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Kinematic analysis of drinking by the lacertid lizard, *Lacerta viridis* (Squamates, Scleroglossa)

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The kinematics of drinking of *Lacerta viridis* were analysed. A drinking bout is composed of four phases: approach, immersion, emersion and withdrawal. The tongue and gravity are central to moving water through successive compartments of the buccal cavity and into the oesophagus. Upon the basis of form/function analysis of water intake and transport, a kinematic model of drinking in lizards is proposed.

Contents

Introduction

In tetrapods the tongue and hyoid apparatus form a morphological complex involved in feeding, drinking, chemoreception and social interactions. In lizards and to some extent snakes, skull form, tongue morphology and the mode of predation have been casually related (Schwenk, 1982, 1987). These morphological and behavioural characters have been used to divide lizards into two sister groups, iguanians (Iguanidae, Agamidae, Chamaeleontidae) and scleroglossans (Estes & Pregill, 1988). Following this division, iguanians possess a fleshy, glandular tongue used

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in prey capture (Schwenk & Bell, 1988; Schwenk & Throckmorton, 1989; Bels, 1990), and to transport food into the buccal cavity, whereas scleroglossans have a tongue with few glands that is generally not used to capture prey (Schwenk, 1988). In general, the scleroglossans catch prey by use of the jaws only (Frazzetta, 1984; Schwenk, 1987; Bels & Goosse, 1990), but exceptions occur in some Gekkonidae which may use the tongue for feeding (Bauer, 1985).

Classification of lizards based on functional specialization of the tongue has been proposed (Underwood, 1971) yielding two different groups: the *ascalabota* (Iguanidae, Agamidae and Gekkonidae) that use the tongue during intrabuccal food reduction and transport, and the *autarchoglossa* (Scincomorpha and Anguimorpha) that mainly use the tongue for chemoreception. But, here too exceptions occur. For example, some scincomorphs such as Teiidae (Smith, 1984) and Lacertidae (Goosse & Bels, 1989) use the tongue also in intrabuccal food reduction and transport. McDowell (1972) proposed that the tongue of the anguimorph varanid lizards (and snakes) is morphologically modified for a chemosensory function. Varanids do not use the tongue during feeding behaviour, and its role in drinking is not yet clearly understood (Smith, 1986). Thus, generally within scleroglossans, the relationship between morphology of the tongue and its use in chemoreception, feeding and drinking is not yet clearly established.

The limited information on the role of the tongue in drinking makes it difficult to evaluate the relative importance of tongue function in feeding and drinking. So far, two modes of drinking have been described in lizards. In the first (iguanians and scleroglossans), the tongue is used directly for lapping water (Smith, 1984). In the second (*Varanus*), the tongue is not used to collect water, but instead the snout is inserted directly into the liquid (Auffenberg, 1981; Smith, 1986). In our study, we selected a scleroglossan lizard, *Lacerta viridis*, for two reasons: (1) *L. viridis* uses the tongue for chemoreception (Goosse & Bels, 1990) but not for prey capture (Bels & Goosse, 1990). Therefore, in contrast to iguanians, the tongue surface is not specialized for an adhesion function related to prey capture (Schwenk, 1988); (2) for a scleroglossan lizard, the hyoid apparatus of *L. viridis* is primitive. It does not exhibit changes in morphological features such as absence of ceratobranchials II and/or lateral or longitudinal expansion of the ceratobranchials I and ceratohyals (Goosse & Bels, 1989).

This paper is part of a series on comparative mechanisms of drinking in lizards. It presents quantitative kinematic analyses of drinking movements in adult *L. viridis* which are intended to contribute to comparative data on the function of the jaw hyo-lingual complex during drinking. In the course of this study, specific questions were addressed: (1) How is the morphology of the tongue related to the mechanism of initial loading and then transporting of water? (2) What is the functional role of the tongue in displacements of the water through the buccal cavity and to the oesophagus? (3) What is the specific role of the throat in water displacements through the buccal cavity to the oesophagus? (4) What method is used to transport water from the buccal cavity to the stomach? and (5) Is the overall drinking mechanism in *L. viridis* similar to other lizards?

