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Modulatory complexity of the feeding repertoire in scincid lizards

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Abstract The kinematics of jaws and tongue, and jaw muscle activity patterns were investigated in the omnivorous lizard *Tiliqua rugosa*, and the herbivorous *Corucia zebrata* (Scincidae) during feeding. Small metal markers were inserted into different parts of the skull, the jaws, and the tongue. Video and cineradiographic images were digitized and displacements of the head, jaws, and tongue were quantified. Additionally, muscle activity patterns were recorded, digitized and several variables were determined quantitatively. The effect of food type on the jaw and hyolingual movement patterns and the jaw muscle activity patterns was investigated for both species. The kinematic data indicate that distinct aspects of gape and tongue cycles are modulated in response to the food characteristics. Similarly, in both species, muscle activity patterns are altered in response to the type of food eaten. A comparison of kinematic and electromyographic patterns during intraoral transport cycles for both species shows that these can be related to food characteristics such as toughness and mobility. Differences between both species in the response to changes in food characteristics are minor. Clearly both species are able to fine tune the activation of the jaw muscles, resulting in the appropriate movement patterns for the type of food eaten.

Key words *Corucia zebrata* · *Tiliqua rugosa* · Electromyography · Kinematics · Food effects

Abbreviations *FC* fast closing phase · *FO* fast opening phase · *HTdispl* horizontal tongue displacement · *LJdepr* lower jaw depression · *SC* slow closing phase · *STD* standard deviation · *SO* slow opening phase · *UJelev* upper jaw elevation · *VTdispl* vertical tongue displacement

Introduction

Feeding is one of the vital functions in animals. Selective pressures on the form and functioning of the feeding apparatus are likely to be high and will, in theory, lead to an optimisation of the design of the system (Thompson 1917; Dullemijer 1974; Lauder 1996). In general, the feeding process can be broken down into several components such as the localisation, collection, digestion and assimilation of the food. After potential food sources are localized, the food must be broken down into digestible components by mastication. The function of this mastication is to increase the digestible area of the food by reducing the size of the particles, or by breaking open indigestible capsules. Still, in order to be efficient a certain increase of the workable surface area should involve minimal costs of energy and time (see Sibbing 1991a).

Biological materials, in general, are composite and heterogeneous, making it hard to predict their mechanical properties. However, four classes of food texture are generally accepted (Lucas 1979; Lucas and Luke 1984; Hiimae and Crompton 1985): hard-brittle, turgid, soft-tough, and tough-fibrous (see also Sibbing 1991a, b), each requiring a specific processing strategy. Tough materials for example, need a lot of mechanical work before fracture occurs as they are generally ductile and resist crack propagation. Similarly, fibrous materials are notch insensitive and cracks are readily absorbed at the matrix-fibre interface (Jeronimidis 1991; Sibbing 1991b). The processing strategy for such materials is to assure tooth penetration as this causes internal crack propagation. However, the capacity for deformation is limited by the size, shape and range of movement of the opposing teeth. To increase local stresses, a set of carefully aligned opposing blades that pass close to each other (i.e. a shearing bite) is presumably optimal (Lucas 1979, 1982; Lucas and Luke 1984; Hiimae and Crompton 1985; Sibbing 1991a, b).

As each food category puts its own specific demands on the feeding apparatus, food specialists are expected to

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show specialisations in the control and functioning of their feeding system. Omnivores, on the other hand, should show a large degree of flexibility in the control and movements of jaws and tongue during feeding.

The aims of the present study are (1) to examine the functional characteristics of the feeding system in scincid lizards, (2) to estimate the physical properties of food items belonging to different functional classes, and (3) to analyse the effects of these properties on the activation patterns and recruitment levels of the jaw muscles and the corresponding movements of the jaw and hyolingual apparatus during intraoral transport in two closely related species of lizards (*Tiliqua rugosa*, *Corucia zebrata*) with a different feeding ecology (omnivorous versus herbivorous). Although the omnivorous *T. rugosa* might not seem a good basis for comparison at first sight, it provides two most valuable extras: (1) as the two species are closely related the phylogenetic effects will be reduced (they share most of their "evolutionary history"), and (2) as it is an omnivore, a comparison based on the same food items is possible. On the basis of the data gathered, the hypothesis that herbivorous specialists show dietary adaptations in the functional properties of the feeding system, related to an extensive mechanical food processing, will be examined.

Materials and methods

Specimens

Five adult specimens (snout-vent length 29 ± 5.0 cm; mass 620 ± 120 g) of *T. rugosa* and two adult *C. zebrata* (snout-vent length 29 ± 0.5 cm; mass 620 ± 20 g) were used in the experiments. The *T. rugosa* specimens were collected in the vicinity of Perth, Western Australia, and provided for us by Dr. C. Gans; specimens of *C. zebrata* were obtained from a commercial dealer. The animals were kept in a glass vivarium on a 12-h light/dark cycle and were offered water and food consisting of a variety of fruits, and vegetables (*C. zebrata*) or fruit, baby mice, and grasshoppers (*T. rugosa*) ad libitum. The environmental temperature varied from 26°C during the day to 20°C at night; an incandescent bulb provided the animals with a basking place at a higher temperature ($35\text{--}40^\circ\text{C}$).

An additional two animals of each species were dissected and stained (Bock and Shear 1972) to characterize all jaw and hyolingual muscles. Drawings were made of all stages of the dissection using a Wild M3Z dissecting microscope with a camera lucida.

Food characteristics

As the aim of this study was to relate the feeding mechanics to the type of food eaten, the mechanical resistance of the food items used was estimated. Properties such as size and shape were controlled for when comparing different fruit types. In order to estimate food toughness, the lower jaw of one specimen of *C. zebrata* was removed and partially embedded in resin, leaving the tooththrows free. The hardened resin was then mounted onto a Kistler force transducer (type 9203, Kistler, Switzerland) connected to a Kistler charge amplifier (type 5058A, Kistler, Switzerland) and PC equipped with an electronic measuring board (PC-Scope T512, IMTEC, Germany). Next, food items were crushed by pushing the jaw onto the food item until structural failure occurred (indicated by a sudden drop in the force recordings). This procedure was then repeated for several pieces of the fruits used. During the recording

sessions food items (except for endive, mice, snails, and grasshoppers) were cut into cubes of the same size ($2 \times 2 \times 2$ cm); similar-sized cubes were used in the toughness recordings and an average toughness value was calculated. For newborn mice, nine previously killed specimens (overdose of Ketalar, 50 mg ml^{-1}) were used, and the toughness at the level of the craniocervical apparatus was determined (i.e. the resistance of the skull bones). For endive, similarly sized pieces (4×4 cm) of leaf from various areas (e.g. near the base, near the edges) were used. Snail hardness (i.e. mechanical resistance of the shell) was measured in a similar way for eight similar-sized *Helix aspersa* (width 34.85 ± 1.79 mm, height 20.16 ± 0.86 mm) using the lower jaw of a *T. rugosa*. For grasshoppers, the data from Herrel et al. (1996b) were used.

Cineradiographic and video recordings

During all recording sessions the animals were offered food items (fruits and vegetables) of a similar size and shape (see above). Cineradiography was accomplished with a Siemens Tridoros-Optimatic 880 x-ray apparatus equipped with a Sirecon-2 image intensifier. Feeding bouts were recorded in lateral view with an Arriflex 16-mm ST camera equipped with a 50-mm lens at a rate of 50 frames per second. Before cineradiography, small metal markers (see Fig. 1A) were inserted subcutaneously on the upper (1, 2) and lower (3, 4) jaws, at the base and the top of the quadrate (5, 6), in the tongue (7, 8), on the frontal and parietal bones (9, 10) and dorsally in the neck just below the skin (11) using a hypodermic needle. During the implantation of the radio-opaque markers, animals were anaesthetized by an intramuscular injection of Ketalar (100 mg kg^{-1} bodyweight). Placement of the markers was checked on dorsoventral and lateral x-rays.

Additional recordings of the feeding process were made using a conventional video system (Panasonic camera and Zoom lens). Video torches (2.4 kW; TRI-LITE, Cool Light, Hollywood, USA) provided the necessary illumination. In both the cineradiographic and the video recording sessions the animals were filmed in an acrylic cage ($40 \times 100 \times 30$ cm).

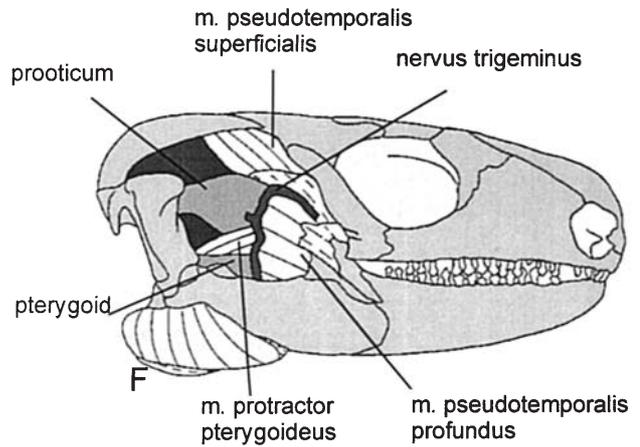
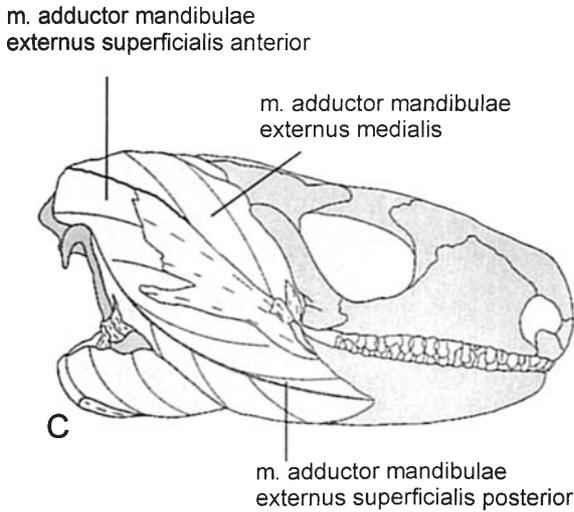
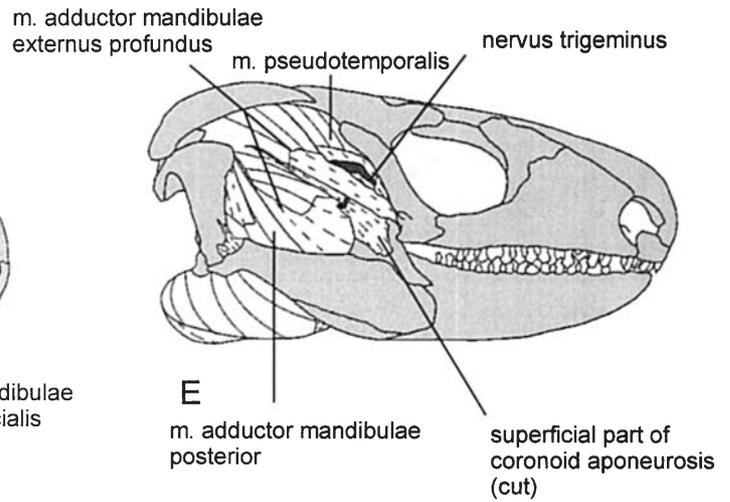
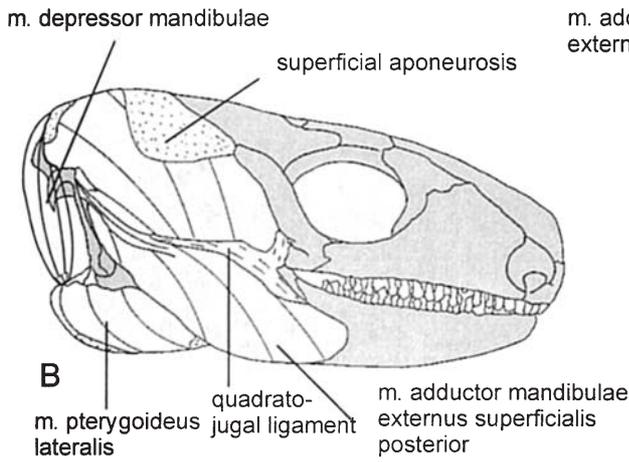
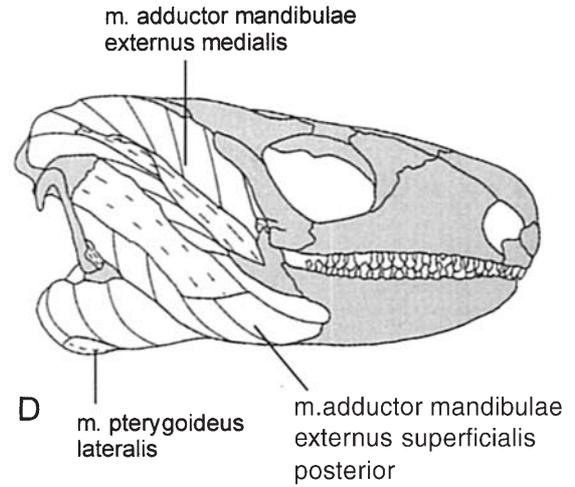
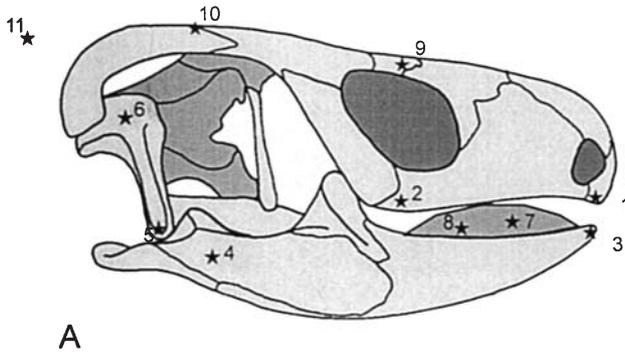
Cineradiographic analysis

