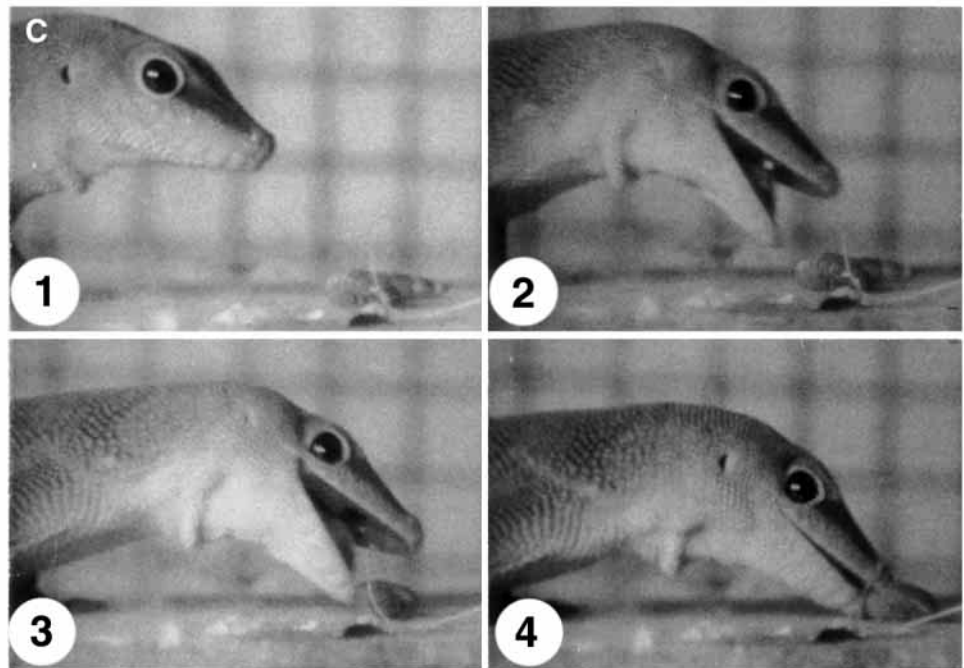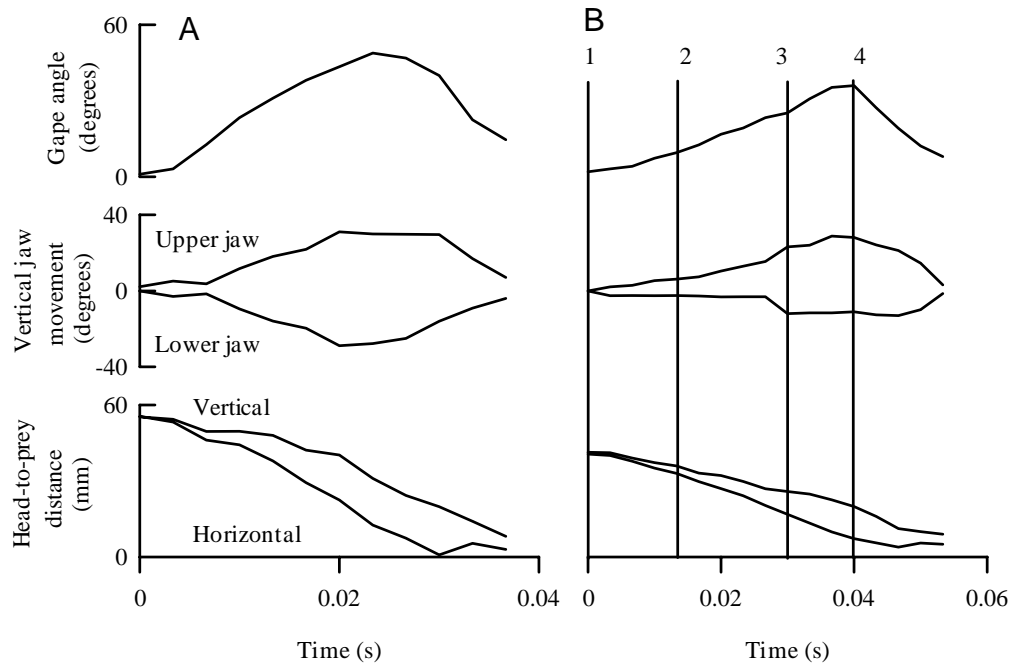
Fig. 3. Kinematic profiles measured from high-speed films depicting prey capture of (A) a cricket and (B) a mealworm by *Phelsuma madagascariensis*. (C) Four frames illustrating successive stages of the capture of a mealworm. These frames refer to the numbers indicated in the kinematic profiles for the mealworm (B). Head-to-prey distance was measured between points P and LJ defined in Fig. 2.

moved its head towards the prey item, as shown by the rapid decrease in distance beween the tip of the upper jaw and a point on the prey.

The gape profile is divided into opening and closing stages with no subdivision of the opening stage (Fig. 3). Lower jaw depression accounts for approximately 70 % of the increase in the gape and upper jaw elevation for approximately 30 %. The mean duration of gape cycle is approximately 200 ms (Table 1).

Reduction

Reduction cycles were divided into four stages: slow opening (SO), fast opening (FO), fast closing (FC) and slow closing (SC). The mean duration of the SO stage represented 96 % (cricket) and 93 % (mealworm) of the mean total duration of the gape cycle (Fig. 4). This stage was divided into slow opening I (SOI) and slow opening II (SOII). During SOI, the gape angle increased linearly; it remained almost constant during SOII. SOI made up approximately 3 % (cricket) and 10 % (mealworm) of the slow opening stage. The duration of SOII was approximately 1000 ms for each prey item. The mean durations of the FO and FC stages were very similar for both prey items. The FO and FC stages made up almost 2 % and 2–5 %, respectively, of the total duration of the cycles (Table 2).
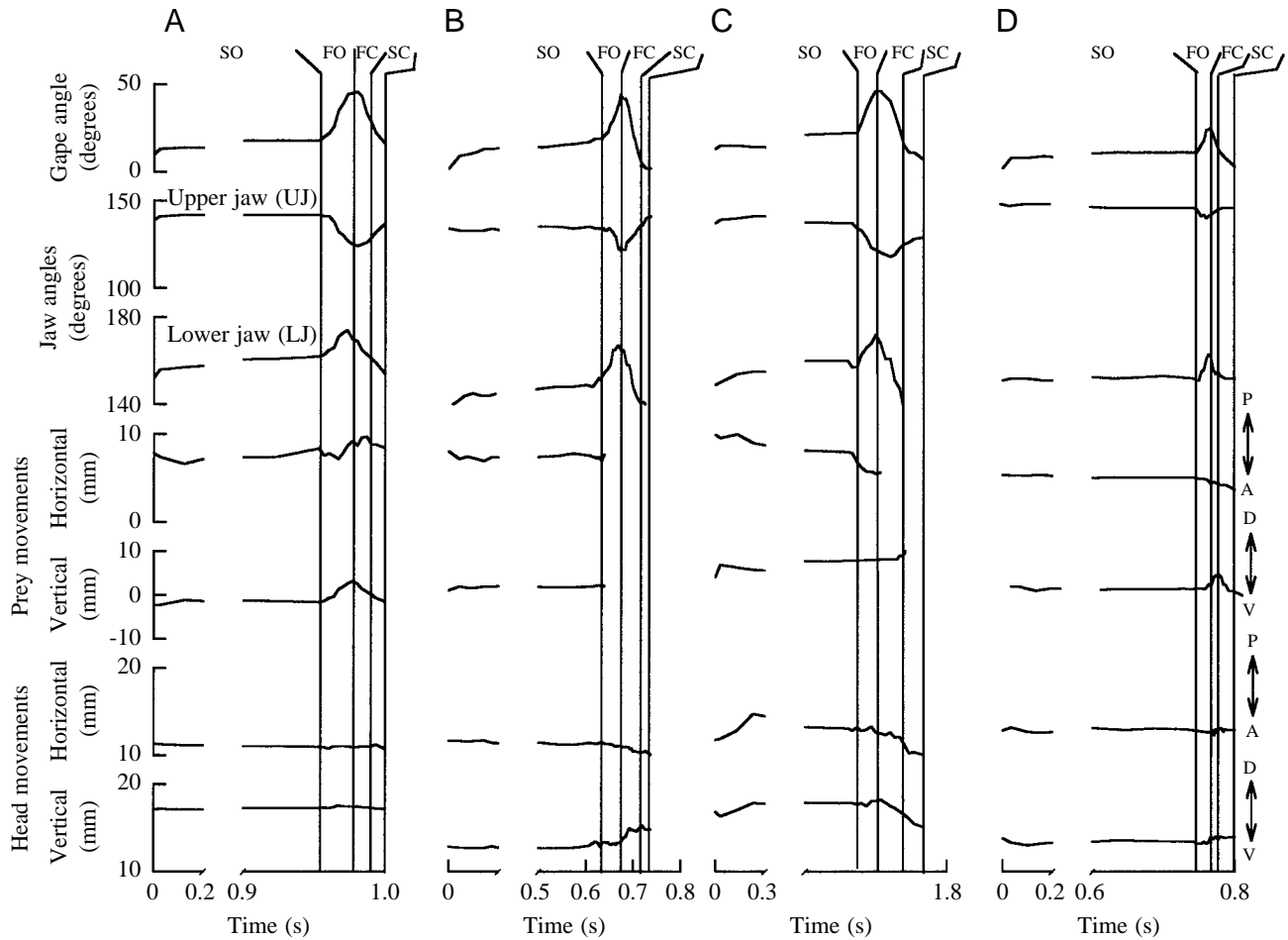
Fig. 4. Kinematic profiles of cricket (A,C) and mealworm (B,D) reduction and transport by *Phelsuma madagascariensis*. Antero-posterior (A–P) and dorso-ventral (D–V) movements of the prey and the head are illustrated in relation to gape and jaw angles. FC, fast closing phase; FO, fast opening phase; SC, slow closing phase; SO, slow opening phases I and II.