Materials and methods

Anatomy

Fresh and preserved specimens of adult male *Lacerta viridis* were used for dissection of the hyoid, tongue and buccal compartment system. Two preserved specimens were cut mid-sagittally and 2 specimens were stained *in toto* with red alizarine to characterize skeletal supports associated with the buccal cavity. Morphology of the tongue was based on 3 anatomical studies. First, gross morphology of the tongue and the

buccal floor were determined by dissection of 2 adult males under a Wild dissecting microscope. Secondly, microscopic analysis was undertaken of fresh tongues of 2 adult specimens paraffin embedded, cut in serial 7 μm transverse sections, and stained by Gallego and Haematoxyline-Eosine by routine methods. Thirdly, 4 tongues were examined by scanning electron microscopy. The tongues were placed for 24 h in 2·0% glutaraldehyde, then rinsed in glass-distilled water, methoxyethanol, and finally in 100% acetone. Thereafter, the tongues were critical-point dried, coated with 5 μm gold-palladium deposit, then ventral and dorsal surfaces were viewed using a JEOL scanning electron microscope.

To determine the position of the successive buccal compartments, the mouths of 3 preserved lizards were filled with liquid synthetic rubber (RTV Cara 502, Moulting Technics SPRL), then solidified using a catalyser (Cara RIY 502). This technique allowed us to obtain 3-dimensional casts of the buccal cavity and the beginning of the oesophagus.

General conditions of filming

Six adult male *Lacerta viridis* (snout–vent length: 107 ± 6 mm) from southern France were used in the filming experiments. Four specimens were filmed using a high-speed 1PL Camera fitted with an Angenieux zoom lens at a rate of 100 frames per second. Drinking movements were cinematically recorded on Kodak 16-mm colour film under 2 1000-Watt tungsten photoflood lights. Two specimens were cineradiographically filmed using a Massiot-Philips cinefluoroscopic apparatus in the Laboratoire d'Anatomie Comparé, Museum National d'Histoire Naturelle in Paris at 70 kV and a speed of 60 frames/s. All the specimens were deprived of water for 1–2 days before filming experiments. In both filming experiments, the lizards were placed in a small Plexiglas cage ($60 \times 10 \times 10$ cm). They drank from both large volumes of water and tiny drops. Thus, each lizard was filmed in 2 conditions: round dish (diameter 5 cm) full of water, and from individual water drops placed on the glass bottom of the cage with a small pipette. Seven sequences with a dish full of water and 8 sequences of drinking drops were filmed. The cycles were filmed at the beginning and at the end of the drinking bout. For cinefluoroscopic films, the water was mixed with barium sulphate. For several high-speed light films, the water was coloured with non-toxic alimentary green dye E102-E131 to visualize better the method by which the tongue was loaded with water. Fixed coordinates in the background were used as the reference system against which selected points on the lizard were compared. In high-speed light analysis, these fixed coordinates consisted of a plastic Cartesian grid of 1 cm^2 placed in view behind the lizard; in high-speed cineradiography these consisted of a fine wire Cartesian grid of 3 cm^2.

Kinematic analysis

All the drinking cycles were analysed using an Old Delft or NAC cine projector. These cycles were studied by digitizing selected points on the skull, mandible, throat and tongue from high-speed frames and also intrabuccal water surface from cinefluoroscopic frames using a graphic table (AGMEE, ULg), with a resolution of 0·14 mm, and a Copam AT or IBM microcomputer. The onset of each cycle was defined as the first frame in which the jaws began to open. To standardize the analysis and facilitate comparison, the following method was used. For each frame, the horizontal (x) and vertical (y) components of the series of points were digitized (Fig. 1a). The head point (HE) was used to compute head horizontal (x) and vertical (y) displacements during jaw cycles. The upper (UJ) and lower (LJ) jaw points and the point of the angulus oris (AO) defined the gape angle (GA). Relative vertical displacement of the points UJ and LJ allowed us to calculate the relative percentage of upper jaw elevation and lower jaw depression contributing to the gape angle. The horizontal and vertical displacements of the point on the tongue tip (TO) were used to compute the displacements of the tongue in drinking cycles from different water volumes (i.e. large volume in a dish, small volume in a drop). The displacements of the throat point (TH) compared to x and y coordinates of the point (TO) allowed us to evaluate the relative movements of the hyoid body (TH) and the tongue (TO) at corresponding intervals of the gape cycle. We computed simultaneously x and y coordinates of points, lengths

of the segments between 2 successive points, and angles between 2 successive segments defined by 3 digitized points. The data were then stored as a series of bipolar coordinates in a data file corresponding to each analysed cycle. A set of computer programs was used to analyse these data.