Only feeding sequences in which the animals remained lateral with respect to the camera were analysed. Röntgen films were projected frame by frame onto a HIPAD-digitizer with a Vanguard projector. The horizontal (x) and vertical (y) coordinates were recorded for each marker in each frame. Video recordings were analysed by digitising seven clearly visible external markers (colour spots) using a NAC X-Y Coordinator. Here, too, horizontal and vertical coordinates were recorded for each external marker for each frame.

From the x - y coordinates of the markers several additional parameters were calculated for both cineradiographic and video recordings: the changes in gape (distance 1–4; angle subtended by the two lines 1–2 and 3–4), the vertical displacement of the upper and the lower jaw (changes in y -coordinates of points 1 and 4), the cranial elevation (angle subtended by line 1–2 and the horizontal) and the lower jaw depression (angle subtended by line 3–4 and the horizontal). On the cineradiographic recordings the displacement of the tongue relative to the lower jaw (horizontal and vertical distance between the tongue markers and the anterior marker on the lower jaw) was also calculated.

From plots of the movements of jaws and tongue against time, an additional number of variables were determined: (1) the dura-

Fig. 1A–F Lateral view of the head of *C. zebrata*. **A** Schematic drawing illustrating the placement of the radio-opaque markers used to quantify displacements of jaws and the tongue (markers 7, 8); **B** (after removal of the skin only) through **E** (deepest dissection level) show sequentially deeper views of the jaw system. *Shaded areas* indicate bony elements; *stippled areas* or *areas with dashed lines* indicate aponeuroses or connective tissue. For an explanation of the numbers in **A** see Materials and methods



tions of the slow opening phase (SO), the fast opening phase (FO), the fast closing phase (FC), the slow closing/power stroke phase and of the total cycle; (2) the maximal values of the gape distance, lower jaw depression, cranial elevation and horizontal and vertical tongue displacement, and (3) the time to the maximal value of the gape distance, time to the most anterior and the most dorsal tongue position, time to the maximal depression of the lower jaw and elevation of the neurocranium. The different phases within a jaw cycle were determined, based on the changes in angular velocity of the jaw movements in conjunction with the changes in tongue movement. When sequences were analysed partially, frame one was arbitrarily chosen at the beginning of the slow opening of the mouth.

Electromyographic recordings and analysis

The animals used in the electromyographic experiments were anaesthetized using an intramuscular injection of Ketalar (100 mg kg⁻¹ body mass) before electrode implantation. Bipolar (Gans 1992) electrodes (50 cm long) were prepared from Teflon-insulated 0.075-mm Stainless steel wire or 0.050-mm NiCr (80%/20%) FORMVAR-insulated wire. The insulation was removed at the tip, exposing 1 mm of electrode wire. The electrodes were implanted percutaneously into each muscle belly using hypodermic needles with 2 mm of the electrode bent back as it emerged from the needle barrel.

During the experiments, electrodes (with a maximum of ten electrodes in one recording session) were placed in groups, including of major jaw closer muscles [musculus adductor mandibulae externus (superficial anterior and posterior, medial and profundus parts), musculus pseudotemporalis (superficial and profundus parts), musculus adductor mandibulae posterior and musculus pterygoideus (lateral and medial parts)] and jaw opener muscles (musculus depressor mandibulae and musculus spinalis capitis). See Fig. 1 for identification of muscles. Electrode placement was confirmed by dorsoventral and lateral x-rays after electrode implantation.

Electrical signals were amplified 2000 times with Gould Bioelectric signal conditioner (model 13-6615-58; range 0.5–5 kHz) and Honeywell Accudata 117 d.c. amplifiers and recorded on a Honeywell 96 FM 14-channel tape recorder (medium bandpass) at a speed of 19.05 cm s⁻¹. The recorded electromyographic signals were digitized at 10 kHz using a Keithley DAS series 500 12-bit A/D convertor. After digitization, the signals were integrated following the procedure of Beach et al. (1982) and the number of spikes as well as the average amplitude and mean number of spikes multiplied by the average amplitude per interval (bin) were calculated.

More than 50 feeding events in over 15 recording sessions were recorded for the five *T. rugosa*. An additional 32 complete feeding events from six recording sessions in two animals feeding on banana (10), tomato (5), baby mice (8), endive (3, but each consisting of 2–5 complete feeding bouts), grasshopper (4), apple (1), and snails (1) were recorded specifically for this study. For *C. zebra* 15 complete feeding events from four recording sessions in two animals feeding on banana (4), tomato (3), endive (2, again consisting of up to 5 complete feeding bouts), apple (1), and kiwi (5) were recorded. For the quantitative analysis five intraoral transport bites representing the ‘‘crushing’’ of the food item were selected from one of the recording sessions in *T. rugosa* and from one of the recording sessions in *C. zebra*. These recording sessions were selected as they included the largest variety of food items eaten by both species. In these sequences the activity from the m. depressor mandibulae, the m. adductor mandibulae externus superficialis, the m. adductor mandibulae externus profundus, the m. pseudotemporalis, the m. adductor mandibulae posterior and the m. pterygoideus lateralis was recorded for *T. rugosa* and the activity in the m. depressor mandibulae (right + left), the m. adductor mandibulae externus superficialis anterior, the m. adductor mandibulae externus superficialis posterior, the m. adductor mandibulae externus

medialis, the m. pseudotemporalis (right + left), and the m. adductor mandibulae posterior for *C. zebra*.

Time-based analysis of electromyograms

From the recorded feeding sequences, five crushing cycles from the intraoral transport stage were selected for all food types. These were selected on the basis of qualitative differences in the intensity of muscular recruitment (i.e. the five cycles which showed the strongest recruitment). Within one crushing cycle, muscle activity patterns were subdivided into several activity bursts (usually three, see Herrel et al. 1997) when abrupt amplitude differences or short periods of silence were present. However, this does not necessarily mean that there was always more than one burst present within each cycle. For each muscle, the onset and the duration of all bursts within one cycle (and for all cycles analysed) were recorded. Onset variables are expressed relative to the onset of the main activity burst in the m. depressor mandibulae (= time 0) as this corresponds well to the beginning of the fast opening of the jaws (see Herrel et al. 1995, 1997).

Intensity-based analysis of electromyograms

As the number of spikes multiplied by the mean amplitude is a measure of the intensity of muscle recruitment (Basmajian and De Luca 1985; Loeb and Gans 1986), further analyses of intensity-related variables were primarily based on this variable. The means, and sums of the recruitment levels were calculated per burst as muscles often showed more than one activity burst during the course of a gape cycle. Within each recording session, the maximal burst values (sum, mean) recorded for each muscle were determined. The burst data for all bite cycles within each recording session were then normalised for each muscle according to their respective maxima. Recruitment levels for each muscle are therefore expressed as a percentage of their maximal burst recruitment level.

Statistical analysis

Several analyses were performed on the kinematic data to explore the effects of the feeding stage and the food type on the feeding kinematics. Analyses of variance and subsequent univariate *F*-tests were performed on the original data. For all univariate *F*-tests performed, the significance level was corrected using a sequential Bonferroni correction (see Rice 1989). As a result of significant interactions between the effects investigated (stage × food type), data sets were subdivided and effects between stages were examined within food types and vice versa (see Table 5).

Similarly, a number of multivariate analyses were performed on the electromyographic data to explore differences in timing, duration and recruitment levels for different food items. To be able to analyse the data statistically, six data sets were constructed on the basis of five selected crushing cycles for each food type from one recording session for each species. The first type of data set (one for both species) consisted of the duration data (in milliseconds) of all activity bursts and for all muscles. The second type of data set consisted of the burst recruitment level data for pre-bursts (activity occurring before the principal activity burst), main bursts (i.e. the principal activity) and post bursts (later activity, usually of a lower amplitude) for all muscles in both species. The third type of data set consisted of the onset data of the pre-main and post-activity bursts for all muscles pooled due to the large number of missing values (i.e. muscles that showed no activity during a certain activity period while eating certain food types). The absence of activity in certain muscles during certain periods was consistently observed for both species and for all food types, but showed no distinct variation between species or food type.

First, a factor analysis (VARIMAX rotation) was performed on the data sets consisting of the duration and intensity-related

variables. An analysis of variance was then performed on the first three (or four, depending on the amount of variation explained by each factor) factors coupled to a Duncan multiple-range significance test (at the 0.55 level) to explore the differences in recruitment pattern as related to the food eaten. Next, an analysis of variance coupled to a Duncan multiple-range significance test was performed on the raw onset data for both species separately.

All analyses were performed using the STATISTICA (Statsoft, version 5.0) statistical package.

Results

Morphology

Wineski and Gans (1984) have given an excellent description of the morphology of the feeding system in *T. rugosa*. Here only a short description of the cranio-cervical system in *C. zebra* will be presented. In our description of the trigeminus-innervated musculature of *C. zebra* we follow the more conventional terminology of Lakjer (1926) rather than that of Wineski and Gans (1984). In general the musculature of *C. zebra* does not differ much from that described for other scincid lizards (see Haas 1973; Gomes 1974). In our description of the cervical musculature we follow the nomenclature of Nishi (1916) and Oelrich (1956).

