rat, the transit time is about 24% of the cycle, or 5–12 times greater than in the poikilotherms. In these low heart rate animals, each pressure wave will be reflected within the aorta 20–50 times before the next cardiac contraction begins. Considering that wave amplitude decreases with each reflection, and that energy losses occur due to hysteresis of the artery wall and blood viscosity[1], each pulse will be almost completely attenuated before the next wave occurs. Therefore, there will be no significant interaction between successive pressure waves; no wave propagation effects, such as pulse amplification, distortion and impedance oscillations will occur, and the arterial systems of these animals should function as simple Windkessels. Indeed, haemodynamic studies of the turtle[16], frog[10], and python snake[24] demonstrate that this is the case for lower vertebrates. In contrast, the much higher heart rate in mammals compared to poikilotherms creates a complex transmission line system in which the interaction of reflected waves with successive pulses produces significant wave propagation effects that are absent from the simpler Windkessel[1,15]. Thus, it is heart rate, rather than differences in the vessel elasticity, which is the major factor determining whether the aorta acts like a Windkessel, as in poikilotherms, or like a transmission line as in mammals. Although the circulatory systems of the toad, lizard, and snake may be described by a much simpler haemodynamic model than can be applied to mammals, the aortae of these lower vertebrates have mechanical design features which are functionally similar to those of mammals.

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A first report of relative movements within the hyoid apparatus during feeding in *Anolis equestris* (Reptilia: Iguanidae)

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Summary. The movements of the hyoid apparatus of *Anolis equestris*, during mechanical reduction of prey, have been studied by cinefluoroscopy. In the SO and FO stages, ceratobranchials I move forward faster than the ceratohyals. Muscle stimulation experiments show that contractions of the m. ceratohyoideus and m. mandibulohyoideus I produce this movement. The other hyoid and extrinsic muscles of the tongue may be divided into protractors and retractors. In the FC-SC stage, the tongue-hyoid complex moves backward. The movements of ceratobranchials II follow those of the other elements after a short delay.
Key words. Lizards; feeding; mechanical reduction; hyoid apparatus; tongue.

The tongue-hyoid complex of early tetrapods seems to have been used in several distinct activities: feeding, drinking, flicking and display. Feeding consists of cyclic movements of the complex co-ordinated with jaw cycles[1-3]. A model of the tongue movement during feeding of a generalized tetrapod has been constructed on the basis of some earlier studies of amphibians and reptiles[3].

In lizards, the wide variation of tongue morphology[4] and its adaptation to their diets have been clearly demonstrated[5]. Only a few studies have presented the movements of the hyoid and the tongue during food manipulation. Dorso-ventral and antero-posterior movements of the whole hyoid-tongue complex have been reported in *Chameleo dilepis*[6], *Ctenosaura similis* and *Tupinambis*

nigropunctatus[1]. Variation in hyoid and tongue morphology has been used in a tentative reconstruction of the evolution of the mechanism of tongue projection from Agamidae to Chamaeleontidae[7, 8], without experimental data. Variations of the angle of the hyoid elements during prey ingestion have also been shown in *Varanus* lizards which are so specialized that the tongue does not participate in intraoral manipulation of food[9]. In fleshy-tongued lizards, the relative movements of the hyoid elements (and the tongue) during the feeding sequence have not been studied adequately.

Our lack of knowledge of hyoid movements from comparative and evolutionary perpectives stems from one main factor: relative movements of the cartilaginous hyoid elements are difficult to observe by cinefluoroscopy in small or middle-sized fleshy-tongued lizards. Only the ceratobranchials I are bony, all other elements being less completely calcified[10]. Markers around the hyoid elements are needed in cinefluoroscopic observations. The cyclic movements of the tongue-hyoid complex involved in food ingestion (from food (prey) capture to pharyngeal packing) are associated with the four stages of the gape cycles : slow open (SO), fast open (FO), fast close (FC) and slow close-power stroke (SC-PS)[1, 3]. In *Anolis equestris*, a typical fleshy-tongued lizard, correlation between the entire hyoid movement and the stages of the gape has been found to be slightly different during the mechanical reduction of the food and during its transport to the esophagus. *A. equestris*, an insectivorous iguanid lizard, was chosen for this research because calcification of the hyoid elements allowed us to obtain good cinefluoroscopic data. Here we report a first analysis of the relative movements of the hyoid elements during cyclic activities of the tongue-hyoid complex in mechanical reduction of the food item. We will compare our observations with the results of previous functional studies of the hyoid movements of other lizards.