Analysis of water displacements through the buccal cavity took advantage of radiopaque water (barium sulphate) visible in the cinefluoroscopic high-speed films. Distinct corners of the radiopaque water were digitized to follow displacements of the water from the tongue to the oesophagus (Fig. 1b). On X-ray frames, the points AO, EY, HE, LJ, UJ, TH and TO were digitized simultaneously with the points D (drop) and ND (new drop) which follow the water volume picked up by the tongue during each protrusion/retraction cycle. Water displacements within the buccal cavity were followed with digitizing points at the anterior and posterior ends of each water compartment (barium shadow). For instance, water volume changes in compartment 1 were obtained by x and y coordinates of points 1 and 2. Displacement of the water between 2 successive compartments was calculated by measuring the x-coordinates of the posterior point of one compartment (for instance, point 2 in C1) and the anterior point of the next compartment (for instance, point 3 in C2). Movement of water into the oesophagus was measured by following displacement of x and y coordinates of point 6. The digitized data were smoothed using a 5-point equation (after Alexander, 1983).

Water surfaces occupying the compartments of the buccal cavity at successive intervals of a drinking bout were digitized for one generalized drinking sequence from a dish by measuring the area of the radiopaque shadow in the buccal compartments (computer program Atlas and Gis). At each successive time interval, the surface area of each barium shadow was measured and expressed as a percentage of the total barium surface area in all the buccal compartments. Regressions between x and y coordinates of the points LJ, TH, TO, UJ, and 1 to 6 were calculated to determine the correlation between tongue (TO), jaw (LJ, UJ), throat (TH) movements, and water displacements (points 1 to 6); the r values are given at probability level $P < 0{\cdot}05$.

Results

Anatomy

Skull

The general shape of the skull of *Lacerta viridis* is elongated and flattened dorsoventrally (Fig. 2). There are no kinetic joints in the adult skull. The widest dimension of the skull is at the level of the suborbital bars posterior to the orbit. The palatal shape defines the bony roof of the buccal cavity (Fig. 2). Anteriorly, each palatine is pierced by a small elongated groove, the fenestrae vomeronasalis, which is also recessed in the palatine. Each vomeronasal duct connects to its respective vomeronasal fenestra. When the mouth is closed, the fleshy body of the tongue makes contact with the roof of the mouth thus temporarily isolating the anterior buccal region, including the fenestrae vomeronasalis, from the posterior portion of the buccal cavity. The posterior margin of the secondary palate is defined in part by the posterior palatines, but mostly by the medial edges of the pterygoids.

Tongue

For descriptive purposes, the lizard tongue can be divided into four regions—forked tip, fore tongue, mid and hind tongue. The dorsal and lateral surface of the tongue tip is covered by strongly keratinized, stratified squamous epithelium (Plate I). Compared to the rest of the tongue, the tip is smooth and without any scales or raised surface texture.

The ventral surface of the fore and hind tongue, like the tongue tip, is covered by stratified squamous epithelium that is smooth and keratinized. However, lateral and dorsal surfaces are