The skull of *C. zebra* is rather thick and most cranial elements are tightly sutured and fused, making intracranial kinesis (meso- and metakinesis) impossible (see Herrel et al. 1998a, b). Characteristics of the skull of *C. zebra* are the absence of contact between the palatine and pterygoid bones from both sides, and the anteriorly oriented ectopterygoid process which touches the palatine bone. The squamosal bone contacts the postfrontal, and the postorbital bone is absent. Teeth are present on the premaxillary, maxillary, dentary and pterygoid bones. The marginal teeth are flattened and show small eccentric cusps which makes them very different from the blunt conical teeth in *T. rugosa*.

The jaw musculature (Fig. 1) is well developed and consists of external, internal and posterior adductor muscle groups. The external adductor consists of a superficial, a medial and a profundus part. The superficial part corresponds to the m. adductor mandibulae externus 1, the medial part to the m. adductor mandibulae externus 2 and 3, and the profundus part to the m. adductor mandibulae externus 4 of *T. rugosa* as described by Wineski and Gans (1984). The internal adductor in *C. zebra* is comparable to the same muscle groups in *T. rugosa* and consists of the pseudotemporal (superficial and profundus parts) and the pterygoid muscles (lateral and medial parts). The posterior adductor in *C. zebra* corresponds more or less to the most posterior part of the m. adductor mandibulae 1 in *T. rugosa*. In *C. zebra*, this muscle originates at the anterolateral side of the quadrate and is covered by the quadrate aponeurosis (medial plate of the quadrate aponeurosis in *T. rugosa*) at its dorsal side. The fibres run anteroventrad and insert on the dorsal side of the lower jaw, behind the coronoid bone.

The jaw opener (m. depressor mandibulae) consists of two distinct but adjacent bundles. The posterior bundle originates at the lateral side of the strongly developed connective tissue covering the dorsal cervical musculature (dorsal neck fascia), and inserts at the posterolateral side of the retroarticular process of the articular bone. The anterior bundle originates partially at the anterolateral side of the dorsal neck fascia and partially at the posterior margin of the quadrate process of the parietal bone. The anterior bundle inserts by means of a short aponeurosis at the dorsal side of the retroarticular process. Although not a part of the jaw musculature sensu stricto, a short description of the dorsal cervical musculature will be given as these muscles produce cranial elevation during mouth opening. The m. spinalis capitis and the m. articulo-parietalis are the two most important muscles producing elevation of the neurocranium. The former originates at the dorsolateral side of the neural spines of cervical vertebrae 2–5 and inserts at the caudomedial side of the parietal bone. The latter muscle originates at the level of the 4th cervical vertebra on the intermediate aponeurosis of the longissimus cervico-capitis complex, and inserts at the posterior side of the entire quadrate process of the parietal bone.

Food characteristics

As indicated earlier (see Materials and methods), all fruit and vegetable food items were cut into cubes of similar size to those fed to the lizards during the recording sessions. Despite the fact that size and shape are thus controlled for, a considerable amount of variation in the mass of the food particles remained. Therefore, the relation between particle mass and toughness was examined.

For all food types tested, except for banana and mice, a clear and significant relation between the size of the particle tested and the force needed to crush it was observed (see Fig. 2). An analysis of covariance on \log_{10} -transformed data (mass as covariate) indicated significant differences between food items (ANCOVA: $F = 378.52$; $P < 0.001$; $df = 6,137$). Although snails require the most force in absolute terms (Table 1), when mass is introduced as a covariate they do not differ from endive (ANCOVA: $F = 2.95$; $P = 0.096$; $df = 1, 29$). Based on the raw data and the results from the ANCOVAs, endive and snails require both more force than apple (endive-apple: $F = 50.73$; $P < 0.000$; $df = 1, 46$; snail-apple $F = 101.07$; $P < 0.000$; $df = 1, 30$), and apple more than tomato ($F = 263.77$; $P < 0.000$; $df = 1, 51$). Remarkably, mice do not differ from either tomato or banana (mice-banana; $F = 0.96$; $P = 0.33$; $df = 1, 31$; mice-tomato; $F = 3.58$; $P = 0.07$; $df = 1, 35$), but tomato requires relatively more force than banana ($F = 20.96$; $P < 0.000$; $df = 1, 51$). However, in absolute terms tomato, banana and newborn mice require the same average amount of force before failure

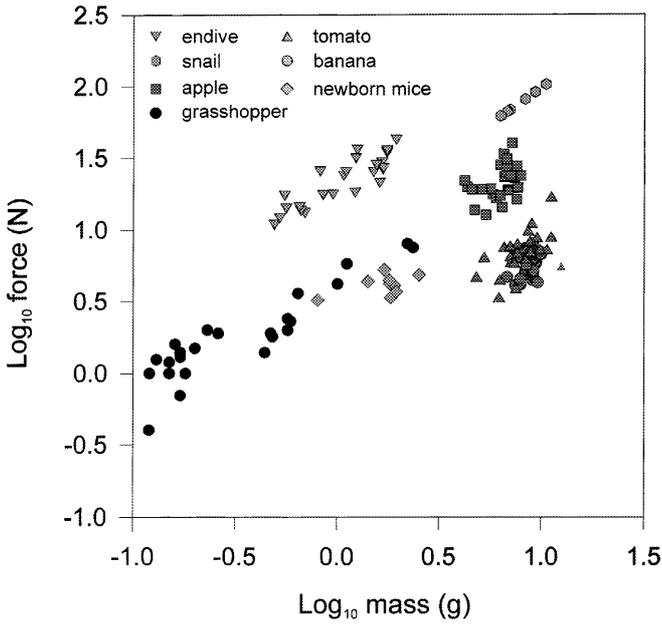


Fig. 2 Results of the food toughness measurements. Note the difference between tough food items such as endive, snails, and apple and others such as tomato, banana, mice and grasshoppers. Note also the log-log scale

(see Table 1). Grasshoppers have the lowest average strength of all items tested, but are just as resistant as banana and newborn mice for a given mass.

Feeding kinematics

Feeding sequence are initiated by the *food prehension* stage during which the food is taken between the jaws, followed by the *intraoral transport* stage where the food is mechanically reduced and transported toward the back of the mouth, and end with the *swallowing* stage where the food mass is transferred from the pharynx to the esophagus (see De Vree and Gans 1989; Herrel et al. 1996a). As for other lizards (see Herrel et al. 1996a) no discrimination between processing or chewing cycles and intraoral transport cycles sensu stricto could be made based on the kinematic data. As no temporal separation

Table 1 Characteristics of food items as used in the experiments. Force is the average force that had to be applied onto the food item to fracture it (see Materials and methods for a more detailed explanation)

Food	Average mass (g) ± SD	Average force (N) ± SD	n
Banana	8.71 ± 0.76	5.63 ± 1.11	25
Apple	6.29 ± 1.08	22.23 ± 6.58	25
Tomato	8.09 ± 1.56	7.09 ± 2.43	29
Endive	1.15 ± 0.47	24.00 ± 8.91	24
Mouse	1.74 ± 0.46	4.17 ± 0.66	9
Grasshopper	0.51 ± 0.60	2.33 ± 2.01	25
Snail	8.13 ± 1.67	79.71 ± 17.54	8

between these two cycle types occurs, intraoral transport in these animals should rather be considered as a continuum where pure physical reduction of food items occurs throughout this feeding stage.

In our description of the jaw and hyolingual kinematics, we adopt the terminology of Bramble and Wake (1985). A jaw cycle is divided into five distinct phases based on the changes in the velocity of mouth opening (Fig. 3). Slow opening of the mouth initiates a cycle and is followed by the fast opening of the mouth. After maximal gape, the mouth is closed rapidly until the jaws touch the prey, initiating the slow closing phase during which the closing speed further decreases. The slow closing phase may be accompanied by a prey crushing phase. For a general description of feeding in *T. rugosa* we refer to Gans et al. (1985). Only intraoral transport and swallowing cycles in *C. zebra* are described here.

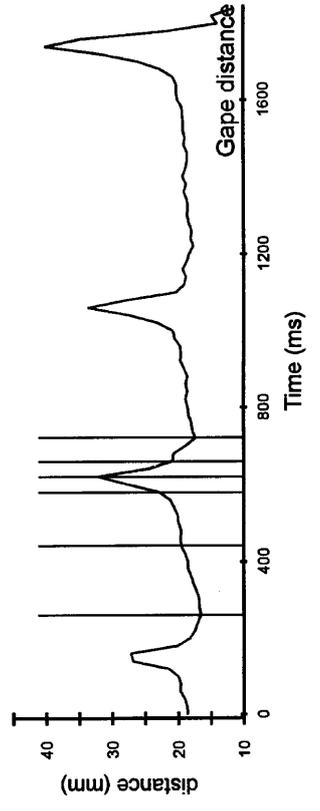
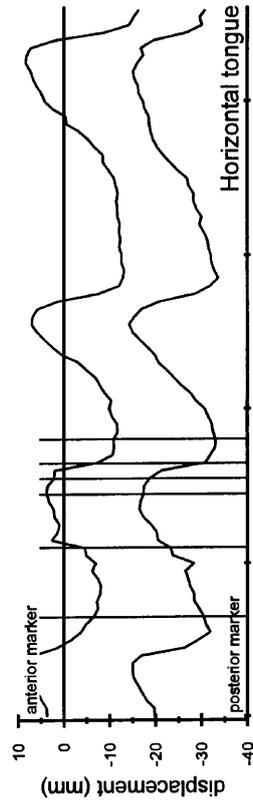
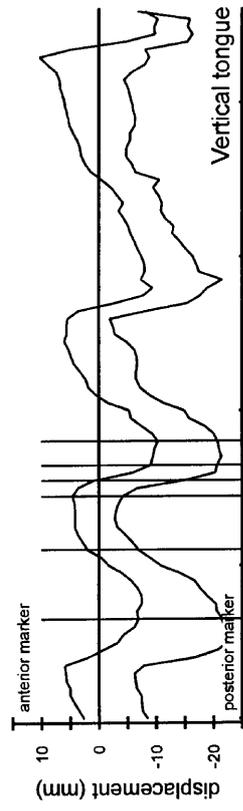
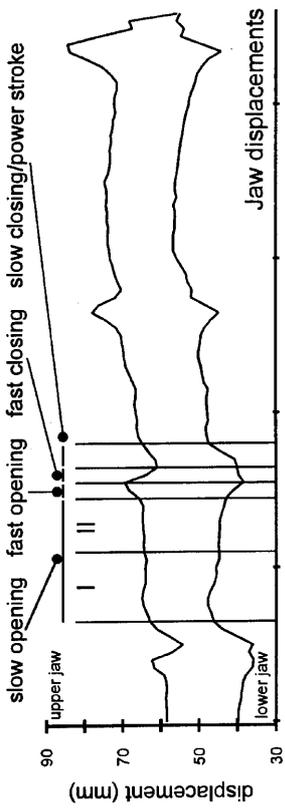
No cranial kinesis (streptostyly, meso- or metakinesis) could be demonstrated during feeding by analysis of the cineradiographic records for either species (see also De Vree and Gans 1987 for *T. rugosa*).