Materials and methods

Two individuals of *A. equestris* feeding on living locusts were filmed by V. Goosse, S. Renous and J. P. Gasc at 61 frames per second using a Massiot-Philips cinefluoroscopic apparatus (41 kV, 0.01 s) in the Laboratory of Comparative Anatomy of the National Museum of Natural History, Paris. The length of the locusts was 3.4 +/ − 0.2 cm (mean and standard deviation). A lead marker was inserted within the prey so that its movements could be followed during the cyclic movements of the feeding behavior. Six feeding cycles were analyzed using a graphic table and a computer program which allowed us to obtain the horizontal (X) and vertical (Y) movements of selected points. The movements of the elements of the hyoid apparatus were observed relative to a metal grid placed behind the lizard. The movements of hyoid elements were recorded by tallying the coordinates of their intersections with the ventral border of the lower jaw. The gape and the movements of the hyoid elements were

plotted against time expressed in frames. A series of electrical experiments was conducted to test the function of the hyoid and extrinsic muscles of the tongue involved during prey manipulation. The contractions of the muscles were produced by using a muscle stimulator (Grass S48).

Results and discussion

The cyclic movement of the jaw in *A. equestris* can be divided into four stages. However, the difference between the FC and SC is not well defined, as stated earlier[11]. The hyoid apparatus of *A. equestris* is typical of the anoles (fig. 1). The ceratobranchials II extend as far as the pectoral girdle. The ceratobranchials I and certohyals run postero-laterally and the lingual process projects anteriorly into the tongue. The ceratohyals are exterior and superior to the ceratobranchials I when the lizard is in its resting position (fig. 1). With the exception of the m. ceratohyoideus which is inserted between the ceratobranchials I and the ceratohyals, the hyoid muscles and the extrinsic muscles of the tongue may be divided into a protractor and a retractor group. The lines of action of the muscles are shown schematically in fig. 2 and their actions summarized in the table. Cinefluoroscopic data and observations of the lines of action of muscles and of the results of stimulating them enabled us to construct a hypothetical kinetic model for tongue and hyoid movements during food manipulation.

When the food item (locust) is within the buccal cavity of the lizard, its mechanical reduction begins. The cerato-
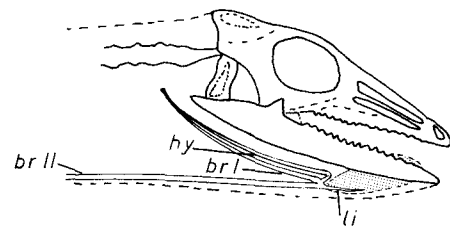

Figure 1. Lateral view of the hyoid apparatus in *Anolis equestris*. *br I*: ceratobranchial I; *br II*: ceratobranchial II; *hy*: ceratohyal; *li*: lingual process. The dashed area is the tongue.
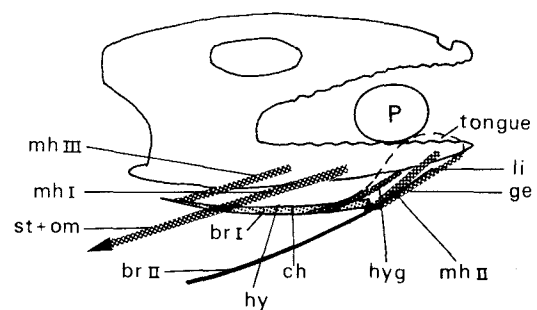