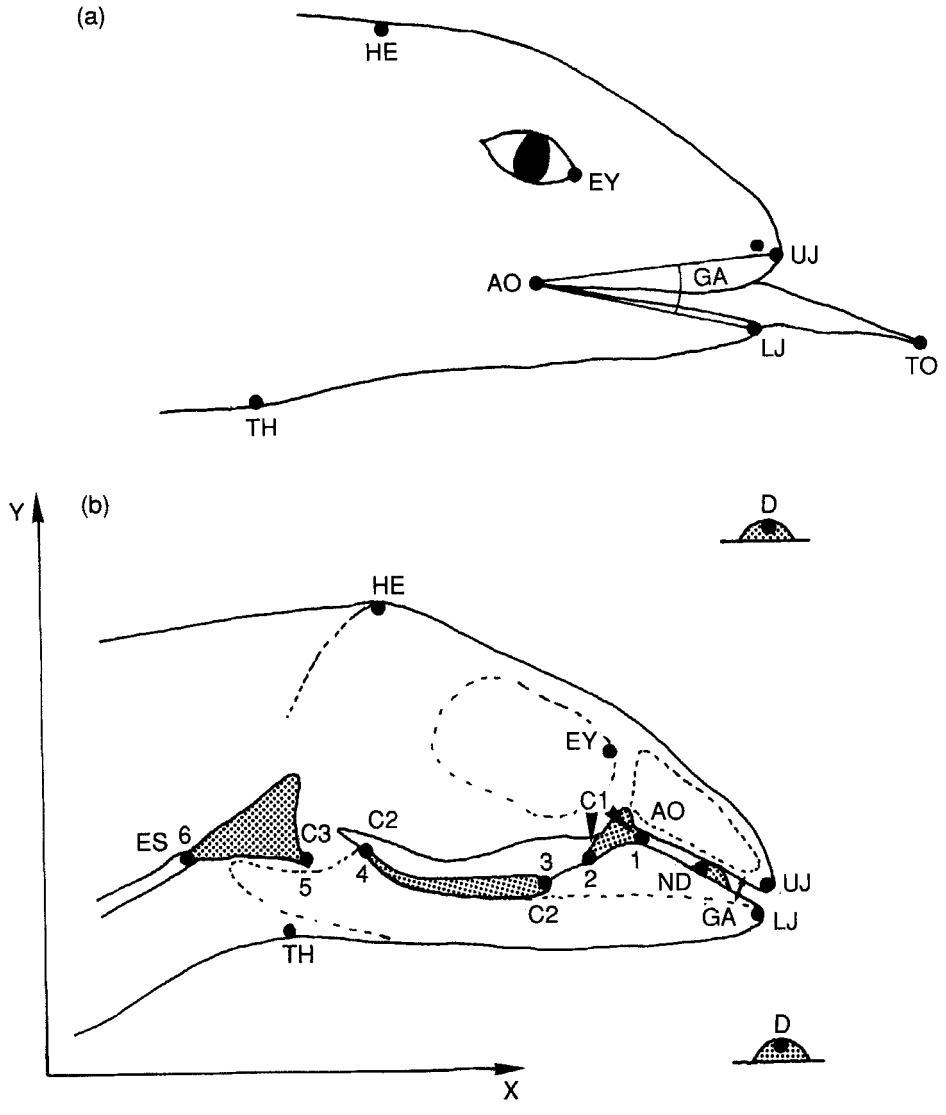

FIG. 1. Lateral head outlines directly from a high-speed (a) and cinefluoroscopic (b) frame of a drinking *Lacerta viridis* showing selected points and angles used to follow head displacements and water transfer. C1, C2 and C3, compartments of the buccal cavity; AO, angulus oris; D, external water drop; ES, oesophagus; EY, eye; GA, gape angle; HE, head; LJ, lower jaw; ND, new drop brought in the buccal cavity by the tongue; TH, throat; TO, tongue; UJ, upper jaw. Points 1–6 are used to examine water displacements successively through the buccal cavity and into the oesophagus.

roughened by the development within the epidermis of broad imbricated folds, the lingual scales. These are small, flat plates in the epithelium that are fixed along their anterior edges but posterior edges are free. Laterally, the fore and mid tongue epithelium forms longer lingual plicae. These plicae are also imbricated folds within the epithelium that extend around the sides of the tongue and continue transversely across the dorsolateral surface of the tongue.