Intraoral transport

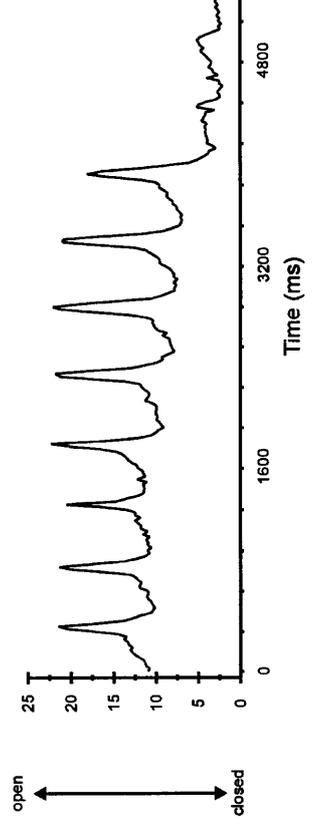
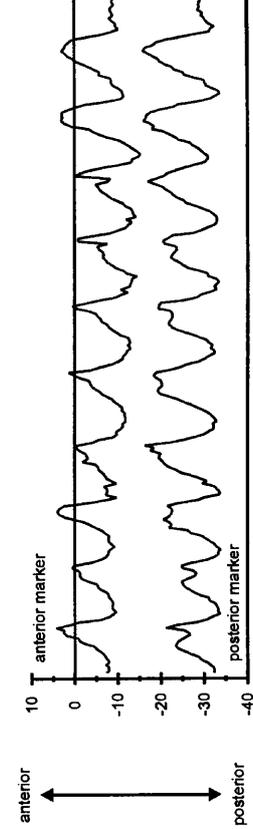
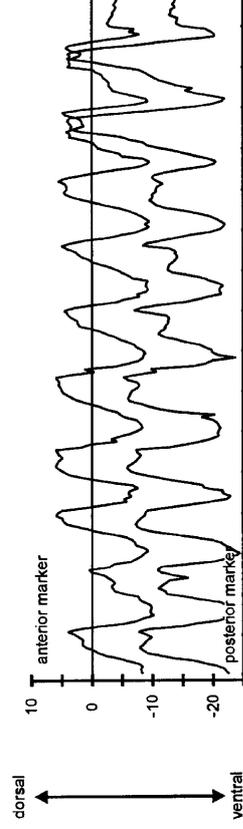
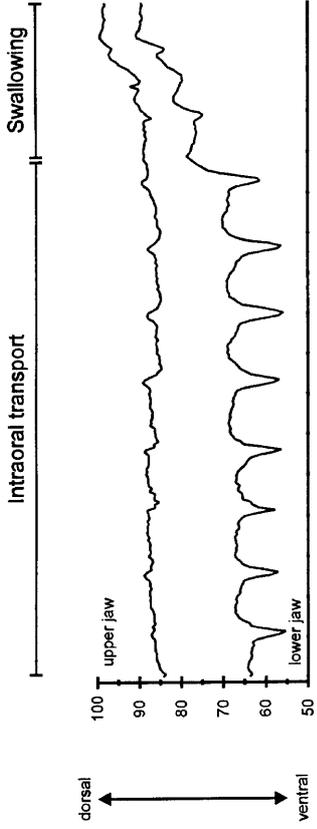
Intraoral transport cycles (Figs. 3, 4; Tables 2, 3) were broadly similar in both species and include SO, FO, FC and slow closing (SC) power stroke phases. A typical intraoral transport cycle was initiated by a SO. During the first part of this phase (generally referred to as slow opening 1) the tongue is protracted and moves upward and forward. As a consequence of this tongue protraction, the lower jaw is pushed down. During the following slow opening 2 phase the anterior part of the tongue stops, but the posterior part of the tongue continues its upward and forward movement, and is fitted against the prey. During the second part of the SO the lower jaw hardly moves downward anymore and the gape distance remains almost constant. The FO was characterized by a simultaneous and fast depression of the lower jaw (LJdepr) and elevation of the neurocranium. Tongue retraction was initiated during this phase. At maximal gape the jaws were closed rapidly by an elevation of the lower and depression of the upper jaw. At the end of this phase the tongue was almost fully retracted. Once the jaws touch the food item the closing speed decreased and the SC, power stroke phase began. This phase is further

Fig. 3 Representative kinematic profiles (based on x-ray films, 50 frames s⁻¹) of vertical displacements of the upper and lower jaw, the vertical displacement of the tongue, the horizontal displacement of the tongue and the gape in *T. rugosa* (all variables are expressed in millimetres). On the *left* a number of intraoral transport cycles while eating a mouse are represented; on the *right* a number of intraoral transport and swallowing cycles are represented with tomato as a food item. Note the different scale on the y-axes for mouse and tomato cycles. Vertical lines delimit kinematic phases (terminology after Bramble and Wake 1985). I and II indicate the slow opening I and II phases as defined by Bramble and Wake (1985)

mouse



tomato



characterized by the return of the tongue to its resting position.

The intraoral transport cycle as described here, is a generalized cycle and bite-to-bite, and food-dependent differences are observed (see Tables 2, 3). Although intraoral transport cycles are similar for both species, consistent species-dependent differences are observed. For example, in *C. zebrata* the slow opening 2 phase is usually more prominent; nevertheless, in both species this phase was sometimes absent (see Figs. 3, 4). Another conspicuous difference between species is the larger contribution of cranial elevation to the total gape distance in *C. zebrata* (e.g. compare tomato intraoral transport cycles on Figs. 3, 4).

Swallowing

Swallowing cycles (Figs. 3, 4; Tables 2, 3) differ from intraoral transport cycles in both species and are generally characterized by a decrease in duration, or the absence of the FO and a smaller gape distance (see Tables 2, 3). Again, LJdepr coincided with tongue protrusion and tongue retraction was initiated just before jaw closure. As no teeth-prey contact occurred during jaw closure, no real slow closing, power stroke phase was present and was replaced by a so-called stationary phase.

At the end of the swallowing stage, usually one or two pharyngeal compression cycles, characterized by a marked pharyngeal constriction, were observed. Such pharyngeal compression cycles were observed in both species, but are most prominent in *C. zebrata*. These cycles usually include several opening and closing phases but the displacements of jaws and tongue and durations of kinematic phases were irregular. The only consistently recurrent element is the strong pharyngeal compression and extension of the cervical region.

Food effects

Within species, distinct effects of the food eaten on the feeding pattern are observed. The number of cycles observed during each feeding stage was affected by the type of food eaten (Table 4). In *T. rugosa* the number of intraoral transport cycles when feeding on apple is significantly greater than when feeding on either tomato, banana, grasshoppers or newborn mice ($F_{4,31} = 4.92$; $P < 0.01$; posthoc Duncan at $\infty = 0.05$). The number of swallowing cycles does not differ for the food types tested ($F_{4,31} = 1.48$; $P = 0.23$). In *C. zebrata* the greatest number of intraoral transport cycles was observed for endive, when compared to banana and tomato ($F_{2,23} = 43.97$; $P < 0.01$; posthoc Duncan test at $\infty = 0.05$). The number of swallowing cycles observed, on the other hand, was less for endive compared to the other food types ($F_{2,23} = 7.83$; $P < 0.01$; posthoc Duncan test at $\infty = 0.05$). Species did not differ from

one another in the number of intraoral transport or swallowing cycles used when eating banana or tomato ($F_{1,86} = 0.61$; $P = 0.44$).

Aspects of jaw and tongue movement patterns were also modulated in response to the food eaten (Tables 2, 3). In *T. rugosa* intraoral transport cycles differed in a few variables while eating different food items. Only the duration of the FC and the gape distance showed significant differences. Whereas the gape distance was significantly smaller during grasshopper intraoral transport cycles, the FC was significantly shorter while eating both grasshoppers and banana (Table 2). Swallowing cycles, on the other hand, were not significantly different for the food items tested.

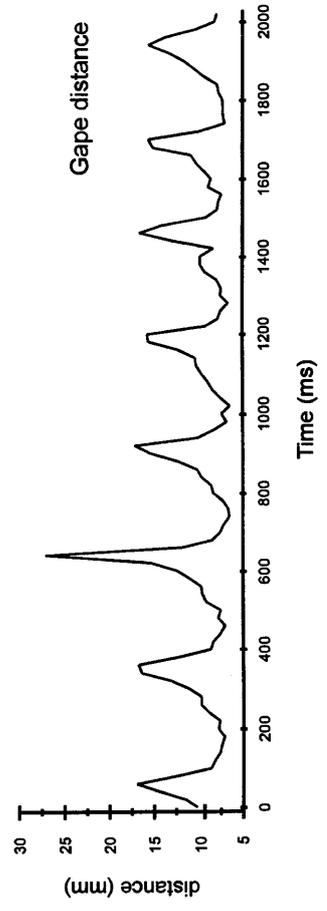
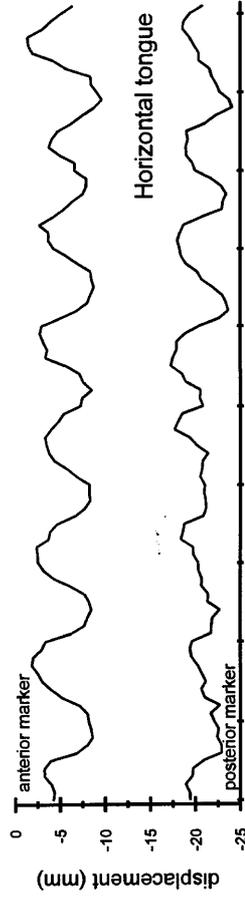
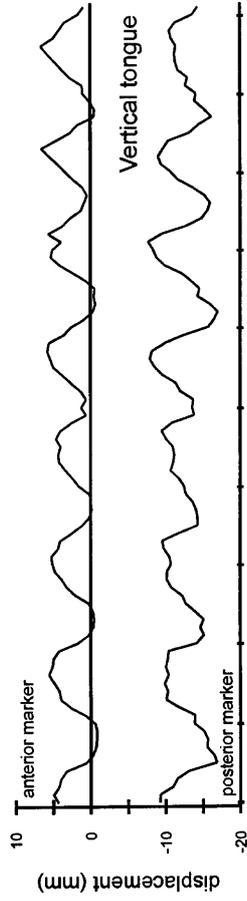
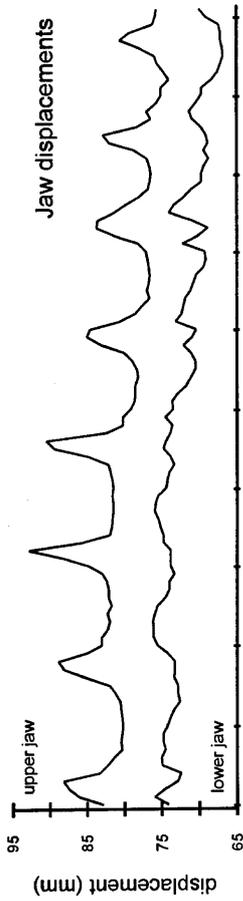
For *C. zebrata* (Table 3) intraoral transport cycles showed significant differences between food types for most variables. Endive intraoral transport cycles differed from apple and tomato intraoral transport cycles by a shorter duration of the total cycle, and the SO resulted in a shorter time to maximal gape, and shorter time to maximal horizontal (HTdispl) and vertical tongue displacement (VTdispl). Additionally, endive differs from banana by a shorter SO, a shorter slow closing, power stroke phase, a more pronounced VTdispl and a shorter time to maximal gape. Banana on the other hand, differs specifically from tomato by a shorter FC, a shorter time to maximal gape and smaller LJdepr. The maximal gape distance is significantly larger for tomato intraoral transport, and the maximal VTdispl significantly smaller for banana intraoral transport. Additionally, the time to maximal LJdepr and HTdispl is smaller for banana compared with apple and tomato. During swallowing, on the other hand, differences were minor. The only differences between swallowing cycles for different food items were the larger maximal gape distances for endive and banana compared to tomato and apple cycles.