Maximal gape angles were 32° for mealworms and approximately 40° for crickets. Changes in gape angle were due to lower jaw depression and upper jaw elevation (Fig. 4). The mean times of lower jaw depression (MLJA) and of maximal upper jaw elevation (MUJA) were similar for both prey items (Table 2). After the FC stage, the gape angle of the next cycle began to increase almost immediately. This increase corresponded to SOI of this next cycle. Prey displacements within the jaws were produced by tongue-mediated displacements (Fig. 5) as suggested by simultaneous tongue and prey displacements. The tongue moved anteriorly at the end of SOII or the beginning of FO as shown by the displacement of the marker in the tongue. During anterior intra-buccal displacement, the tongue marker elevated slightly. During the FO stage, the tongue suddenly retracted. The increase in the vertical distance between the tongue and the lower jaw at the beginning of the retraction of the tongue corresponds to the period when the tongue bulged at the beginning of its retraction; the tongue then moved downwards (Fig. 5). Horizontal and vertical movements of the tongue resulted in slight movements of the prey as it was ground by

the teeth (Fig. 4). For each reduction cycle, the profiles of the tongue and prey displacements were similar. The mean vertical prey displacements (between 2.5 and 2.3 mm) within the buccal cavity were similar for both food types, while horizontal displacement was larger for the mealworm. Vertical and horizontal displacements of the head were rather variable between cycles and never exceeded 1.6 mm.

Transport

Transport cycles with both prey types involved slow opening (SO), fast opening (FO) and fast closing (FC) stages (Fig. 4). In contrast to the majority of reduction cycles, no slow closing stage was observed at the end of the gape cycle. The SO stage was divided in a short SOI (Table 2) and a long and variable SOII (coefficient of variation for crickets, 61 %; for mealworms, 77 %). The mean duration of the SO stage was 88 % of the mean total duration of the cycle for the cricket and 92 % for the mealworm. The mean durations of the FO and FC stages represented 4–5 % and 5–6 % of the mean total duration of the gape cycle respectively (Table 2).

Mean peak gape angle for crickets was approximately 40°,

Table 1. *Statistical variables of the gape cycle during cricket capture and transport behaviour by* Phelsuma madagascariensis *and* Oplurus cuvieri

| Variable | P. madagascariensis (Scleroglossa) | | O. cuvieri (Iguania) | |
	Capture (N=10)	Transport (N=28)	Capture* (N=10)	Transport‡ (N=40)
GA (degrees)	39.30±5.11	39.78±5.06	33.10±5.11	31.60±9.53
MGA (s)	0.14±0.04	0.77±0.40	0.45±0.07	0.16±0.11
MLGA (s)	0.14±0.04	0.77±0.40	0.40±0.08	0.21±0.11
TC (s)	0.18±0.06	0.82±0.39	0.50±0.07	0.31±0.13
SOI+SOII (s)		0.72±0.29	0.42±0.09	0.18±0.10
FO (s)	0.03±0.01	0.04±0.02	0.04±0.01	0.06±0.04
FC (s)	0.03±0.01	0.05±0.02	0.04±0.01	0.07±0.04

Values are means ± S.D.

*Capture cycles included the seven cycles studied by Delheusy and Bels (1992).

‡Data from Delheusy and Bels (1992).

FC, fast closing stage; FO, fast opening stage; GA, maximal gape; MGA, time of maximal gape; MLJA, time of maximal depression of the lower jaws; SOI, slow opening stage I; SOII, slow opening stage II; TC, total duration of the gape cycle.

tongue followed an intra-buccal anterior–posterior cyclic displacement, as shown by the lead marker placed within the mid-tongue. The tongue began its retraction at the end of SOII or the beginning of FO, and the prey moved posteriorly during the sudden posterior displacement of the tongue marker. Then, the tongue moved slowly forwards during SOI and SOII of the following cycle to be positioned anteriorly before retraction. The prey remained in almost the same position as the tongue moved slightly forwards during the SO stage (SOI and SOII) and followed the tongue displacement (Figs 4, 5). The action of the tongue resulted in a 'step-by-step' posterior movement of the prey towards the pharynx (Fig. 5). The amplitude of this posterior displacement of the prey was variable from one cycle to another (Fig. 5; Table 2). The coefficient of variation for crickets was 44.8 % and that for mealworms was 65.0 %. The amplitude of posterior displacement of cricket and mealworm prey were different, as determined from X-ray images. Posterior movement of mealworms decreased linearly from the first to the last transport cycle, whereas movement of crickets, which quickly fill the pharyngeal cavity, was rather similar during the three first cycles and then decreased drastically. Vertical and horizontal displacements of the head varied between 1.5 and 0.8 mm. As in reduction cycles, these movements were negligible and had no effect on prey displacement because we were unable to find any correlation between these movements and posterior displacements of the prey.