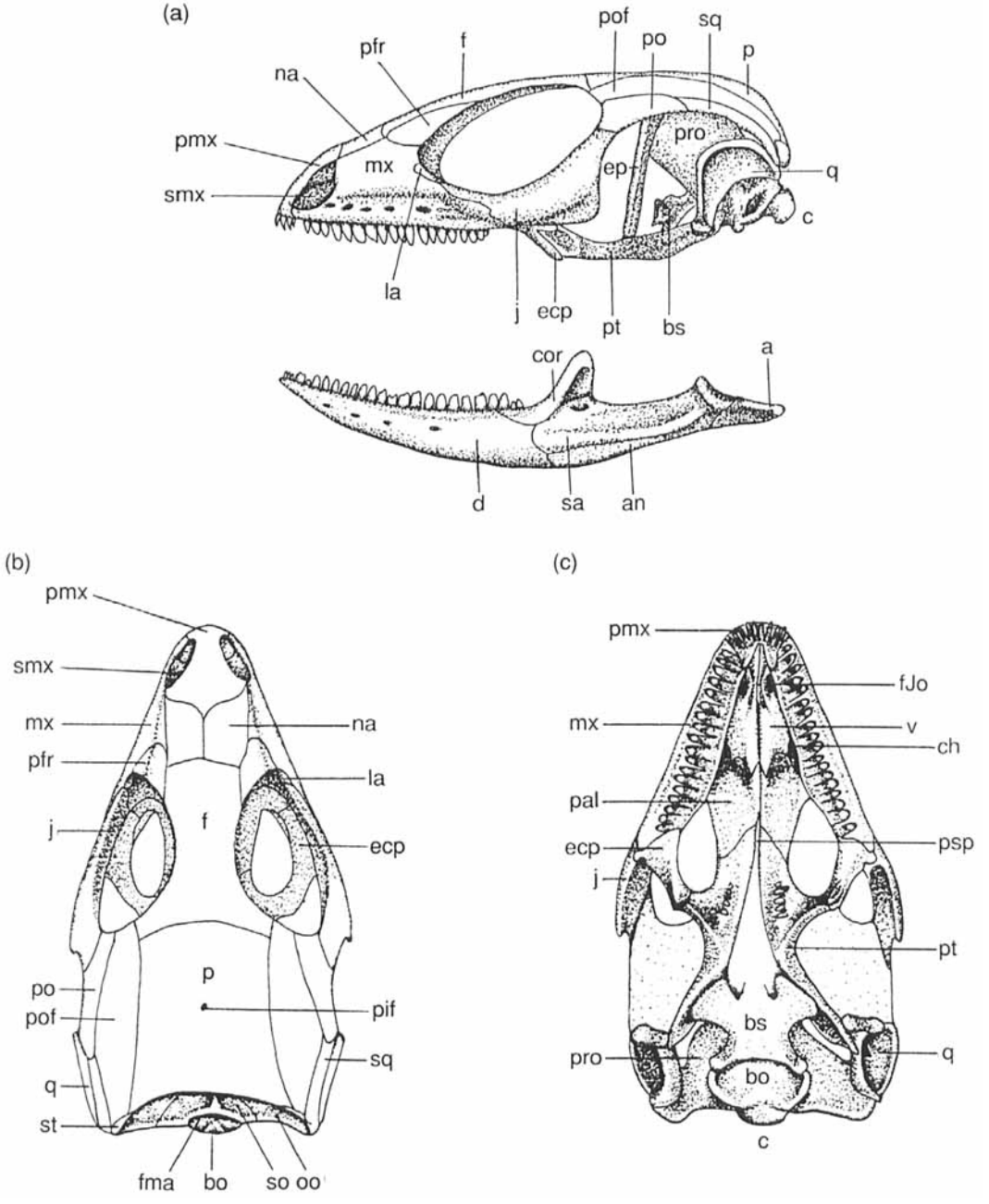

FIG. 2. Skull of *Lacerta viridis*. (a) Lateral view. (b) Dorsal view. (c) Ventral view. a, articular; an, angular; bo, basioccipital; bs, basisphenoid; c, condyle; ch, choana; cor, coronoid; d, dentary; ecp, ectopterygoid; ep, epipterygoid; f, frontal; fJo; fenestra of the Jacobson's organ; fma, foramen magnum; j, jugal, la lacrimal; mx, maxillary; na, nasal; oo, ootic; p, parietal; pal, palatine; pfr, prefrontal; pif, pineal foramen; po, postorbital; pof, postfrontal; pmx, premaxillary; pro, prootic; psp, parasphenoid; pt, pterygoid; q, quadrate; sa, surangular; smx, submaxillary; so, supraoccipital; sq, squamosal; st, supratemporal; v, vomer.