Electromyography

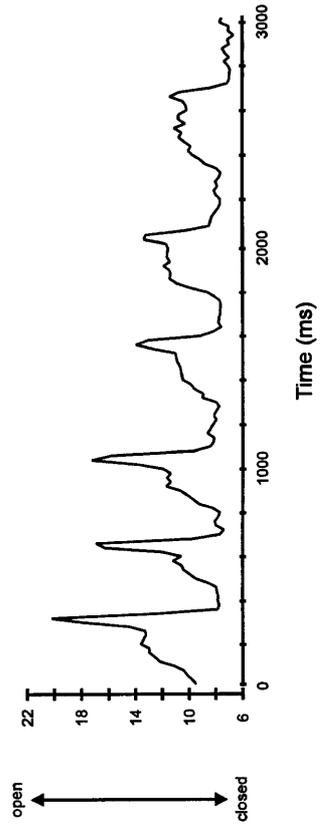
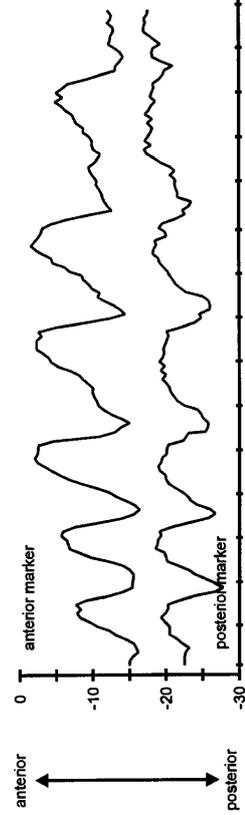
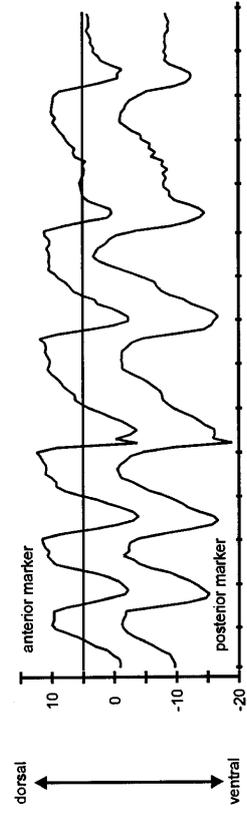
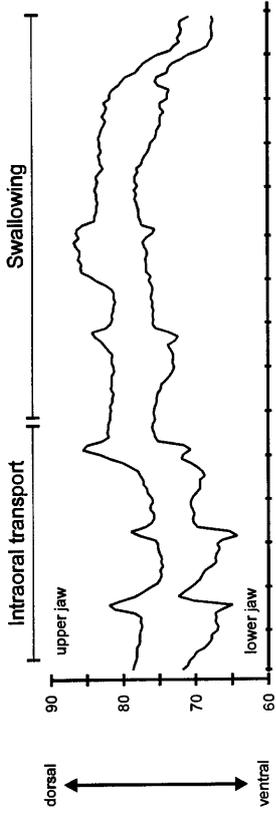
For a general description of jaw muscle activity patterns during feeding in *T. rugosa* we refer to Gans et al. (1985) and Gans and De Vree (1986). Here, the activity patterns of the jaw muscles in *C. zebrata* during the different feeding stages will be described first. The descriptions are based on endive feeding cycles as these probably correspond best to the feeding cycles of *C. zebrata* in natural circumstances (see Kinghorn 1928; Honegger 1975; Parker 1983). In the subsequent section, the effect of food structure and type on the jaw muscle

Fig. 4 Representative kinematic profiles (based on x-ray films, 50 frames s^{-1}) of vertical displacements of the upper and lower jaw, the vertical displacement of the tongue, the horizontal displacement of the tongue and the gape in *C. zebrata* (all variables expressed in millimeters). On the *left* a number of intraoral transport cycles while eating endive are represented; on the *right* a number of intraoral transport and swallowing cycles are represented with tomato as a food item. Note the different scale on the *y*-axes for endive and tomato

endive



tomato



activity patterns during intraoral transport cycles for both species is analysed.

Intraoral transport

During the SO no or very little activity is present in the jaw muscles (Fig. 5). Occasionally the jaw closers (mainly the *m. pterygoideus*) show a short activity burst of about 250 ms. The first high-intensity burst during an intraoral transport cycle is a bilaterally synchronous activity in the jaw opener and a strong and simultaneous activity burst in the *m. spinalis capitis*, initiating the FO. At maximal gape the jaw openers become silent and after maximally 75 ms the jaw closers become active. During this FC all jaw closers are active and remain active throughout the FC. After a short pause the jaw closers become active again and show an activity burst of variable duration. During this phase the *m. adductor mandibulae posterior* usually remains active about twice as long as the other jaw closers. Both the *m. depressor mandibulae* and the *m. spinalis capitis* generally no longer show any activity during the FC. However, both muscles often show renewed activity during the slow closing, power stroke phase.

Swallowing

As in other lizards, swallowing in *C. zebra* is characterized by the absence of a slow closing, power stroke phase (teeth no longer contact the food upon jaw closure) and smaller jaw opening distances (Fig. 5). Differences in tongue movement patterns are due to the position of the food with respect to the tongue (the tongue now moves under and past the food before being retracted). The first muscles to become active during a swallowing cycle are the lateral and medial parts of the

m. pterygoideus. These muscles generally show prolonged activity bursts (up to 200 ms) of low amplitude. After an activity pause of about 250 ms the jaw openers (*m. depressor mandibulae* and *m. spinalis capitis*) become active simultaneously. Unlike during intraoral transport, the *m. spinalis capitis* ceases its activity before the *m. depressor mandibulae* and is generally activated at a much lower intensity level. Shortly after the offset of the *m. depressor mandibulae* (about 75 ms), the *m. adductor mandibulae externus complex* (mainly the superficial anterior part) and the *m. pterygoideus* (mainly the medial part) become active. In general, the *m. adductor mandibulae externus complex* remains active about three times as long as the *m. pterygoideus* at a fairly high activity level. However, the *m. pterygoideus* may show low to very low activity up to 2 s after jaw closure (i.e. during the stationary phase).

After most feeding sequences one or two pharyngeal compression cycles (Smith 1984) are observed (Fig. 5). These cycles always occur after swallowing i.e. after passage of the food from the oral cavity to the esophagus. These pharyngeal compression cycles consist of several opening and closing actions. However, the most striking feature of these cycles is the strong pharyngeal compression and/or constriction, and the extension of the head-neck region. Jaw muscle activity patterns diverge strongly from the activity patterns during other feeding stages. Pharyngeal compression cycles are initiated by a "regular" open-close phase. During this first part of the cycle, jaw openers (*m. depressor mandibulae*, *m. spinalis capitis*) are active during opening and most jaw closers show moderate (*m. adductor mandibulae externus superficialis anterior*) to low (*m. adductor mandibulae externus superficialis posterior*, *m. pseudo-temporalis*, *m. adductor mandibulae posterior*, *m. pterygoideus*) activity during closing. The subsequent part of the cycle is characterised by prolonged and intense activity in the jaw openers. Usually, this prolonged

Table 2 Effect of food type on the kinematic variables during intraoral transport and swallowing *Tiliqua rugosa*. All times are measured from the beginning of the cycle (all values based on x-ray data, 50 frames s⁻¹). *n* = number of cycles used

Variable	Mouse		Banana				Grasshopper		Tomato			
	Intraoral transport (<i>n</i> = 13)		Intraoral transport (<i>n</i> = 17)		Swallowing (<i>n</i> = 8)		Intraoral transport (<i>n</i> = 13)		Intraoral transport (<i>n</i> = 23)		Swallowing (<i>n</i> = 9)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Duration of the SO phase (ms)	240.0	97.7	218.8	110.3	110.0	152.3	270.8	68.2	260.9	71.9	60.0	113.1
Duration of the FO phase (ms)	60.0	22.2	50.6	13.9	225.0	158.4	47.7	12.5	60.0	14.5	255.6	142.0
Duration of the FC phase (ms)*	56.9	17.3	47.1	11.8	65.0	29.6	41.5	12.3	57.4	10.7	100.0	26.7
Duration of the SC phase (ms)	52.3	32.9	105.9	68.9	77.5	64.4	78.5	41.1	92.2	35.3	17.8	34.6
Maximal gape distance (mm)*	28.5	7.2	30.6	5.5	14.6	2.3	20.5	2.3	29.1	2.9	14.0	1.4

* Indicates significant food effects during intraoral transport; bold values indicate significant differences between intraoral transport and swallowing cycles. Note that no significant food effects were observed during swallowing

Table 3 The effect of food type on the kinematic variables during intraoral transport and swallowing in *Corucia zebrata*. All times are measured from the beginning of the cycle (all values based on x-ray data, 50 frames s⁻¹), *n* = number of cycles used

Variable	Endive			Apple			Tomato			Banana				
	Intraoral transport (<i>n</i> = 82)		Swallowing (<i>n</i> = 4)	Intraoral transport (<i>n</i> = 6)		Swallowing (<i>n</i> = 3)	Intraoral transport (<i>n</i> = 25)		Swallowing (<i>n</i> = 5)	Intraoral transport (<i>n</i> = 2)		Swallowing (<i>n</i> = 8)		
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD		
Duration of the total cycle (ms)*	264.9	68.7	355.0	202.7	363.3	35.4	431.2	92.3	572.0	250.6	350.0	130.0	632.5	262.7
Duration of the SO phase (ms)*	108.3	49.7	85.0	63.8	193.3	45.7	232.8	73.3	356.0	172.7	180.0	120.0	52.5	92.2
Duration of the FO phase (ms)	59.5	20.0	140.0	140.7	43.3	18.0	63.2	10.9	40.0	21.9	40.0	0.0	405.0	276.0
Duration of the FC phase (ms)*	48.3	11.7	55.0	16.6	46.7	9.4	65.6	27.4	60.0	17.9	40.0	20.0	85.0	45.6
Duration of the SC phase (ms)*	47.6	28.2	80.0	104.9	80.0	41.6	72.8	32.9	116.0	87.1	110.0	50.0	112.5	109.6
Maximal gape distance (mm)*	21.4	3.9	24.4	2.8	16.4	2.5	26.5	3.7	15.7	3.7	20.5	0.2	22.1	3.7
Maximal Ljdepr (mm)*	4.4	3.5	8.7	3.4	5.9	3.7	7.2	2.9	4.1	1.7	2.2	1.3	5.1	3.6
Maximal VTdspl (mm)*	8.2	3.0	7.1	3.9	8.8	2.0	10.2	3.0	8.0	2.2	4.6	0.3	10.7	2.0
Time to maximal gape distance (ms)*	169.0	49.9	220.0	94.9	236.7	42.3	292.8	71.3	396.0	185.6	220.0	120.0	457.5	215.3
Time to the maximal Ujelev (ms)*	167.6	50.7	175.0	49.8	216.7	49.6	288.8	76.3	388.0	174.2	260.0	140.0	467.5	220.7
Time to the maximal HTdispl (ms)*	151.2	61.6	215.0	86.5	246.7	44.2	296.0	72.0	404.0	186.1	150.0	110.0	402.5	188.0
Time to the maximal VTdispl (ms)*	158.8	41.5	165.0	45.6	230.0	57.5	266.4	88.7	368.0	207.3	130.0	90.0	362.5	161.4
Time to the maximal HTdispl (ms)*	135.4	41.2	175.0	77.9	216.7	61.6	218.4	62.0	368.0	194.2	190.0	110.0	345.0	185.4
Time to the maximal VTdispl (ms)*														