Figure 2. Schematic lateral view of the hyoid and extrinsic tongue muscles in *Anolis equestris*. *br I*: ceratobranchial I; *br II*: ceratobranchial II; *hy*: ceratohyal; *li*: lingual process; *ch*: m. ceratohyoideus; *ge*: m. genioglossus; *hyg*: m. hyoglossus; *mh I, II* and *III*: m. mandibulohyoideus I, II, III; *P*: prey in the buccal cavity; *st + om*: m. sternohyoideus + m. omohyoideus.
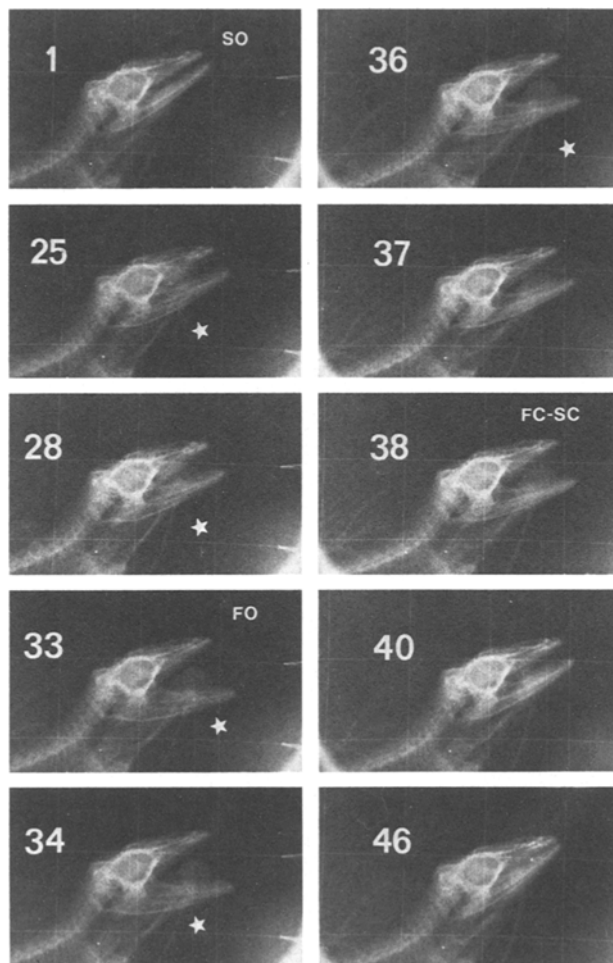
Figure 3. Lateral cinefluoroscopic views of a typical mechanical reduction in *Anolis equestris*. The prey is not visible in the successive frames because the marker is masked by the upper jaws. The number in the upper corner corresponds to the frame number. FC: fast close FO: fast open, SC: slow close, SO: slow open. The stars indicate the frames where the ceratobranchial I and the ceratohyal are laterally mid-crossed.
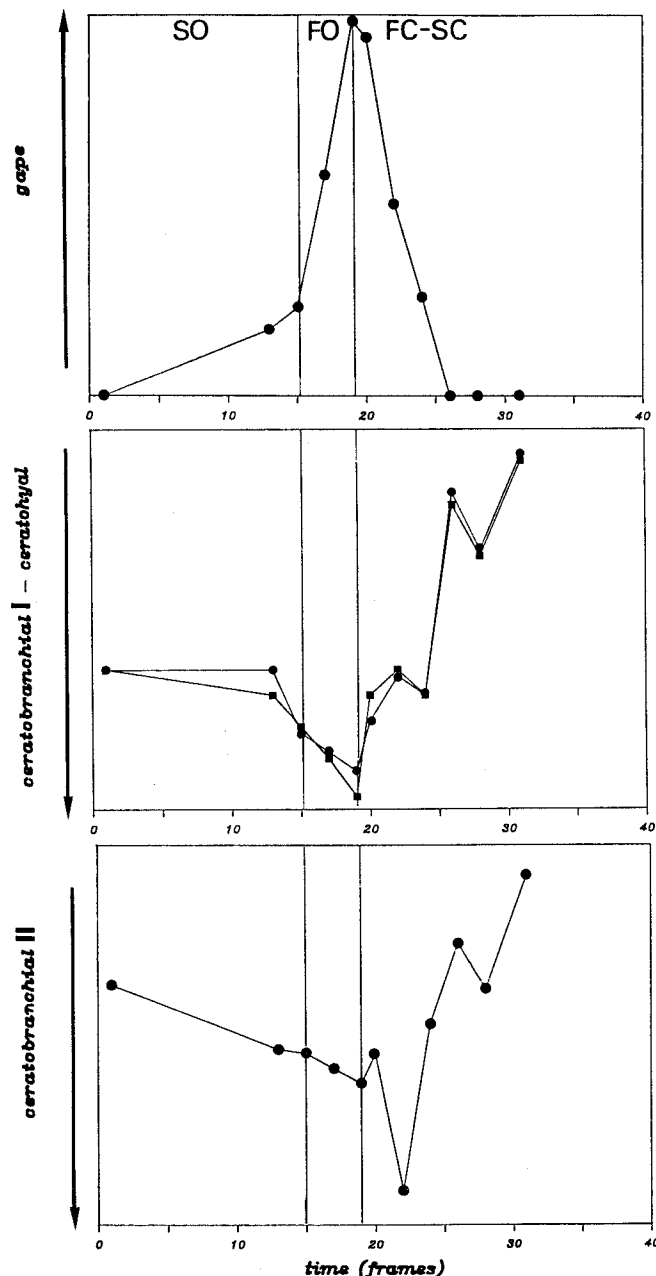