Fig. 6 shows individual variations in the gape cycle for four *P. madagascariensis.*

whereas the mean value for mealworms was only 28°. Changes in gape angle were caused by lower jaw depression and upper jaw elevation. The amplitude of lower jaw depression LGA was more than twice that of upper jaw elevation UJA (Table 2). During each transport cycle, the

Table 2. *Summary statistics for 14 kinematic variables describing three feeding phases in* Phelsuma madagascariensis *eating crickets and mealworms*

| Variable | Cricket | | | Mealworm | | |
	Reduction (N=28)	Transport (N=28)	Licking (N=28)	Reduction (N=28)	Transport (N=28)	Licking (N=28)
GA (degrees)	39.53±6.75	39.78±5.06	9.78±3.06	32.07±6.72	27.92±4.23	10.79±4.49
LJA (degrees)	26.79±4.80	27.63±4.06	8.26±2.60	21.79±6.15	20.85±5.21	7.93±3.16
UJA (degrees)	12.82±4.14	11.78±4056	1.52±0.80	10.29±2.42	8.85±2.20	2.86±1.63
MGA (s)	1.15±0.65	0.77±0.40	0.15±0.10	1.23±0.77	0.72±0.21	0.20±0.13
MLGA (s)	1.15±0.65	0.77±0.40	0.15±0.11	1.18±0.80	0.72±0.21	0.12±0.04
MUJA (s)	1.15±0.64	0.77±0.40	0.15±0.10	1.19±0.80	0.72±0.21	0.12±0.04
TC (s)	1.18±0.65	0.82±0.39	0.45±0.12	1.23±0.79	0.76±0.21	0.31±0.18
SOI (s)	0.03±0.01	0.06±0.04		0.08±0.04	0.08±0.06	
SOII (s)	1.08±0.66	0.68±0.41		1.07±0.82	0.62±0.18	
FO (s)	0.03±0.01	0.04±0.02		0.03±0.01	0.03±0.01	
FC (s)	0.03±0.01	0.05±0.02		0.05±0.01	0.04±0.01	
OPENING (s)			0.15±0.10			0.12±0.04
PLAT (s)			0.21±0.05			0.16±0.07
CLOSING (s)			0.09±0.04			0.10±0.05

Values are means ± S.D.

CLOSING, closing stage of the gape cycle (licking); FC, fast closing stage; FO, fast opening stage; GA, maximal gape; LJA, maximal depression of the lower jaws; MGA, time of maximal gape; MLJA, time of maximal depression of the lower jaws; MUJA, time of maximal elevation of the upper jaws; OPENING, opening stage of the gape (licking cycle); PLAT, 'plateau' between opening and closing stages (licking); SOI, slow opening stage I; SOII, slow opening stage II; TC, total duration of the gape cycle; UJA, maximal elevation of the upper jaws.
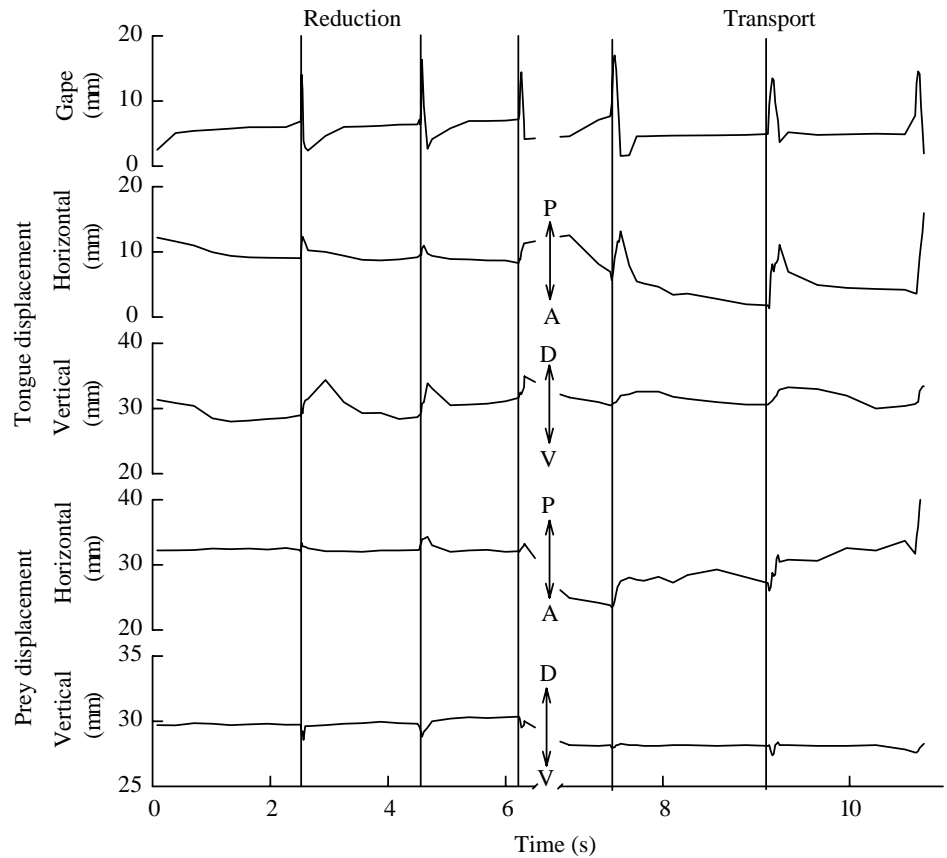
Fig. 5. Kinematic profiles of three successive reduction and transport cycles by *Phelsuma madagascariensis* obtained from X-ray films during a sequence of intra-oral manipulation of a cricket. A–P, antero-posterior movement; D–V, dorso-ventral movement.

Licking

The licking cycle consisted of a protraction of the tongue out of the mouth followed by wrapping of the tongue around the lower jaw or the upper jaw before retraction. Tongue movement was highly variable, and we did not observe any relationship between its amplitude or its direction with prey type. Gape increased only slightly during licking cycles (Table 2), and the head remained almost stationary during each cycle. Gape profiles were rather different from capture, reduction and transport cycles because they were characterised by the presence of a 'plateau' of approximately 20 ms between opening (approximately 13 ms) and closing (approximately 10 ms).

Effects of phase and prey
Capture and intra-oral processing of crickets

Significant effects of capture, reduction and transport phases were observed on kinematic variables depicting the durations of the stages of the gape cycle (TC, FO, FC) ($P<0.0045$) (Table 3). The *post-hoc* Newman–Keuls test separates capture from reduction plus transport for gape angle (GA), time to maximal gape angle (MGA), time to maximal lower jaw depression (MLGA), the total duration of the gape cycle (TC) and FO (percentage) and FC (duration and percentage). Comparison of means shows that the maximal gape angle during capture ($49.0\pm6.7\,°$) is significantly greater than during reduction ($39.5\pm6.8\,°$) and during transport

($39.8\pm5.1\,°$) (Table 2). Time variables (MGA, MLGA, TC and the durations of the gape stages) were signifcantly shorter for capture cycles.

Table 3. *Results of a three-way analysis of variance contrasting kinematic variables from capture, reduction, transport and licking cycles in* Phelsuma madagascariensis

Variable	Phase d.f.=2,6	Individual d.f.=3,108	Interaction d.f.=6,108	Post-hoc Newman–Keuls test results for phase
GA (degrees)	6.2*	6.6**	1.9	C; R—T
MGA (s)	6.6*	8.1**	1.7	C; R—T
MLGA (s)	5.4*	7.5**	1.9	C; R—T
TC (s)	22.7**	1.9	4.9*	C; R—T
FO (s)	111.6**	50.0**	3.1*	C—R; R—T
FC (s)	23.9**	193.2**	0.5	C; R—T
FO (%)	549.1**	3.1*	1.4	C; R—T
FC (%)	294.8**	0.5	2.9*	C; R—T

C, capture; R, reduction; T, transport.
Phases belonging to same group are connected by a line.
*$P<0.05$; **$P<0.006$.