* Indicates significant food effects during intraoral transport; bold values indicate significant differences between intraoral transport and swallowing cycles. Note that the maximal gape distance is the only variable showing significant food effects during swallowing cycles

Table 4 Number of jaw cycles observed for both species for the food types studied. Data are based on observational video recordings (50 frames s^{-1}). The number of feeding bouts used is indicated between brackets after each foodtype

	<i>T. rugosa</i>			
	Intraoral transport		Swallowing	
	Mean	\pm SD	Mean	\pm SD
<i>T. rugosa</i>				
Apple (5)*	22.60	8.78	4.00	2.51
Tomato (10)	9.60	6.15	5.50	1.36
Banana (8)	8.25	7.58	4.75	1.20
Mouse (9)	8.78	2.48	4.00	1.70
Grasshopper (4)	7.75	3.11	5.75	2.59
<i>C. zebrata</i>				
Endive (9)**	22.44	4.35	2.78	0.63
Tomato (7)	8.57	3.46	5.14	1.55
Banana (10)	6.40	3.23	4.30	1.19

* Indicates that significantly more intraoral transport cycles are observed during apple feeding when compared to other food types

** Indicates that significantly more intraoral transport but significantly less intraoral transport cycles are observed during endive feeding compared to other food types. Note also that the number of cycles observed during banana and tomato feeding is the same for both species

activity is repeated and followed by a short activity burst of moderate to high amplitude in all jaw closers. The prolonged activity in the jaw opener usually coincides with head-neck extension and pharyngeal compression.

In general, the first muscles to cease their activity during the course of a feeding sequence are in chronological order: the m. pseudotemporalis, the medial and deep parts of the m. adductor mandibulae externus complex (medial and profundus parts), the m. adductor mandibulae posterior, and the m. adductor mandibulae externus superficialis posterior. The anterior superficial part of the external adductor usually remains active longer in *C. zebrata* (Fig. 5). These muscles still contribute to jaw closing only during the first few swallowing cycles. Unlike during intraoral transport cycles, variation in both intensity and timing/duration of muscle activity patterns due to differences in food type is limited.

Food effects

For both species the effects of changes in food type are very clear even at a qualitative level (see Fig. 6 as an example for *T. rugosa*). However, in order to be able to evaluate the magnitude of these effects within and between species a quantitative analysis of both the timing of muscular activation (onset and duration of muscular activity) as well as the recruitment levels is required.

Timing of muscle activation Using duration data for *C. zebrata* significant food type effects could be demonstrated (Rao's $r = 7.58$ $df = 9, 29$; $P < 0.01$). Post-hoc Duncan tests showed that, on the first factor, no signi-

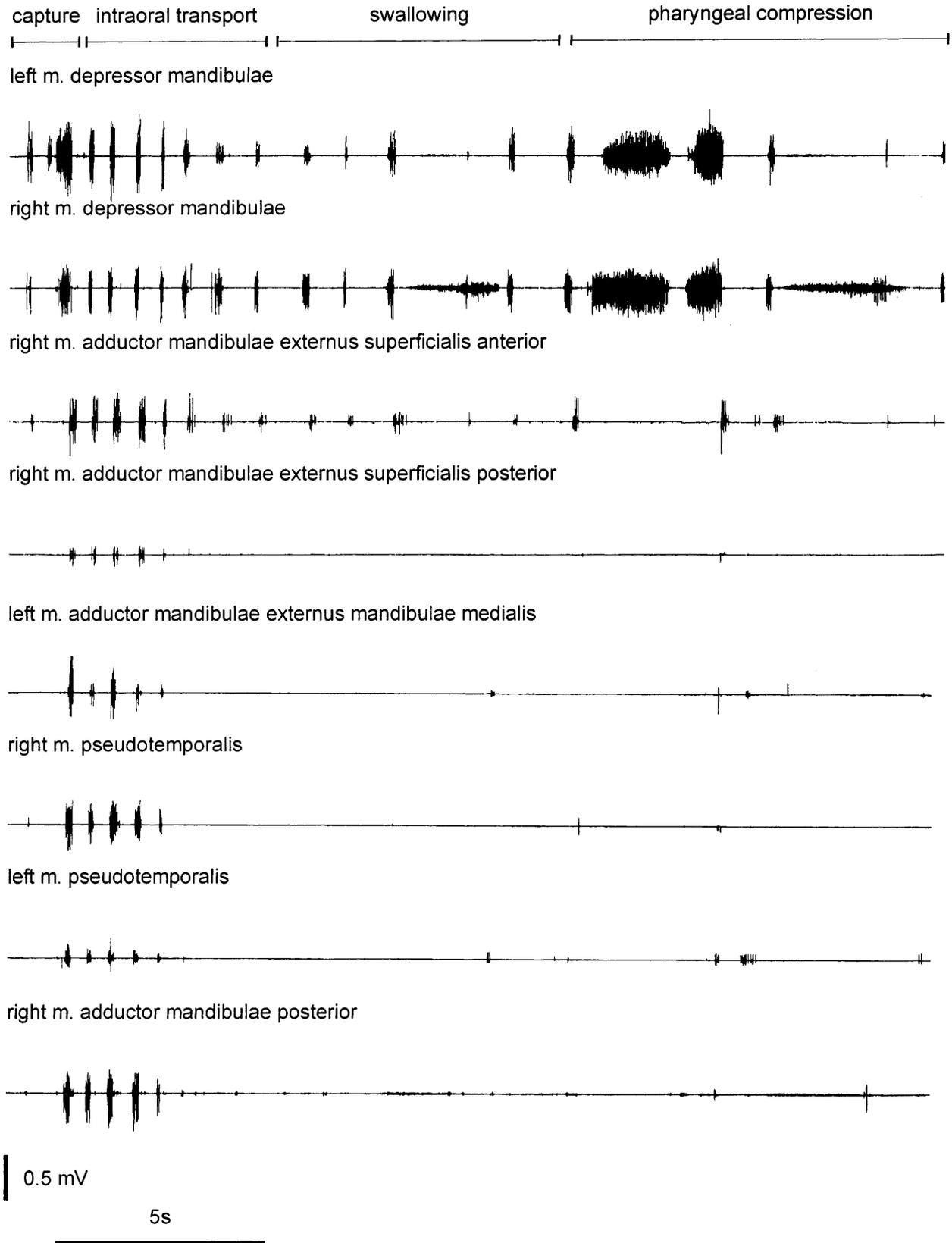
Fig. 5 Representative original EMG traces of a complete kiwi feeding cycle in *C. zebrata*. Feeding stages are indicated at the top of the figure

ficant food type effects were present. However, on the second factor endive crushing cycles were significantly different from apple and kiwi cycles. These differences between food types are situated in an increase of the duration of the main bursts of all jaw closers. On the third factor banana and kiwi cycles differ from apple and endive due to an increase in the duration of the main burst in both (right + left) jaw openers.

For *T. rugosa* significant food type effects are also observed (Rao's $r = 4.87$ $df = 16, 49$; $P < 0.01$). Post-hoc significance tests on the factor loadings show that on the first factor snail-crushing cycles differ from all others, and mouse differs from tomato-crushing cycles. These differences are due to an increase in the duration of the main bursts in all jaw closers and the post-burst in the jaw opener for snail- and mouse-crushing cycles. An increase in the duration of the post-bursts in the medial and profundus parts of the external adductor complex and the m. pterygoideus lateralis, and the pre-burst in the m. adductor mandibulae externus profundus cause the differences between mouse and other crushing cycles on the second factor. On the third factor no significant differences between food types could be demonstrated.

Based on the onset data for *C. zebrata* on food effects could be demonstrated, indicating that no significant differences in onset times were observed between food types (Rao's $r = 1.63$ $df = 9, 14$; $P > 0.05$). For *T. rugosa*, on the other hand, significant differences are observed (Rao's $r = 5.13$ $df = 12, 169$; $P < 0.05$). However, the subsequent post-hoc Duncan tests no longer discriminated between food types.

Recruitment levels In *C. zebrata* significant effects of food type on the recruitment of the jaw muscles are observed (Rao's $r = 19.78$ $df = 12, 34$; $P < 0.01$). Post-hoc tests on the factor loadings showed that on the first factor endive cycles differ from all others. These differences are due to an increase of the recruitment levels during the main burst in the m. adductor mandibulae posterior and the m. adductor mandibulae externus medialis and during the post bursts in the m. adductor mandibulae posterior, the m. pseudotemporalis, the m. adductor mandibulae externus medialis and the m. adductor mandibulae externus superficialis (both parts) when eating endive. On the second factor, kiwi differed from all other food types because the recruitment levels during the main burst in the m. depressor mandibulae increased. Although food types did not differ on the third factor, the fourth factor indicated that during banana crushing cycles the post-burst of the m. depressor mandibulae is stronger than that during crushing on other food types. Similarly, kiwi-crushing cycles showed a larger recruitment of the m. depressor mandibulae than apple-crushing cycles during the post-burst.



Similarly, significant food type effects in the recruitment levels of the jaw muscles in *T. rugosa* are present due to differences in the food eaten (Rao's $r = 5.13$ $df = 16, 49$; $P < 0.01$). The greatest differences were

observed in the recruitment of the m. adductor mandibulae externus medialis, the m. pseudotemporalis, the m. adductor mandibulae externus profundus and the m. pterygoideus lateralis which all showed high loadings on