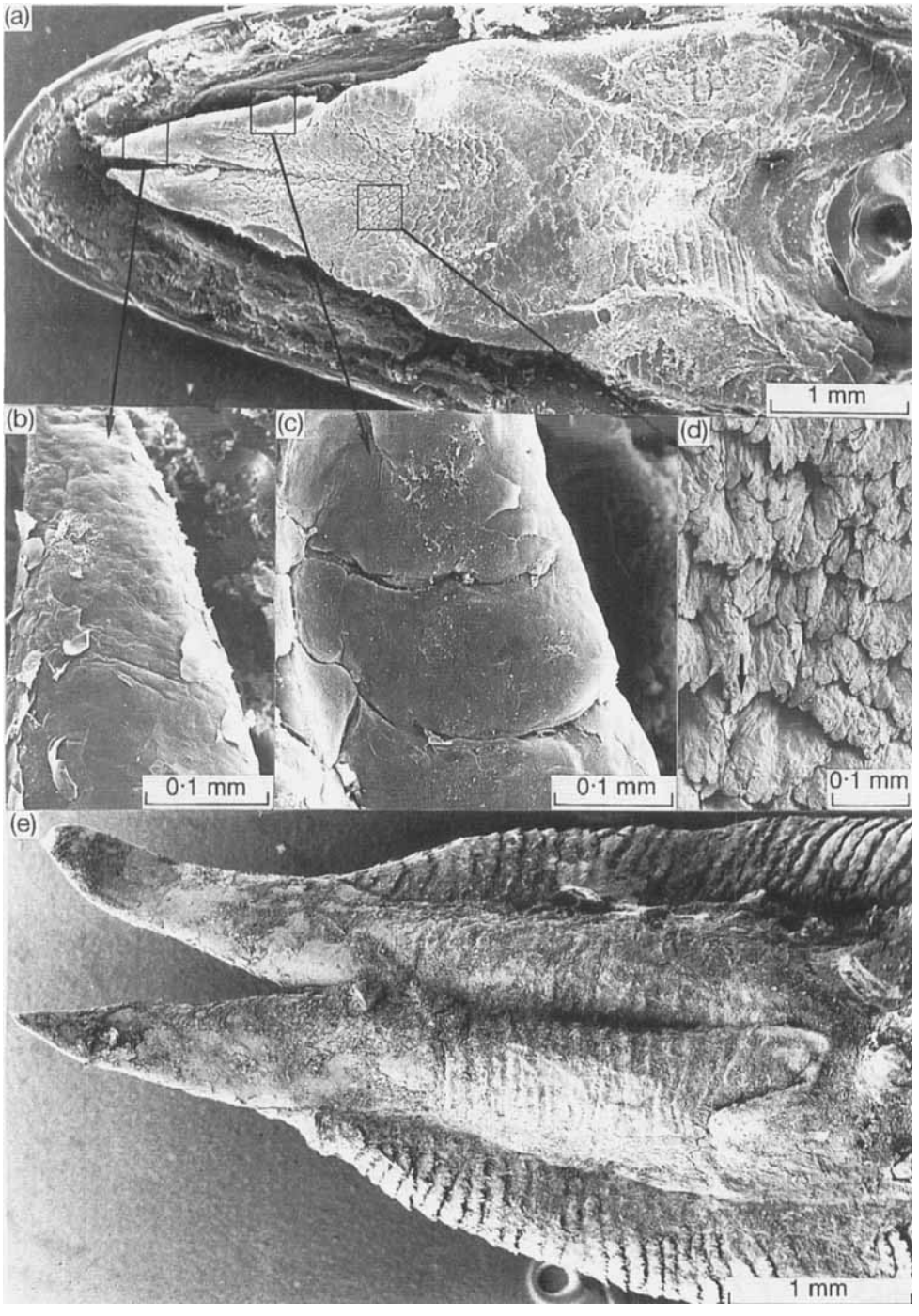

PLATE I. Scanning electron micrographs of the tongue in *Lacerta viridis*. (a) Dorsal view showing the tongue in resting position within the floor of the buccal cavity. (b) Stratified squamous epithelium of the tongue tips. (c) Lateral stratified squamous epithelium of the fore tongue. (d) Lingual scales of the fore tongue. Arrow points to the posterior free edge of one of these imbricated scales. (e) Ventral view of the tongue tips and fore tongue. Rows of imbricated lingual plicae form the lateral edges of the fore and hind tongue. The cut root of the tongue is at the far right.

The hind tongue is rooted ventrally into the floor of the mouth (Plate I). Lingual plicae continue around the lateral edge of the hind tongue and extend across its dorsal surface. The lingual scales and plicae have a 'grain'. If combed forward, their free posterior edges tend to lift up; if combed back, they lie flat. In the dermis immediately beneath the epidermis are found numerous spaces, devoid of erythrocytes, presumably lymphatic sinuses. These spaces are most numerous in the fore tongue, less so in the hind tongue, and absent in the forked tongue tip. The core of the tongue contains the glossal musculature. The lingual process of the hyoid apparatus runs through the hind tongue and into the caudal fore tongue, but does not enter the tongue tip.

Compartments of the buccal cavity

Water, laced with barium sulphate and followed by cinefluoroscopy, moved sequentially through three dynamic compartments within the buccal cavity (Fig. 3) during drinking. The most anterior and smallest of these was the buccal region termed *compartment* 1 (C1) that lay dorsal to the fore tongue (when retracted) and beneath the recessed vomeronasal fenestra. The second buccal compartment, *compartment* 2 (C2), was larger and more posteriorly positioned. When filling, it was crescent-shaped, and was connected to the first compartment through both dorsal and ventral channels. Dorsally, the second compartment included the posterior nasopharynx, a single, medial space behind and above the posterior edge of the secondary palate. During drinking, this dorsal space connected with spaces adjacent to the sides of the tongue along arching lateral channels located within the sides of the buccal cavity. *Compartment* 3 (C3) was the largest and the most posterior of the three. It included all of the posterior buccal cavity situated within the throat. Its anterior walls were rounded by the protruding swollen bellies of the paired pterygoideus muscle. Laterally, its walls were reinforced internally by the ceratobranchials of the hyoid apparatus that arched upward into the sides of the throat. The oesophagus departed from the centre of its posterior wall.