FC, fast closing stage; FO, fast opening stage; GA, maximal gape; MGA, time of maximal gape; MLJA, time of maximal depression of the lower jaws; SOI, slow opening stage I; SOII, slow opening stage II; TC, total duration of the gape cycle.
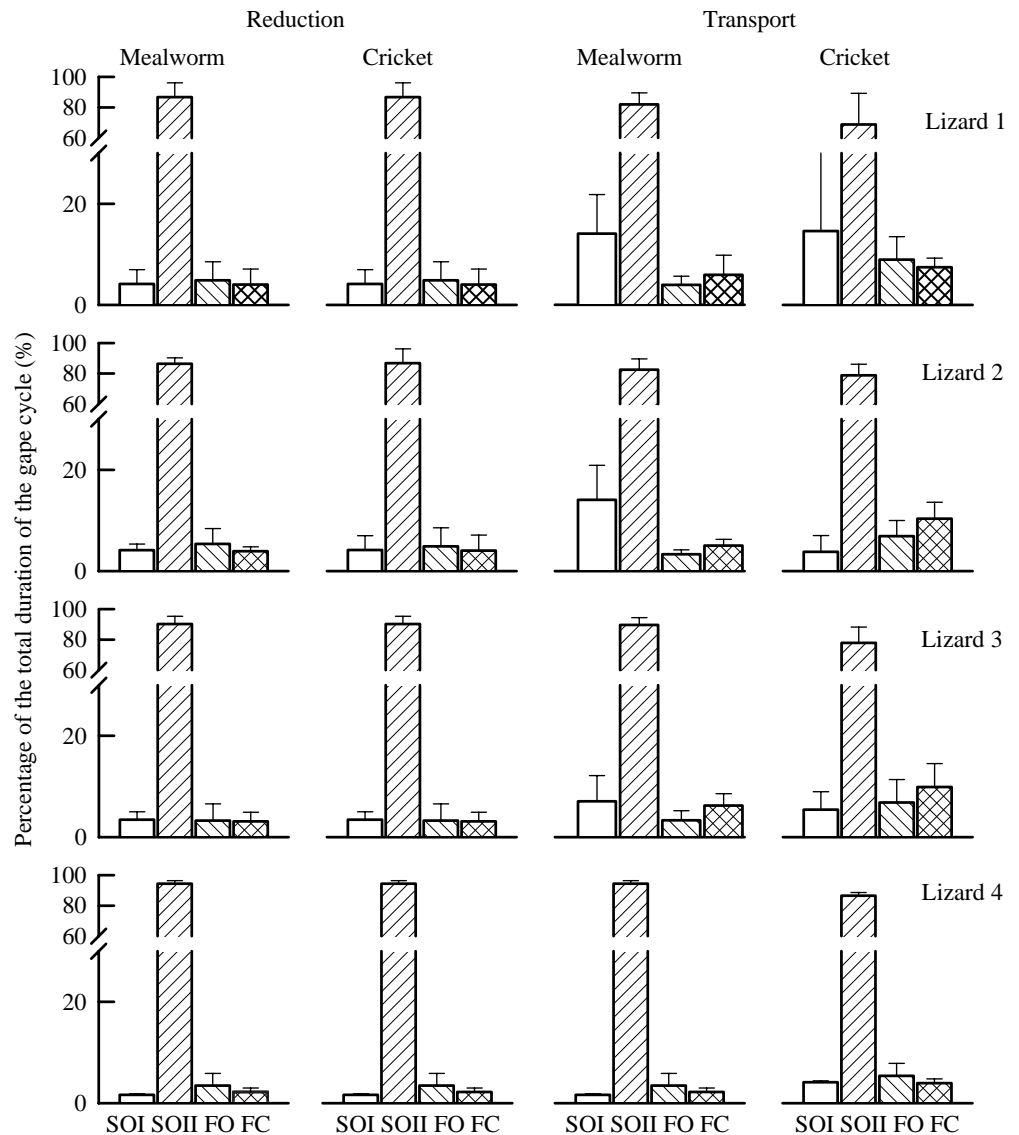
Fig. 6. Individual variation in the duration of the gape stages for four *Phelsuma madagascariensis* (percentage of the total duration of gape cycle). Each column corresponds to the mean (+ S.D.) percentage of the four stages of the gape. Different stages are represented by different shading. FC, fast closing phase; FO, fast opening phase; SOI, slow opening phase I; SOII, slow opening phase II.

Intra-oral processing of crickets and mealworms

In the first three-way ANOVA comparing the effects of phase (reduction, transport and licking), prey (crickets and mealworms) and individual (four lizards), seven variables (GA, UJA, MGA, MLGA, MUJA, TC and SOII) differed significantly among phases at $P \leq 0.05$ (Table 4), four of these (MGA, MLGA, MULA and TC) at $P \leq 0.0045$ (Bonferroni correction). At $P \leq 0.0045$, prey type had a significant effect on two variables, GA and LJA (d.f.=1,3). Individual had a significant effect ($P \leq 0.0045$) on all variables except LJA ($P \leq 0.05$) (Table 4). The following *post-hoc* tests showed that the licking phase was always distinct from a group formed by the reduction and transport phases for the seven variables influenced significantly by phase at $P \leq 0.0045$.

In the second three-way ANOVA we compared reduction and transport phases only. Although no variables were significantly influenced by phase at $P \leq 0.0045$, the individual effect remained significant for four variables at $P \leq 0.0045$

(GA, UJA, SOII and TC). In this ANOVA, the prey-type effect was also observed for two variables (GA and LJA). Two groups of two lizards were defined by the *post-hoc* tests. Within each group, six kinematic variables were significantly different among phases at $P \leq 0.0045$ (UJA, MGA, MLGA, MUJA, TC and SOII). Gape amplitude (GA, LJA) and SOI (s) were significantly influenced by prey type in both groups (Table 5).

Comparison between O. cuveri and P. madagascariensis

Table 1 shows a comparison of seven common variables of the gape cycle between capture and transport phases for a representative iguanid (*O. cuveri*) and a representative gekkonid (*P. madagascariensis*). In the principal components analysis of capture and transport kinematics based on these data, the axis PC1 accounts for 63 % and PC2 for 18 % of the variation of the set of data (Fig. 7). Variables TC and MGA, the related variables MLJA and MUJA, and SOII have

Table 4. *Results of a three-way analysis of variance contrasting kinematic variables from reduction, transport and licking cycles in* Phelsuma madagascariensis

| Variable | Phase (Ph) d.f.=2,6 | Prey type (Pr) d.f.=1,3 | Individual (In) d.f.=3,96 | First-order interactions | | | Second-order interaction |
				Ph×Pr d.f.=2,6	Ph×In d.f.=6,6	Pr×In d.f.=3,6	Ph×Pr×In d.f.=6,96
GA (degrees)	6.4*	151.1**	16.3**	7.1*	3.8*	7.1*	4.2**
LJA (degrees)	0.1	58.8**	3.4*	1.7	4.4*	7.8*	6.6**
UJA (degrees)	8.1*	30.6*	16.9**	0	21.1*	1.8	1.1
MGA (s)	24.2**	0.1	9.5**	0.6	2.6	2.8*	1.9
MLGA (s)	23.0**	0	10.5**	0.3	3.3*	2.9*	2.5*
MUJA (s)	22.8**	0.1	10.4**	0.3	3.3*	2.9*	2.5*
TC (s)	21.5**	10.2*	10.1**	0.5	3.3*	2.4*	2
SOI (s)	0.3	20.9*	5.6**	0.6	5.6*	3.2*	0.7
SOII (s)	6.4*	0.1	12.8**	0.1	2	3.7*	2.5*
FO (s)	2.2	29.3*	10.8**	9.1*	5.6*	1.4	1.6
FC (s)	4.9	2.7	16.7**	76.7**	1.4	2.4	10.3**

In, individuals; Ph, phase (reduction, transport, licking); Pr, prey type (mealworm or cricket).
*$P<0.05$; **$P<0.0045$.
FC, fast closing stage; FO, fast opening stage; GA, maximal gape; LJA, maximal depression of the lower jaws; MGA, time of maximal gape; MLJA, time of maximal depression of the lower jaws; MUJA, time of maximal elevation of the upper jaws; SOI, slow opening stage I; SOII, slow opening stage II; TC, total duration of the gape cycle; UJA, maximal elevation of the upper jaws.

considerable loading on PC1 (Table 6). PC1 distinguishes most of the cycles (capture and transport) of the iguanid *O. cuvieri* from cycles (capture and transport) of the gekkonid *P. madagascariensis*. There is only a small region of overlap between the transport cycles of the iguanid and the gekkonid. Capture cycles from the two species show complete separation along PC1. Prey capture and transport in *O. cuvieri* are very similar, as suggested previously by Delheusy and Bels (1992).