Figure 4. Kinematic patterns of selected hyoid and cranial (gape) components during a typical mechanical reduction in *Anolis equestris* feeding on a living locust: gape cycle, horizontal movement of the ceratobranchial I (■) and ceratohyal (●), horizontal movement of the ceratobranchials II. FC: fast close, FO: fast open, SC: slow close, SO: slow open. FC and SC stages are not clearly different. The arrow on the upper graph is directed upwards and the arrows on the other graphs are anteriorly directed.

branchials II are depressed relative to the hyoid body whereas the other elements (ceratobranchials I and ceratohyals) remain roughly parallel to the jaw (fig. 3, frame 2). During the SO and the main part of the FO stages, the hyoid elements move forward (figs 3 and 4). The movement of ceratobranchials I and ceratohyals is more rapid during the FO stage (fig. 3, frames 25–37). The ceratobranchials I move further anteriorly than the ceratohyals so that the two elements seem to be crossed in their mid-portion in figure 3 (frames 25–36). The hyoid body is therefore forced upward (fig. 3, frames 28–36). Stimulation experiments show that m. mandibulohyoideus II protracts the entire hyoid apparatus. M. mandibulohyoideus I protracts ceratobranchials I and m. mandibulohyoideus III the ceratohyals. During their protraction, ceratobranchials I and ceratohyals are slightly abducted (table). M. genioglossus protracts the tongue (table).
The hyoid elements cease to cross as they move backward at the beginning of the FC stage (fig. 3, frames 37–40).

Because the digitized points on the hyoid elements were above the crossing (along the lower jaw), figure 4 does not show this movement. The backward movement begins during the FO stage[4] or just at the maximal gape (fig. 4). The ceratobranchials I and the ceratohyals move to a position posterior to the one they occupied at the start of the cycle (fig. 3). M. sternohyoideus and omohyoideus retract the whole hyoid apparatus (table). M. hyo-

Effects of contraction of the hyoid and extrinsic muscles of the tongue obtained in the stimulation experiments. The muscle coding corresponds to figure 2.