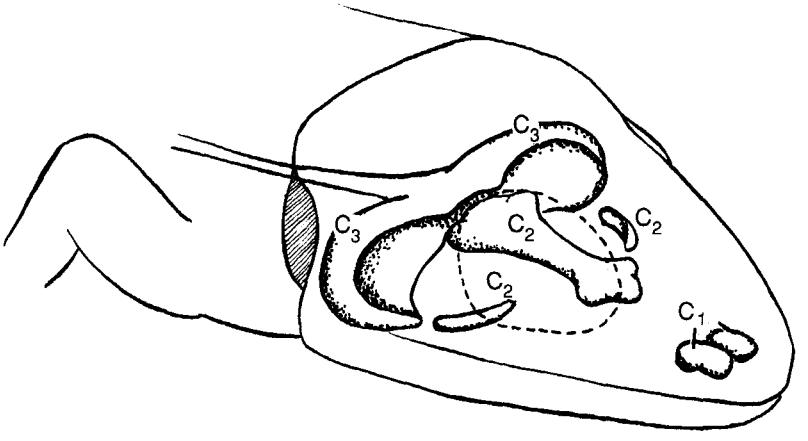

FIG. 3. Compartments of the buccal cavity in *Lacerta viridis*. Shapes are based upon casts of compartments from preserved specimens interpreted from direct inspection of cinefluoroscopic films. C1 is located within the recessed fenestrae vomeronasalis. C2 includes large, unpaired mid-dorsal and paired lateral, crescent-shaped spaces. C3 is the largest compartment; the oesophagus departs from its posterior wall and the belly of the pterygoideus muscle protrudes into its anterior wall.

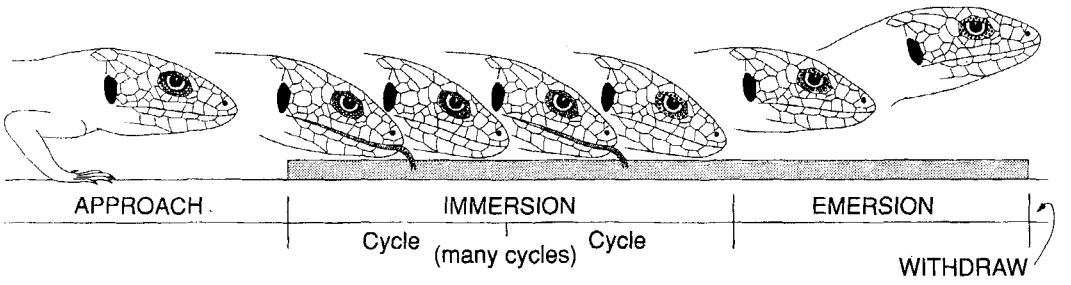

FIG. 4. Generalized drinking bout in *Lacerta viridis*. A drinking bout divides into four phases—approach, immersion, emersion, withdrawal. Repeated cycles of tongue protraction/retraction occur during immersion phase but diminish during emersion phase as the head is raised. Following emersion phase, immersion may be repeated or if completed the lizard withdraws.

The three compartments were connected, each representing parts of the buccal cavity. During drinking, each was used as a temporary holding area for incoming water that collected in the third compartment before entering the oesophagus and passing to the stomach.

Behaviour

General observation

Drinking bout: A drinking bout typically included four phases: approach, immersion, emersion, withdrawal (Fig. 4). The approach and withdraw phases, respectively, began and ended the drinking bout; immersion and emersion phases were occasionally repeated together in separate episodes of water intake and swallowing during a drinking bout. After a first drinking episode, the lizard occasionally remained in the same position before the water dish to begin a second episode of drinking.

During the approach phase, the lizard moved about the cage producing occasional tongue flicks at irregular intervals. Body transport eventually carried the head of the lizard into the proximity of the water. Contact of the tongue tip with the water was accompanied by cessation of movement about the cage, and the head was brought to a fixed position just above the water. This ended the approach phase and marked the onset of immersion phase. Specifically, the immersion phase started when water was first conveyed into the mouth by the tongue.