Discussion

The data for *P. madagascariensis* described in this study (i) compare the feeding phases within the Gekkota and (ii) test the effects of prey characteristics on three feeding phases in comparison with previous studies in iguanians and other scleroglossans. They also permit us to discuss the evolutionary transformations of tetrapod feeding models (Bramble and Wake, 1985; Reilly and Lauder, 1990) and the plesiomorphic characters of feeding suggested for

Table 5. *Results of a two-way analysis of variance (ANOVA) contrasting kinematic variables from reduction and transport in the two groups of lizards detected by the Newman–Keuls analysis (tested factor: individual) following the three-way ANOVA contrasting kinematic variables from reduction and transport cycles in* Phelsuma madagascariensis

| Variable | Group 1 | | | Group 2 | | |
	Phase d.f.=1,24	Prey type d.f.=1,24	Interaction d.f.=1,24	Phase d.f.=1,24	Prey type d.f.=1,24	Interaction d.f.=1,24
GA (degrees)	3.1	10.4**	9.8**	1.2	128.9**	0.2
LJA (degrees)	0.3	12.2**	11.1**	0.3	35.9**	3.9*
UJA (degrees)	15.5**	0.2	0.3	0.2	3.5	0.1
MGA (s)	15.4**	0.8	1.9	17.6**	0.3	2.1
MLGA (s)	24.3**	3.2	4.8*	17.2**	0.4	2.3
MUJA (s)	14.3**	3.4	5.1*	17.1**	0.5	2.3
TC (s)	13.1**	2.3	2.7	17.3**	0.4	2.3
SOI (s)	0.1	12.9**	13.0**	0.1	15.1**	0.2
SOII (s)	18.4**	0.2	2.2	13.6**	4.5*	5.5*
FO (s)	0.1	1.2	2.9	3.5	0.5	0.3
FC (s)	0.9	0.1	4.9*	2	1.6	5.8*

*$P<0.05$; **$P<0.0045$.
FC, fast closing stage; FO, fast opening stage; GA, maximal gape; LJA, maximal depression of the lower jaws; MGA, time of maximal gape; MLJA, time of maximal depression of the lower jaws; MUJA, time of maximal elevation of the upper jaws; SOI, slow opening stage I; SOII, slow opening stage II; TC, total duration of the gape cycle; UJA, maximal elevation of the upper jaws.

Table 6. *Factor loading of the eleven variables used in the comparative analysis for the two principal components that explain the most variance (PC1 and PC2)*

Variable	PC1 (63.3%)	PC2 (18.1%)
GA (degrees)	0.31	−0.35
LJA (degrees)	0.3	−0.33
UJA (degrees)	0.28	−0.31
MGA (s)	0.34	0.28
MLGA (s)	0.35	0.27
MUJA (s)	0.35	0.27
TC (s)	0.32	0.35
SOI (s)	−0.18	0.24
SOII (s)	0.35	0.25
FO (s)	0.23	−0.36
FC (s)	−0.24	0.26

FC, fast closing stage; FO, fast opening stage; GA, maximal gape; LJA, maximal depression of the lower jaws; MGA, time of maximal gape; MLJA, time of maximal depression of the lower jaws; MUJA, time of maximal elevation of the upper jaws; SOI, slow opening stage I; SOII, slow opening stage II; TC, total duration of the gape cycle; UJA, maximal elevation of the upper jaws.

Fig. 7. Principal components analysis (PC1 *versus* PC2) of cricket capture and transport in *Phelsuma madagascariensis* and *Oplurus cuvieri* based on seven kinematic variables. Each symbol corresponds to one feeding cycle from all four individuals of each species. Factor loadings for each variable are presented in Table 6.

Amniota by Lauder and Gillis (1997) in terminal groups of squamates.

Prey processing in lizards

On the basis of the sudden changes in the rate of increase in gape angle, jaw opening is divided into slow (SO) and fast (FO) stages in iguanians, and slow opening is often divided in SOI and SOII stages (Bels and Baltus, 1989; Schwenk and Bell, 1988; Schwenk and Throckmorton, 1989; Bell, 1990; Bels, 1990; Kraklau, 1991; Wainwright et al., 1991; Bels and Delheusy, 1992; Wainwright and Bennett, 1992; Herrel et al., 1995). Profiles of capture by *P. madagascariensis* (Fig. 3) show no marked modifications in the increase of the gape angle as previously reported for other scleroglossans (Frazzetta, 1983; Bels and Goosse, 1990; Goosse and Bels, 1992a; Smith, 1986; Urbani and Bels, 1995). Consequently, the total duration of the gape cycle and the related time to reach maximum gape are at least twice as long in iguanians as in scleroglossans, even though the movement is of similar amplitude (maximum gape angle is approximately 30° in representative species). The durations of the FO (approximately 40 ms) and FC (approximately 40 ms) stages are approximately the same (Table 7). The differences in gape between Gekkota and Scleroglossa (Scincomorpha and Anguimorpha) compared with Iguania suggest different adaptive strategies during prey capture. In essence, the presence of the SO stage of capture in iguanians is related to the positioning the tongue at the tip of the jaws before protraction out of the buccal cavity towards the prey. As suggested by Schwenk and Throckmorton (1989), this protrusion of the tongue can be modulated in response to sensory feedback (e.g. visual and olfactory) except in the Chamaeleontidae. However, we suggest that this modulation is
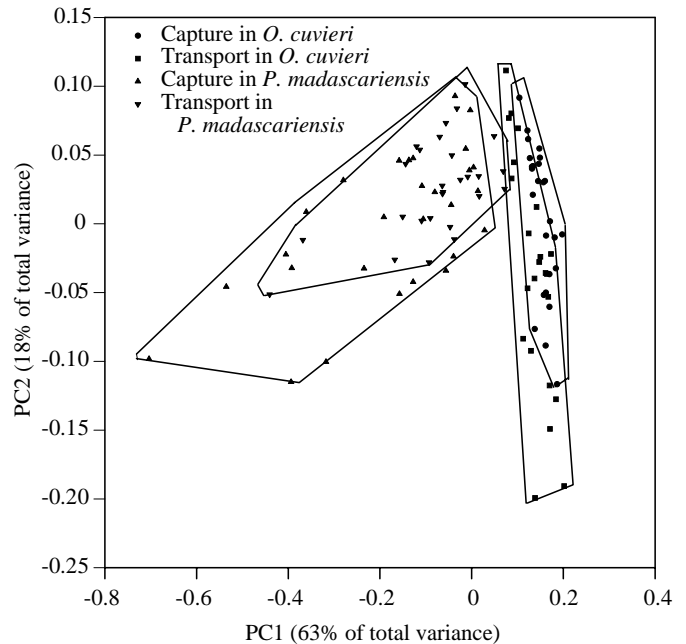
probably limited to the period of protraction of the tongue within the buccal cavity to the tips of the jaw apparatus during the SO stage. Once the FO stage has been initiated, the protruding tongue is aimed towards the prey. This SO stage may be useful for accurate tongue protrusion in association with sit-and-wait (ambush) behaviour, which is recognized as the basic foraging mode in Iguania by lizard ecologists (Cooper, 1994).