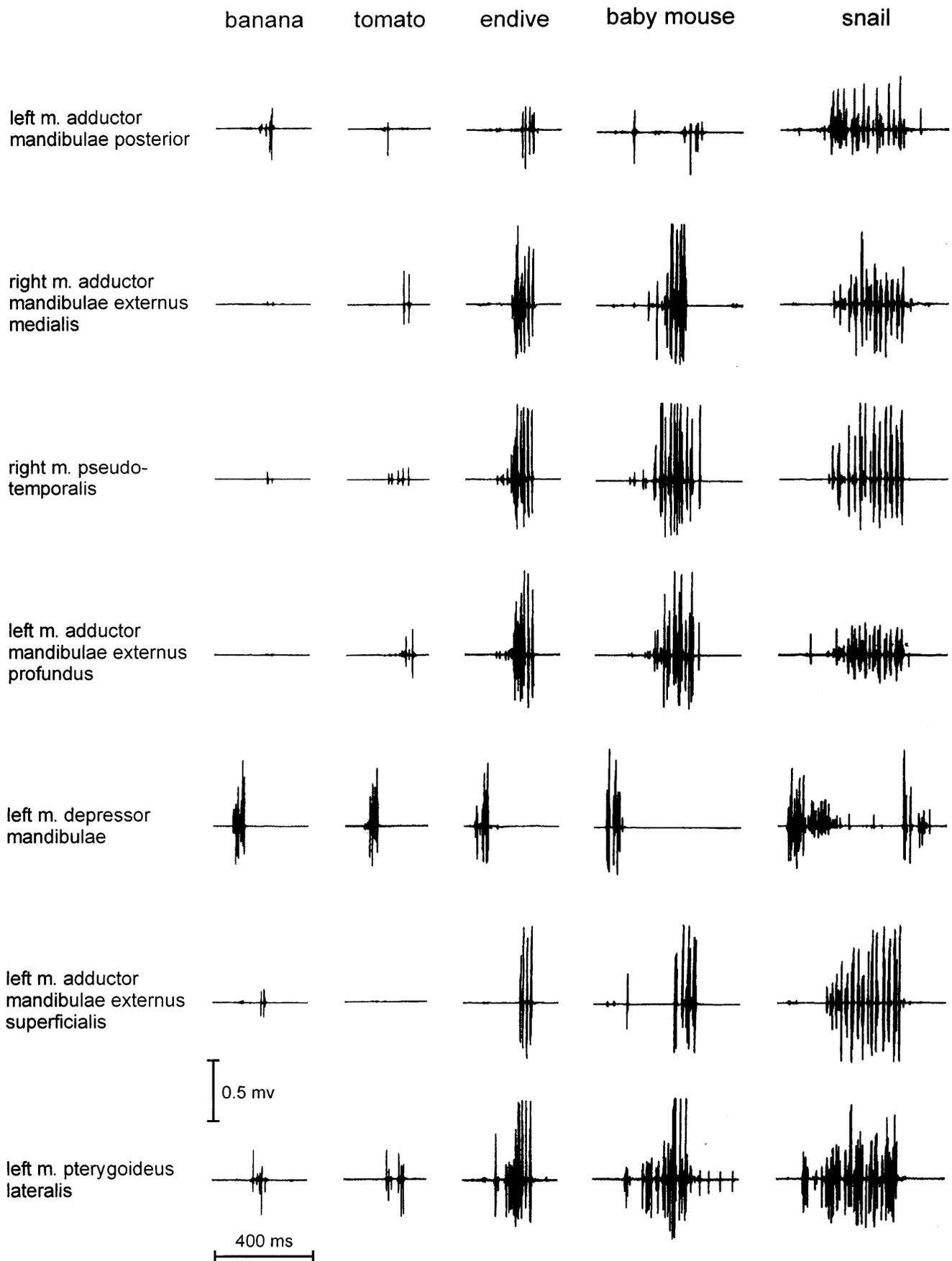




Fig. 6 Representative original EMG traces of intraoral transport cycles, illustrating food type effects in *T. rugosa*. The EMG traces are based on one recording session in one animal. The food type is indicated at the top of the figure

the first factor. Although both mouse-snail, and endive-crushing cycles differed significantly (stronger recruitment) from both tomato and banana, they did not differ from one another. On the second factor, crushing cycles for snails differed from those for all other food types except endive. The increase of the recruitment of the m. adductor mandibulae posterior during the post-burst was the only variable to show high loadings on this factor, and is thus causing the observed differences. On the third factor, endive differed from tomato in a decreased recruitment of the m. adductor mandibulae externus medialis during the pre-burst and an increase in the recruitment of the m. adductor mandibulae externus superficialis (both parts) during the post-burst. On the fourth factor, an increase in the recruitment of the m. adductor mandibulae posterior causes snails to differ from both mouse- and banana-crushing cycles.

Discussion

General

One major difference between the kinematical data gathered here for scincid lizards and previously published data is the strong kinematic similarity between intraoral transport and swallowing cycles. Only the gape distance and the duration of kinematic phases differ between behaviours. For other lizards such as *Ploceoderma stellio* nearly all kinematic variables determined differ between intraoral transport and swallowing (see Herrel et al. 1996a). However, the apparent kinematic similarity in scincids is not reflected in the activation patterns, which indicate that in both species, not only the number of active jaw closers but also the intensity of contraction differs markedly when comparing intraoral transport and swallowing cycles at a qualitative level.

One very special feature of the feeding cycle in scincid lizards, when compared to iguanian lizards such as *P. stellio* (Herrel et al. 1996a, 1997), is the presence of a number of pharyngeal compression cycles. These swallowing cycles are especially clear in *C. zebra* due to the large gular area, and correspond to the pharyngeal compression cycles as described by Smith (1984, 1986) for lizards such as *Tupinambis* and *Varanus*. Differences are mainly in the absence of head/neck extension in both the latter species. As for *P. stellio*, in *Ctenosaura* (Smith 1984) these pharyngeal compression cycles seem to be absent or at least less prominent. Extensive pharyngeal compression might thus be a derived feature of feeding in non-iguanian lizards and might be linked to the less-developed tongue, and the gradual decrease of its importance during feeding in scleroglossan lizards.

Despite the previously cited differences, the general jaw and tongue movement patterns observed in this study for scincids correspond to those observed for members of the more basal lizard clade of iguanian lizards (Throckmorton 1976; Smith 1984; Schwenk and Throckmorton 1989; Delheusy and Bels, 1992; Herrel et al. 1996a), and also fairly well to those for the more derived scleroglossan lizards (Smith 1984; Goosse and Bels 1992; Urbani and Bels 1995; Delheusy et al. 1995). This is corroborated by the results from the electromyographic analyses as these correspond generally well to previously reported data for other lizards (Throckmorton 1978; Smith 1982; Gans et al. 1985; Gans and De Vree 1986; Herrel et al. 1997) and seem to support the proposal of a common basic pattern of jaw muscle activity patterns in lizards as put forward by Bramble and Wake (1985).

Relation between food structure, movements and activation patterns

Swallowing

Given that, before swallowing, food items are already largely mechanically reduced, it is hardly surprising that few differences are observed when comparing the number of swallowing cycles for different food items. Only with endive were significantly fewer swallowing cycles observed. Here the size and weight of the food may come into play, leading to a reduction in the number of swallowing cycles for the lightest and smallest food. Similarly, the movements of the jaws and tongue did not differ greatly during swallowing. Whereas in *T. rugosa* no differences were observed between swallowing cycles for different food items, in *C. zebra* only the gape distance was modulated, resulting in an increased mouth opening during endive and banana swallowing. In the case of banana this is most likely the result of the sticky nature of the food. A larger mouth opening will then simplify the passage of the food upon tongue retraction. During endive swallowing, on the other hand, it is unclear why the animals should open their jaws further.

Intraoral transport

During intraoral transport, on the other hand, the differences in the properties of the food affect the kinematic patterns of jaws and tongue in many ways. However, the extent of modulation observed was different in both species. In *C. zebra* the most striking food effects are the decrease of the duration of the total cycle and the SO while feeding on endive, and the decreased tongue displacement and reduced duration of the FC during banana intraoral transport. In contrast, the most notable food effects in *T. rugosa* are the shortening of the FC and a decrease of the gape distance while feeding on grasshoppers (see below).

As has been argued previously, the main function of the SO is to assure a good tongue-food contact (Bramble and Wake 1985). A reduction of the duration of this phase while feeding on endive indicates that either the tongue of *C. zebra* adheres better to leaf-like foods, or that lighter foods do not require such a tight adherence and are easier to transport. In general, the variation in cycle time is caused by differences in the duration of the SO, which is in turn related to food type (e.g. Thexton et al. 1980; Herrel et al. 1996a).

The results of the electromyographic analysis in *C. zebra* indicate that all jaw closers show higher recruitment levels for a longer period of time while eating endive. This strong response for endive is most likely related to the toughness of the food. In *T. rugosa*, on the other hand, jaw closers are mainly recruited for a longer period while eating snails (which is due to the tetanic activation of the jaw closers, see Gans and De Vree 1986) and endive. While eating mice, on the other hand, post-bursts are more prominent. These observations correspond to previously reported qualitative differences in the EMG traces of some jaw closers in the lizard *Uromastix aegyptius* while feeding on different food items (Throckmorton 1978). Apparently, most lizards respond to changes in food characteristics by modulating their basic motor pattern, resulting in the observed variation in the jaw and hyolingual kinematics.

Food characteristics

Previously, the physical features of food items such as the size and weight (Urbani and Bels 1995), the shape (Goosse and Bels 1992), the mechanical resistance (Herrel et al. 1996a) and the physical properties of the food item in general (Bels and Baltus 1988) have been forwarded as playing an important role in triggering the modulation of the feeding cycle. However, the food characteristics were generally not quantified in these studies, and thus these hypotheses remain largely speculative. In this study, it is demonstrated that lizards are clearly able to respond to the mechanical resistance of the food by differentially recruiting their jaw closers. When crushing together food items such as apple, the recruitment of the jaw closers of both species is more intense for longer periods of time than when crushing pieces of banana or tomato of a similar mass, size and shape (Figs. 2, 6). Since, in general, the toughness of food increases with mass, it is likely that animals will bite harder on larger food items. That the toughness of the food item is a very important characteristic for the animals, is nicely demonstrated in the case of endive. Although pieces of endive are relatively light and not bulky, they are very tough (Fig. 2, Table 1). Both animals respond to this by recruiting their jaw muscles maximally. For example, in *T. rugosa*, the intensity of the jaw muscle recruitment is just as strong when feeding on either snails or endive. Presumably, the lizards are capable of evaluating the mechanical resistance of the

food. This might be mediated through muscle spindles or tendon organs associated with the jaw closer muscles (see Crowe 1992 for an overview).

However, food toughness or mass are clearly not the only factors that affect the motor pattern and kinematic output. Surprisingly, although newborn mice should be classified as soft food items (see Fig. 2), *T. rugosa* still responds with a very strong recruitment of the jaw closers which cannot be discerned from muscular recruitment during snail- or endive-crushing cycles (Figs. 3, 5). Presumably, the animals respond to the mobility of the prey. When feeding on mobile prey, a maximal or near-maximal activation of the jaw closers will result in the death of the prey after one or two bites. The recognition (through visual and/or vomerolfactory stimuli) of the food as mice, apparently results in the maximal activation of the jaw closers. Presumably, the jaw closers will continue to be recruited at such high levels as long as cues from a struggling prey are perceived, as has been observed in constricting snakes (B. Moon, personal communication). As these lizards are rather clumsy (see Gans et al. 1985), a quick killing of a potentially mobile prey is undoubtedly the best way to assure that it will not escape. Indirect support for this is the observation that *T. rugosa* responds to grasshoppers by decreasing the gape distance, and thus the duration of the FC, during intraoral transport cycles. By decreasing the time that the prey is not in contact with the jaws (i.e. during FOs and FCs) the chances that a mobile prey can escape are likely to be reduced. Qualitative observations of EMG recordings of the jaw closers of *T. rugosa* while eating grasshoppers show similar results. Although grasshoppers are rather soft food items, the jaw closers still seem to be recruited near maximally.

Effects of specialisation?

One peculiar feature observed is that whereas in *C. zebra* the onset-offset pattern does not differ while eating different foods, in *T. rugosa* it clearly does. It has been proposed previously that the trophic breadth of an organism might be related to behavioural and functional versatility or flexibility (Liem 1978, 1984). Theoretically, this implies that dietary specialists are less flexible or versatile in their feeding capabilities than generalists (see Ralston and Wainwright 1997). In our study we would thus predict that *C. zebra*, being a food specialist, would exhibit less diversity in motor and kinematic patterns while feeding on a range of prey types. Although the variety of food items presented is smaller, there seems to be some kind of limitation of the versatility in motor pattern in *C. zebra* when compared to *T. rugosa*. Whereas *C. zebra* apparently only modulates the recruitment levels and the duration of jaw muscle activity, *T. rugosa* alters both the complete timing (onset and duration) as well as the recruitment levels. A similar observation was made in pufferfish, where a direct relationship between trophic breadth of the species and its

functional versatility for buccal manipulation could be demonstrated (Ralston and Wainwright 1997). Yet, for the scincids studied here, the EMG data are not supported by the kinematics. The observed variability in jaw and tongue movement patterns is equally large or larger in the food specialist. Possibly the reduced versatility of the motor control of the jaw system in *C. zebtrata* is compensated by an increased flexibility and versatility of the hyolingual apparatus. However, as no data on hyolingual muscle activity patterns are available, this hypothesis remains purely speculative.