| Muscles	Coding	Actions
M. ceratohyoideus	ch	Relative protraction of the ceratobranchials I
M. genioglossus	ge	Protraction of the tongue out of the mouth
M. hyoglossus	hyg	Retraction of the tongue
M. omohyoideus	om	Retraction of the hyoid apparatus
M. mandibulohyoideus I	mh I	Protraction of the hyoid apparatus, abduction of the ceratobranchials I
M. mandibulohyoideus II	mh II	Protraction of the hyoid body (and apparatus)
M. mandibulohyoideus III	mh III	Abduction of the ceratohyals
M. sternohyoideus	st	Retraction of the hyoid apparatus
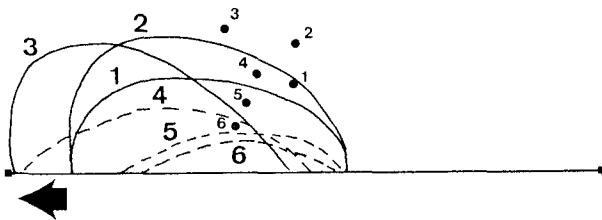
Figure 5. Lateral movement of the tongue within the buccal cavity during a typical cyclic movement of the mechanical reduction of the prey in *Anolis equestris*. The numbers 1 to 3 (normal lines) correspond to movements during the SO (1) and FO (2, 3) stages and the numbers 4 to 6 (dashed lines) correspond to the movements during the FC-SC stages. The horizontal line represents the lower jaw drawn between the symphysis and the articular bone (squares). The numbered points represent the movement of the marker introduced into the prey item for the corresponding position of the tongue. The arrow indicates the postero-anterior direction of the movement of the tongue.

glossus retracts the tongue on ceratobranchials I. Stimulation experiments did not show any clear adduction. The antero-posterior cyclic movements of ceratobranchials II are similar to those of the other hyoid elements, except that the posterior movement begins later. Apart from the insertion of m. mandibulohyoideus II at their anterior ends, the ceratobranchials II are free of muscle insertions. During the mechanical reduction of the prey item, it seems that the anterior movement of the ceratobranchials I relative to the ceratohyals produces the protraction of the tongue-hyoid complex. The more rapid protraction of the ceratobranchials is produced by stimulation of m. ceratohyoideus and/or m. mandibulohyoideus I. Relaxation of those muscles allow the movement to be reversed.

The protracted tongue is arched during the FO stage (fig. 5). This confirms our previous hypothesis, based on high speed cinematographic analysis of the same species[1,2]. The force exerted by the ceratobranchials I against the hyoid body should be greater than that exerted by the ceratohyals because the contracting m. ceratohyoideus and/or m. mandibulohyoideus I protract(s) the ceratobranchials I against the ceratohyals. This produces a forward and upward force acting on the tongue. The forward component results in the protraction of the lingual process and the tongue and the upward component elevates the lingual process (fig. 3). The tongue is then elevated during the FO stage (fig. 3). At the same time, the intrinsic musculature of the tongue would act to produce the hump-backed shape (figs 3 and 5).

Our data seem to confirm the model proposed for a generalized tetrapod[3], emphasizing the variability in the relative movements of the tongue-hyoid complex during each gape cycle (i.e., mechanical reduction). However, we show the importance of the relative movement during the cyclic displacement of the ceratobranchials I and ceratohyals in producing the cyclic movement of the tongue previously reported[3].

According to the previous data on food transport in *Ctenosaura similis* and *Tupinambis nigropunctatus*[1], the backward movement of the tongue begins during the FO stage (fig. 4). In the study presented here, it begins just at the end of this stage (maximal gape). The rhythmic activities of the oscillators producing the movements should be influenced by the relative position of the food item within the buccal cavity. The upper and forward movement of the tongue during the FO stage may push the prey item against the palatal structures and the dorsal maxillary teeth. When the backward movement of the tongue (and the hyoid) occurs during the FC and SC stages, shearing forces act on the prey aiding its reduction. Repositioning movements during mechanical reduction would change the points of application of these shearing forces. The hypothetical model has to be tested by quantitative electromyography and confirmed or not in other specialized lizards.

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