In a majority of scleroglossans, the tongue is not used to catch prey. During jaw prehension, it may be more advantageous to have a rapid continuous increase in gape, represented by the FO stage, while the advancing body causes the jaws to close around the prey. Since the tongue is used for pinning the prey to the substratum (e.g. in the Cordylidae) and possibly briefly for preventing any defence or escape response of the prey, a rapid increase in gape involving simply the FO stage is also advantageous (Urbani and Bels, 1995). During the evolution of squamates, jaw prehension has probably been associated with active foragers such as Scleroglossa because these predatory lizards are able to catch prey very rapidly without targeting the prey with the tongue. Many Gekkota are known to be ambush foragers. This mode of capture is probably derived from actively foraging ancestral geckos (Cooper, 1994). Under this hypothesis, the arboreal diurnal *P. madagascariensis* displays conserved jaw prehension. The locomotor abilities of these lizards (e.g. the presence of subdigital lamellae) permit gekkos to approach their prey slowly before catching it rapidly. This technique is probably

Table 7. *Comparative data for prey capture by two sister groups of lizards (Iguania and Scleroglossa) reported in the literature*

Variable	Range		References
	Scleroglossa	Iguania	
Total duration of the gape cycle (ms)	35–85[1], 213[2]	174–500[3], 949	Bels (1990), Kraklau (1991), Wainwright et al. (1991), Delheusy and Bels (1992), Urbani and Bels (1995), Herrel et al. (1995)
Duration of the slow opening stage (ms) (SOI + SOII)		65, 265–420	Bels (1990), Kraklau (1991), Wainwright et al. (1991), Delheusy and Bels (1992), Herrel et al. (1997)
Duration of the fast opening stage (ms)	19–48	38–40	Bels (1990), Kraklau (1991), Wainwright et al. (1991), Delheusy and Bels (1992), Urbani and Bels (1995), Herrel et al. (1995)
Duration of closing			Bels (1990), Kraklau (1991), Wainwright et al. (1991), Delheusy and Bels (1992), Urbani and Bels (1995), Herrel et al. (1995)
Fast closing (ms)	16–48	32–40	
Fast + slow closing (ms)		68–80	
Time to maximum gape angle (ms)	19–48	300–450, 870	Bels (1990), Kraklau (1991), Wainwright et al. (1991), Delheusy and Bels (1992), Urbani and Bels (1995), Herrel et al. (1995)
Time to tongue–prey contact (ms)		170–250	Bels (1990), Kraklau (1991), Wainwright et al. (1991), Delheusy and Bels (1992), Urbani and Bels (1995), Herrel et al. (1995)
Maximum gape angle (degrees)	16–30	23–42	Bels (1990), Kraklau (1991), Wainwright et al. (1991), Delheusy and Bels (1992), Urbani and Bels (1995), Herrel et al. (1995)

[1]Jaw prehension, [2]tongue pinning, [3]lingual prehension.

efficient enough for gekkos to acquire sufficient energy by catching moving prey and liberates the tongue from food capture. The tongue may be used to gain energy from other food sources (e.g. juices of fruits) and is also used for other behavioural activities (e.g. eye cleaning).

Comparison of intraoral processing and swallowing in lizards

The results of this study confirm previous reports of the quantitative kinematics of prey reduction and transport in Scincomorpha (Goosse and Bels, 1992a; Urbani and Bels, 1995): (i) mastication and transport cycles are organized into successive phases; (ii) jaw cycles are divided into SO, FO, FC and SC stages (Fig. 4); and (iii) profiles of reduction and transport cycles are kinematically similar (Figs 4, 5), although these cycles are influenced by the fixed effect of phase in the two groups of lizards compared here (Table 5).

The division of intraoral process into phases has been reported not only in scleroglossans but also in all iguanians (Smith, 1984; Bels and Baltus, 1989; Delheusy and Bels, 1992; So et al., 1992) and *Sphenodon punctatus* (Gorniak et al., 1982). However, Herrel et al. (1996) were not able to separate clearly reduction and transport phases during the intraoral processing of food in *Agama stellio*, although Kraklau (1991) noted that chewing (reduction) cycles differ significantly from transport cycles in another agamid (*A. agama*). It is now known that reduction cycles (crushing cycles in *A. stellio*: Herrel et al., 1996, 1997) occurring before any food transport derive from transport cycles, as suggested from kinematic data

(Delheusy and Bels, 1994; Urbani and Bels, 1995) and electromyographic data (Herrel et al., 1997). This sequential organization was not observed in terrestrial feeding in *Terrapene carolina* reducing food (e.g. mealworms) during transport (Bels et al., 1997). It is possible that the sequential organization of oral processing is a novel feature of the feeding mechanism in amniotes (Lauder and Gillis, 1997). But it is not present in terrestrial turtles. Consequently, this feature could be present at the base of the amniote radiation and lost in terrestrial turtles. Further studies on terrestrial feeding in turtles remain to be made to test this hypothesis.

In the reduction and transport cycles of *P. madagascariensis*, the tongue and jaws follow the same basic profiles (Figs 4, 5) as in the previously studied gekkotan *Eublepharis macularius* (Delheusy et al., 1994). These profiles are also similar to those described in other scleroglossans that have tongues of different shape (Urbani and Bels, 1995). They are also similar to kinematic profiles of iguanians with a fleshy tongue, indicating that, in all lizards, feeding cycles during intraoral reduction and transport are probably controlled by similar sequential muscular contractions according to the suggestions of Bels and Baltus (1989) and Delheusy and Bels (1992) and recent electromyographic data presented by Herrel et al. (1997).

During both phases of intraoral processing, the tongue of *P. madagascariensis* plays a major role, mainly acting in manipulation of food, as in other lizards (Bels and Goosse, 1989; Delheusy and Bels, 1992; Goosse and Bels, 1992a; Bels

et al., 1994; Delheusy et al., 1994; Herrel et al., 1996, 1997). The retraction of the tongue occurs towards the end of the SO stage or the beginning of the FO stage, as in *O. cuvieri* (Delheusy and Bels, 1992), resulting in posterior displacements of the prey into the buccal cavity. The reduction and transport phases do not involve elevation of the head (Figs 4, 5). In contrast to previous studies of iguanians (Schwenk and Throckmorton, 1989; Delheusy and Bels, 1992), head movements do not contribute to prey displacements during either phase. Consequently, posterior movements of the prey into the buccal cavity are produced by tongue retraction only.

The SO (SOI+SOII) stage during reduction and transport in *P. madagascariensis* (although variable, coefficient of variation of approximately 50–60 %, see Table 2) is rather longer than that previously reported for several iguanians such as *O. cuvieri* (Tables 1, 2). It has been suggested that SOI may be (i) a reopening (i.e. a by-product of the strong contractions by adductor muscles) during the closing stage of the previous cycle in scleroglossans; and (ii) a jaw displacement resulting from active forward displacement of the tongue and connected hyoid within the buccal cavity in iguanians (Bels and Goosse, 1990; Bels et al., 1994, 1997). Recent data for *A. stellio* support the second suggestion. The protractor muscles of the hyoid apparatus and the external and internal protractors (m. verticalis) of the tongue contract during the SO stage, and the jaw openers (m. depressor mandibulae and m. depressor mandibulae accessorius) and craniocervical muscles become active at the end of the SO stage corresponding to the beginning of the FO stage (Herrel et al., 1997). In *P. madagascariensis*, the mean duration of the SOII stage was different among phases (Table 5). The duration of SOII was longer for reduction than for transport (Table 2). Because reduction follows immediately after capture, the prey is not yet dead and continues to attempt to escape by making movements of its head, legs and body (V. Delheusy and V. L. Bels, unpublished observations). In contrast, during transport, the prey is probably dead and does not move. Previous studies have shown that the tongue moves forwards under the prey during the SO stage (Bels et al., 1994). Modulation in this movement may result from efforts to deal with the prey attempting to escape during reduction and may explain the longer SOII. Furthermore, SOII (and consequently TC) was shorter during prey transport than during reduction (Tables 2, 5). The orientation of the prey along the long axis of the tongue may facilitate tongue movement under the prey and explain this difference between the reduction and transport phases.