Specialised fixed motor patterns, as observed for fish (Grobeck 1983), and salamanders (Reilly and Lauder 1989) were not observed in *C. zebtrata* during feeding on its preferred prey type (i.e. leaves, see Honegger 1975; Parker 1983). In lizards the use of feedback mechanisms to fine-tune the feeding cycle is apparently widely used (Schwenk and Throckmorton 1989; Herrel et al. 1997; this study). It has, for example, been demonstrated that changes in food type may result in an increase of the cycle duration, an increase in the duration of subsets of a feeding cycle and changes in maximal excursions of jaws and tongue during feeding (Urbani and Bels 1995; Herrel et al. 1996a; this study). This variety of patterns observed while feeding on different food types is a nice reflection of the modulatory capabilities of lizards. In many of the vertebrate groups studied to date, extensive modulation seems to be the rule rather than the exception (e.g. see Aerts 1990 for fish; Herrel et al. 1997 and this study for lizards; Van Damme and Aerts 1997 for turtles; Gorniak and Gans 1980; Thexton et al. 1980 for mammals). However, as argued by Galis (1996) one should be cautious when considering the presence/absence of stereotypy of motor patterns. Further research on other lizards is clearly required to allow an evaluation of the results in a strict phylogenetic context.

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References

- Aerts P (1990) Variability of the fast suction feeding process in *Astatotilapia elegans* (Teleostei: Cichlidae): a hypothesis of peripheral feedback control. *J Zool (Lond)* 220: 653–678
- Basmajian JV, De Luca CJ (1985) *Muscles alive: their functions revealed by electromyography*. Williams and Wilkins, Baltimore
- Beach J, Gorniak GC, Gans C (1982) A method for quantifying electromyograms. *J Biomech* 15: 611–617
- Bels V, Baltus I (1988) The influence of food items on the feeding cycle in *Anolis equestris* (Reptilia: Iguanidae). *Copeia* 2: 479–481
- Bock WJ, Shear CR (1972) A staining method for gross dissection. *Anat Anz* 130: 222–227
- Bramble D, Wake DB (1985) Feeding mechanisms of lower tetrapods. In: Hildebrand M, Bramble D, Liem K, Wake D (eds) *Functional vertebrate morphology*. Harvard University Press, Cambridge, MA, pp 230–261
- Crowe A (1992) Muscle spindles, tendon organs, and joint receptors. In: Gans C, Ulinski PS (eds) *Biology of the reptilia*, vol 17. University of Chicago Press, Chicago, pp 454–495
- Delheuy V, Bels VL (1992) Kinematics of feeding behaviour in *Oplurus cuvieri* (Reptilia: Iguanidae). *J Exp Biol* 170: 155–186
- Delheuy V, Brillet C, Bels VL (1995) Etude cinématique de la prise de nourriture chez *Eublepharis macularius* (Reptilia, Gekkonidae) et comparaison au sein des gekkos. *Amphibia-Reptilia* 16: 185–201
- De Vree E, Gans C (1987) Kinetic movements in the skull of adult *Trachydosaurus rugosus*. *Anat Hist Embryol* 16: 206–209
- De Vree F, Gans C (1989) Functional morphology of the feeding mechanisms in lower tetrapods. In: Splechna H, Hilgers H (eds) *Fortschritte der Zoologie*, vol 35. Fischer, New York, pp 115–127
- Dullemeijer P (1974) *Concepts and approaches in animal morphology*. Van Gorcum, Assen
- Galis F (1996) The application of functional morphology to evolutionary studies. *TREE* 11: 124–129
- Gans C (1992) *Electromyography: structures and systems, a practical approach*. Oxford University Press, Oxford, pp 175–204
- Gans C, De Vree F, Carrier D (1985) Usage pattern of the complex masticatory muscles in the shingleback lizard, *Trachydosaurus rugosus*: a model for muscle placement. *Am J Anat* 173: 219–240
- Gans C, De Vree F (1986) Shingle-back lizards crush snail shells using temporal summation (tetanus) to increase the force of the adductor muscles. *Experientia* 42: 387–389
- Gomes NMB (1974) Anatomie comparée de la musculature trigéminal des lacertiliens. *Mem Mus Natl Hist Nat, Ser A (Zool)* 90: 1–107
- Goosse V, Bels VL (1992) Kinematic and functional analysis of feeding behaviour in *Lacerta viridis* (Reptilia: Lacertidae). *Zool Jb Anat* 122: 187–202
- Gorniak GC, Gans C (1980) Quantitative assay of electromyograms during mastication in domestic cats (*Felis catus*). *J Morphol* 163: 253–281
- Grobeck DB (1983) The “lie-in-wait” feeding mode of a cryptic teleost, *Synanceia verrucosa*. *Env Biol Fishes* 8: 191–202
- Haas G (1973) Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. In: Gans C, Parsons T (eds) *Biology of the Reptilia*, vol 4. Academic Press, London, pp 285–490
- Herrel A, Cleuren J, De Vree F (1995) Prey capture in the lizard *Agama stellio*. *J Morphol* 224: 313–329
- Herrel A, Cleuren J, De Vree F (1996a) Kinematics of feeding in the lizard *Agama stellio*. *J Exp Biol* 199: 1727–1742
- Herrel A, Van Damme R, De Vree F (1996b) Sexual dimorphism of head size in *Podarcis hispanica atrata*: testing the dietary divergence hypothesis by bite force analysis. *Neth J Zool* 46: 253–262
- Herrel A, Cleuren J, 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
- Herrel A, Aerts P, De Vree F (1998a) Static biting in lizards: functional morphology of the temporal ligaments. *J Zool (Lond)* 224: 135–143
- Herrel A, Aerts P, De Vree F (1998b) Ecomorphology of the lizard feeding apparatus: a modelling approach. *Neth J Zool* 48: 1–25
- Hiiemae KM, Crompton AW (1985) Mastication, food transport and swallowing. In: Hildebrand M, Bramble D, Liem K, Wake D (eds) *Functional vertebrate morphology*. Harvard University Press, Cambridge, pp 181–208
- Honegger RE (1975) Beitrag zur Kenntnis des Wickelskinnes *Corucia zebtrata*. *Salamandra* 11: 27–32
- Jeronimidis G (1991) Mechanical and fracture properties of cellular and fibrous materials. In: Vincent JFV, Lillford PJ (eds)

- Feeding and the texture of food. Cambridge University Press, Cambridge, pp 1–17
- Kinghorn JR (1928) Herpetology of the Salomon Islands. *Rec Aust Mus* 16: 123–178
- Lakjer T (1926) Studien über die Trigemini-versorgte Kaumuskulatur der Sauropsiden. Carlsbergstiftung, CA Rietzel, Kopenhagen
- Lauder GV (1996) The argument form design. In: Rose MR, Lauder GV (eds) *Adaptation*. Academic Press, London, pp 55–91
- Liem KF (1978) Modulatory multiplicity in the functional repertoire of the feeding mechanism of chlid fishes. I. Piscivores. *J Morphol* 158: 323–360
- Liem KF (1984) Functional versatility, speciation and niche overlap: are fishes different? In: Meyers DG, Strickler JR (eds) *Trophic interactions within aquatic ecosystems*. Westview Press, Boulder, Colorado, pp 269–305
- Loeb GE, Gans C (1986) *Electromyography for experimentalists*. University of Chicago Press, Chicago
- Lucas PW (1979) The dental-dietary adaptations of mammals. *Neues Jahrb Geol Palaeontol Monatsh* 8: 486–512
- Lucas PW (1982) Basic principles of tooth design. In: Kurten B (ed) *Teeth: form, function and evolution*. Columbia University Press, New York, pp 154–162
- Lucas PW, Luke DA (1984) Basic principles of food break down. In: Chivers DA, Woods BA, Bilsborough A (eds) *Food acquisition and processing in primates*. Plenum Press, New York, pp 283–301
- Nishi S (1916) Zur vergleichenden Anatomie der eigentlichen Rückenmuskeln. *Morphol Jahrb* 50: 219–247
- Oelrich TM (1956) The anatomy of the head of *Ctenosaura pectinata*. *Misc Publ Mus Zool Univ Mich* 94: 1–122
- Parker F (1983) The prehensile tailed skink (*Corucia zebrata*) on Bougainville island, Papua New Guinea. In: Rhodin A, Miyata K (eds) *Advances in herpetology and evolutionary biology*, Smithsonian Institution Press, Washington DC, pp 435–440
- Ralston KR, Wainwright PC (1997) Functional consequences of trophic specialisation in pufferfishes. *Functional Ecology* 11: 43–52
- Reilly S, Lauder G (1989) Physiological bases of feeding behaviour in salamanders: do motor patterns vary with prey type? *J Exp Biol* 141: 343–358
- Rice WR (1989) Analyzing tables of statistical tests. *Evolution* 43: 223–225
- Schwenk K, Throckmorton GS (1989) Functional and evolutionary morphology of lingual feeding in squamate reptiles: phylogenetics and kinematics. *J Zool (Lond)* 219: 153–175
- Sibbing FA (1991a) Food processing by mastication in cyprinid fish. In: Vincent JFV, Lillford PJ (eds) *Feeding and the texture of food*. Cambridge University Press, Cambridge, pp 57–92
- Sibbing FA (1991b) Food capture and oral processing. In: Winfield IJ, Nelson JS (eds) *Systematics, biology and exploitation*. Chapman and Hall, London, pp 377–412
- Smith KK (1982) An electromyographic study of the function of the jaw adducting muscles in *Varanus exanthematicus*. *J Morphol* 173: 137–158
- Smith KK (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 KK (1986) Morphology and function of the tongue and hyoid apparatus in *Varanus* (Varanidae, Lacertilia). *J Morphol* 187: 261–287
- Thexton AJ, Hiemae KM, Crompton AW (1980) Food consistency and bite size as regulators of jaw movement during feeding in the cat. *J Neurophysiol* 44: 456–474
- Thompson D'AW (1917) *On growth and form*. Cambridge University Press, Cambridge
- Throckmorton GS (1976) Oral food processing in two herbivorous lizards, *Iguana iguana* (Iguanidae) and *Uromastix aegyptius* (Agamidae). *J Morphol* 148: 363–390
- Throckmorton GS (1978) Action of the pterygoideus muscle during feeding in the lizard *Uromastix aegyptius* (Agamidae). *Anat Rec* 190: 217–222
- Urbani JM, Bels VL (1995) Feeding behaviour in two scleroglossan lizards: *Lacerta viridis* (Lacertidae) and *Zonosaurus laticaudatus* (Cordylidae). *J Zool (Lond)* 236: 265–290
- Van Damme J, Aerts P (1997) Kinematics and functional morphology of aquatic feeding in Australian snake-necked turtles (Pleurodira; *Chelodina*). *J Morphol* 233: 113–125
- Wineski LE, Gans C (1984) Morphological basis of the feeding mechanics in the shingle-back lizard *Trachydosaurus rugosus* (Scincidae, Reptilia). *J Morphol* 181: 271–295