As in iguanians, swallowing cycles in scleroglossans relate mainly to tongue movements. We did not succeed in recording any marked difference between intraoral transport and swallowing cycles in *P. madagascariensis*. In *Sphenodon punctatus*, classical swallowing cycles typically involve SO, FO, FC and SC/PS phases (PS is the power stroke of the SC phase) (Gorniak et al., 1982). In *Uromastix aegyptius* (Throckmorton, 1980) and *Agama stellio* (Herrel et al., 1996), swallowing cycles contain a rather long SO stage. This stage in *A. stellio* represents approximately 65 % of the total cycle, but only 20–46 % during intraoral transport (Herrel et al., 1996). In *Oplurus cuvieri*, Delheusy and Bels (1992) did not record any difference in the duration of the SO stage between intraoral transport and swallowing. In contrast, Herrel et al. (1997) have demonstrated considerable variation in the duration of muscle contractions of the swallowing phase in an agamid (e.g. intensity, duration, onset), suggesting that this feeding phase is variable not only among species but within species. In scleroglossans, except varanids (Smith, 1986), jaw and tongue actions also plays a major role during swallowing. In *P. madagascariensis*, we were unable to relate licking tongue cycles with any posterior movement of the prey towards the oesophagus. As in other scleroglossans (Smith, 1984, 1986; Goosse and Bels, 1992b; Urbani and Bels, 1995), swallowing is performed by tongue and jaw cycles at the end of the intraoral transport phase, resulting in posterior displacement of the prey through the buccal cavity. The licking cycles may also help regular and slow movement of the prey into the oesophagus (Smith, 1984; Delheusy and Bels, 1992).

Modulation of intraoral processing

As in several previous studies of feeding kinematics in squamates (Delheusy and Bels, 1992; So et al., 1992; Herrel et al., 1996, 1997), a number of kinematic variables of food manipulation were significantly different among prey types within categories of individuals (Tables 4, 5). The effects of prey characteristic (i.e. type, size, volume, hardness) are rather different among species, affecting not only the kinematics of the jaw and hyo-lingual apparatus but also the number of cycles per reduction and transport phase (Bels and Baltus, 1988). Urbani and Bels (1995) showed limited effects of prey type on kinematics in *Zonosaurus laticaudatus* (Cordylidae). According to Herrel et al. (1996), feedback from the prey within the buccal cavity may modulate the kinematic response during food manipulation. The range of modulation is probably strongly related to the structural properties of the feeding apparatus (i.e. musculature, volume of the buccal cavity, size of the teeth), explaining differences within species. In *P. madagascariensis*, the amplitude variables of the gape cycle (GA, LJA) were related to the characteristics of the prey, which are very different between crickets and mealworms. The size of the prey may be the main factor influencing these variables because they were always larger for the cricket during reduction and transport phases (Table 2). For reduction and transport cycles, the lizards can be divided into two categories. Within each category, prey type has similar effects on kinematic variables (Table 5), supporting the above hypothesis of modulation of kinematics by prey characteristics. Such individual variability has previously been reported for some variables in Chameleontidae (So et al., 1992) and the majority of Iguanidae (Delheusy and Bels, 1992; Herrel et al., 1997). For each animal, the spatiotemporal network that activates and coordinates the motor pattern may be strongly modulated by internal (i.e. stress, training experience, satiety level) and external (i.e. temperature, relative humidity) factors. For the

quantitative study based on high-speed cinematographic films, *P. madagascariensis* were not trained to catch prey in fixed conditions (i.e. on a table or in a small cage in front of the table) before filming, and they were filmed in their home vivarium at different times of day. Insects were gently presented moving slowly on the branch where the lizard sat as a typical sit-and-wait predator. Further studies on feeding in lizards should help to explain individual differences in feeding kinematics in relation to filming conditions.

Evolution of feeding in Squamata

Kinematically, transport cycles are almost separated, and separation between capture cycles is complete in *O. cuvieri* and *P. madagascariensis* along PC1, which accounted for 48 % of the total variance. This difference may be related to the shape and function of the tongue. In *O. cuvieri*, the tongue is fleshy and used mainly for prey capture. In *P. madagascariensis*, the non-fleshy tongue plays a major role in vomerolfaction, as suggested for all Gekkota. The tongue of Gekkota shows three of nine expected adaptations to vomerolfaction: high extensibility, modification of the intrinsic musculature to promote extensive protrusion, and a relatively smooth surface (Schwenk, 1993a,b). During food transport, a tongue such as this does not make the same contact with the prey as the fleshy, less extensible and mucous tongue of *O. cuvieri* (Delheusy et al., 1994). This difference in contact between the food within the buccal cavity and the tongue of the lizard may explain effects on kinematic variables. Concomitantly, the relationships between movements of the hyo-lingual and jaw apparatus are not greatly transformed among species, as suggested from the comparison of kinematic profiles (compare Figs 4, 5 in this paper with Figs 8, 9 in Delheusy and Bels, 1992).

Several features of the primitive generalized transport model of Bramble and Wake (1985) are recognizable in our data in *P. madagascariensis*, a squamate with a highly transformed tongue compared with that of the Iguania. The principal implications of this model are (i) that the gape angle is divided into five stages (SOI, SOII, FO, FC and SC/PS); (ii) that, during SOII, there is a slight depression of the lower jaw, and the upper jaw is stationary; (iii) that the upper jaw elevates during FO and depresses during FC; (iv) that hyoid/tongue retraction begins during FO; (v) that hyoid/tongue protraction occurs during the SC power stroke (SC/PS), SOI, SOII and the beginning of FO; and (vi) that the head is elevated at the end of FO and during FC (see Fig. 13-3 in Bramble and Wake, 1985). These authors speculate that the tongue moves anteriorly under the food during SOI, fits round the food during SOII, retracts during FO and FC, and reaches its maximal posterior position during SC/PS (Fig. 13-5 in Bramble and Wake, 1985). They also speculate that SOII increases for larger or heavier food items.

We found in *P. madagascariensis*, as in several other iguanians (Smith, 1984; Schwenk and Throckmorton, 1989), that the SOII stage occurs during transport cycles (Fig. 5). A majority of the characteristics of the Bramble and Wake (1985) model are supported by the data for iguanians (Smith, 1984; Schwenk and Throckmorton, 1989; Delheusy and Bels, 1992; So et al., 1992) and scleroglossans (Goosse and Bels, 1992a; this study). Modulations of this model (i.e. the absent or short SOII stage) could be related to the contact between the tongue and the food within the buccal cavity (Delheusy and Bels, 1992; Delheusy et al., 1994).

Schwenk and Throckmorton (1989) and Kraklau (1991) have compared the capture cycle of Iguania with the model of Bramble and Wake (1985). The capture cycle in scleroglossans is completely different because the SO stage is always absent during jaw prehension (Goosse and Bels, 1992a; this study). Because the tongue is not used for prey capture in scleroglossans, this SO stage is absent (Bels and Goosse, 1989; Goosse and Bels, 1992a; this study). This absence could be related to the optimization of capture, as discussed above.

Reilly and Lauder (1990) proposed two synapomorphic characters for all tetrapods (tongue-based intraoral prey transport, and a long preparatory phase prior to the FO stage) and five derived characters for all Amniota (an SO stage prior to the FO stage, gape increase mainly by depression of the lower jaw, a recovery stage compressed into the gape cycle, the presence of inertial feeding, and extensive intraoral food processing). The data for *P. madagascariensis* correspond most closely to the features of the model of Reilly and Lauder (1990). However, as in *O. cuvieri*, the tongue retracts at the end of the SOII stage or at the beginning of the FO stage and not always at the end of the SOII stage as proposed by Reilly and Lauder (1990). This discrepancy between our data and the model could simply be related to prey types and to the frictional relationship between prey characteristics and tongue displacements. For example, worms and crickets eaten by *Ambystoma tigrinum* may move easily through the buccal cavity because this cavity is large. The tongue is therefore not largely restricted in its anterior displacement and in its anteriormost position prior to retraction at the end of the SOII stage.

References

Bell, D. A. (1990). Kinematics of prey capture in the chameleon. *Zool. Jb. Anat.* **94**, 247–260.

Bels, V. L. (1990). Quantitative analysis of prey-capture kinematics in *Anolis equestris* (Reptilia: Iguanidae). *Can. J. Zool.* **68**, 2192–2198.

Bels, V. L. (1997). L'étonnante langue des lézards. *La Recherche* **290**, 62–67.

Bels, V. L. and Baltus, I. (1988). The influence of food items on the

feeding cycle in *Anolis equestris* (Reptilia: Iguanidae). *Copeia* **1988**, 479–481.

Bels, V. L. and Baltus, I. (1989). First analysis of feeding in *Anolis* lizards. In *Fortschritte der Zoologie/Progress in Zoology*, Band/vol. 35, *Trends in Vertebrate Morphology* (ed. H. Splechna and H. Hilgers), pp. 141–145. Stuttgart: Gustav Fisher Verlag.

Bels, V. L., Chardon, M. and Kardong, K. (1994). Biomechanics of the hyolingual system in Squamata. In *Biomechanics of Feeding in Vertebrates* (ed. V. Bels, M. Chardon and P. Vandewalle), pp. 197–240. Berlin: Springer-Verlag.

Bels, V. L., Davenport, J. and Delheusy, V. (1997). Kinematic analysis of the feeding behavior in the bow turtle *Terrapene carolina* (L.) (Reptilia: Emydidiae). *J. Exp. Zool.* **277**, 198–212.

Bels, V. L. and Delheusy, V. (1992). Kinematics of prey capture in iguanid lizards: comparison between *Anolis carolinensis* and *Oplurus cuvieri* (Oplurinae). *Belg. J. Zool.* **122**, 223–234.

Bels, V. L. and Goosse, V. (1989). A first report of relative movements within the hyoid apparatus during feeding in *Anolis equestris* (Reptilia: Iguanidae). *Experientia* **45**, 1088–1091.

Bels, V. L. and Goosse, V. (1990). Comparative kinematic analysis of prey capture in *Anolis carolinensis* (Iguania) and *Lacerta viridis* (Scleroglossa). *J. Exp. Zool.* **255**, 120–124.

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

Cooper, W. E., Jr (1994). Prey chemical discrimination, foraging mode and phylogeny. In *Lizard Ecology* (ed. L. J. Vitt and E. R. Pianka), pp. 95–116. New Jersey: Princeton University Press.

Cooper, W. E., Jr (1995a). Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Anim. Behav.* **50**, 973–985.

Cooper, W. E., Jr (1995b). Evolution and function of lingual shape in lizards, with emphasis on elongation, extensibility and chemical sampling. *J. Chem. Ecol.* **21**, 477–505.

Dial, B. E. and Schwenk, K. (1996). Olfaction and predator detection in *Coleonyx brevis* (Squamata: Eublepharidae), with comments on the functional significance of buccal pulsing in geckos. *J. Exp. Zool.* **276**, 415–424.

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

Delheusy, V. and Bels, V. L. (1994). Comportement agonistique du gecko géant diurne *P. madagascariensis madagascariensis grandis*. *Amphibia – Reptilia* **15**, 63–79.

Delheusy, V., Brillet, Ch. 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.

Delheusy, V., Toubeau, G. and Bels, V. L. (1994). Tongue structure and function in *Oplurus cuvieri* (Reptilia: Iguanidae). *Anat. Rec.* **238**, 263–276.

Estes, R., De Queiroz, K. and Gauthier, J. (1988). Phylogenetic relationships within Squamata. In *Phylogenetic Relationships in the Lizard Families* (ed. R. Estes and G. Pregill), pp. 119–281. Stanford: Stanford University Press.

Frazzetta, T. H. (1983). Adaptation and function of cranial kinesis in reptiles: a time–motion analysis of feeding in alligator lizards. In *Advances in Herpetology and Evolutionary Biology: Essays in Honor of E. E. Williams* (ed. A. G. J. Rhodin and K. Myata), pp.

222–244. Cambridge, MA: Museum of Comparative Zoology Publications.

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

Goosse, V. and Bels, V. L. (1992b). Tongue movements during chemosensory behavior in the European green lizard *Lacerta viridis*. *Can. J. Zool.* **70**, 1886–1896.

Gorniak, G. C., Rosenberg, H. I. and Gans, C. (1982). Mastication in the tuatara, *Sphenodon punctatus* (Reptilia: Rynchocephalia), structure and activity of motor system. *J. Morph.* **171**, 321–353.

Gove, D. (1979). A comparative study of snake and lizard tongue-flicking with an evolutionary hypothesis. *Z. Tierpsychol.* **51**, 58–76.

Greer, A. (1985). The relationships of the lizard genera *Anelytropsis* and *Dibamu*s. *J. Herpetol.* **19**, 116–156.

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., Cleuren, J. and De Vree, F. (1997). Quantitative analysis of jaw and hyolingual muscle activity during feeding in the lizard *Agama stellio*. *J. Exp. Biol.* **200**, 101–115.

Hiiemae, K. M. and Crompton, A. W. (1985). Mastication, food transport and swallowing. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 262–290. Cambridge, MA: Harvard University Press.

Iwasaki, S. (1990). Fine structure of the dorsal epithelium of the lizard *Gekko japonicus* (Lacertilia, Gekkonidae). *Am. J. Anat.* **187**, 12–20.

Kardong, K. V., Kiene, T. L. and Bels, V. L. (1997). Evolution of the trophic systems in squamates. *Neth. J. Zool.* **47**, 411–427.

Kiene, T. L., Kardong, K. V. and Bels, V. L. (1996). Evolution of lizard feeding systems: testing a model. *Am. Zool.* **36**, 440.

Kiene, T. L., Kardong, K. V. and Bels, V. L. (1999). Prey capture behavior in the blue-tongued skink*, Tiliqua scincoides*. *J. Herpetol.* **33**, 362–369.

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

Lauder, G. and Gillis, G. B. (1997). Origin of the amniote feeding mechanism: experimental analysis of outgroup clades. In *Amniotes Origins. Completing the Transition to Land* (ed. S. S. Sumida and K. L. M. Martin), pp. 169–206. New York: Academic Press.

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

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

Russell, A. P. (1977). The genera *Rhotropus* and *P. madagascariensis* (Reptilia: Gekkonidae) in Southern Africa: a case of convergence and a reconsideration of the biogeography of *P. madagascariensis*. *Zool. Africana* **12**, 393–408.

Schwenk, K. (1988). Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny. In *Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp* (ed. R. Estes and G. Pregill), pp. 569–598. Stanford: Stanford University Press.

Schwenk, K. (1993a). The evolution of chemoreception in squamate reptiles: a phylogenetic approach. *Brain Behav. Evol.* **41**, 124–137.

Schwenk, K. (1993b). Are geckos olfactory specialists? *J. Zool., Lond.* **229**, 289–302.

Schwenk, K. (1994). Comparative biology and the importance of cladistic classification: a case study from the sensory biology of squamate reptiles. *Biol. J. Linn Soc.* **52**, 69–82.

Schwenk, K. and Bell, D. A. (1988). A cryptic intermediate in the evolution of chameleon tongue projection. *Experientia* **44**, 697–700.

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

Smith, K. K. (1984). The use of the tongue and hyoid apparatus during feeding in lizards (*Ctenosaura similis* and *Tupinambis nigropunctatus*). *J. Zool., Lond.* **202**, 115–143.

Smith, K. K. (1986). Morphology and function of the tongue and hyoid apparatus in *Varanus* (Varanidae, Lacertilia). *J. Zool., Lond.* **187**, 261–287.

So, K.-K. J., Wainwright, P. C. and Bennett, A. F. (1992). Kinematics of prey processing in *Chamaeleo jacksonii*:

conservation of function with morphological specialization. *J. Zool., Lond.* **226**, 47–64.

Sokal, R. R. and Rohlf, F. J. (1995). *Biometry*. New York: W. H. Freeman & Co.

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

Toubeau, G. and Bels, V. L. (1994). Morphological and kinematic study of the tongue and buccal cavity in the lizard *Anguis fragilis* (Reptilia: Anguidae). *Anat. Rec.* **240**, 423–433.

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 Bennett, A. F. (1992). The mechanism of tongue projection. I. Electromyographic tests of functional hypotheses. *J. Exp. Biol.* **168**, 1–21.

Wainwright, P. C., Kraklau, D. M. and Bennett, A. F. (1991). Kinematics of tongue projection in *Chamaeleo oustaleti*. *J. Exp. Biol.* **159**, 109–133.