The occasional tongue flicks exhibited during the approach phase became very regular during the immersion phase, establishing a rhythmic pattern of protrusion/retraction cycles. Each such cycle consisted of two stages. During the first, the protraction stage, the jaws parted just enough to permit protrusion of the tongue that arched out and downward, entering the water. During the second, the retraction stage, the tongue carrying water was retracted into the mouth and the jaws closed. Each immersion phase consisted of 20–30 jaw/tongue cycles, each cycle taking about $0{\cdot}6 \pm 0{\cdot}4$ sec ($N = 15$). Some repositioning of the head occurred during immersion, but characteristically the head was held in a fixed position above the water throughout this phase while jaw/tongue cycles alone brought water into the mouth. The immersion phase ended and emersion phase began when the protruded tongue ceased to make regular contact with the water. Tongue contact with the water ceased initially as a result of shorter protrusions. This was followed by elevation of the head so that the snout tilted upward bringing it above the level of the throat and

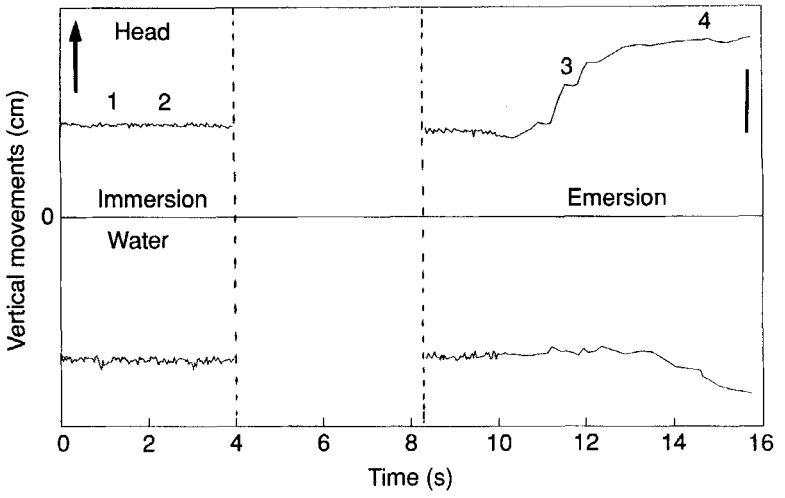

FIG. 5. General overview showing water movement correlated with head tilting. The head (HE, Fig. 1) and water (point 5, Fig. 1) are followed during a drinking bout. In the immersion phase, the horizontal slope of both plots indicates that the head is held fixed and the water begins to fill but does not move from C3. During emersion phase, the head is elevated, but note that water, for the first time, begins to flow downward (towards opening to oesophagus) filling now C3. Vertical bar at right equals 1 cm. The arrow indicates the up–down direction.

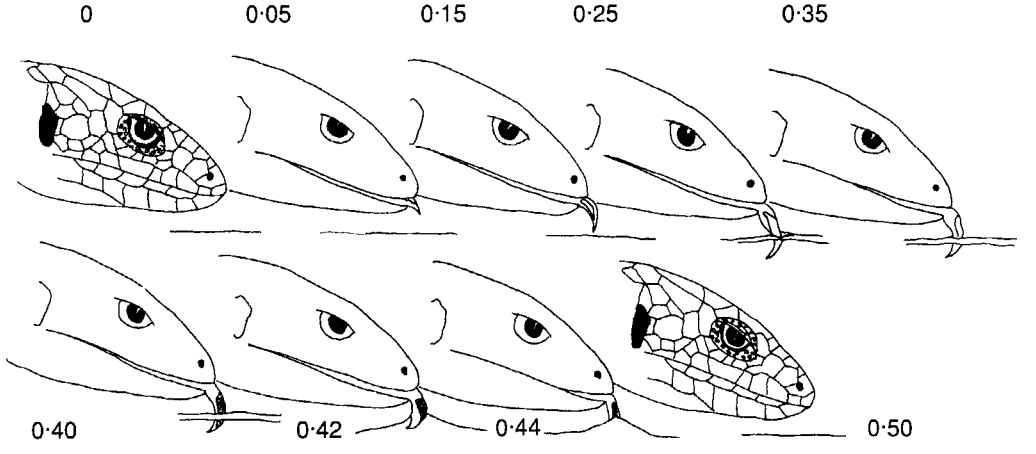

FIG. 6. Immersion Phase: Successive movements of the tongue in *Lacerta viridis* drinking from a dish. One protraction/retraction cycle is shown; shading on tongue indicates location of water. The successive outlines of the head were made directly from cinematographic film and above each is the successive running time(s) during this cycle.

lifting the tongue farther from the water (Fig. 5). Tongue protractions and retractions continued during emersion, but progressively became less frequent.

Within a drinking bout, the lizard occasionally exhibited successive episodes of water intake and swallowing. Water taken in and transported to successive buccal compartments (immersion) was moved to the oesophagus and swallowed (emersion). Occasionally, the lizard remained in the same

position before the water dish to initiate a second episode (immersion, emersion) of drinking. Thus, at the end of emersion the head might again be lowered and the lizard begin a second drinking episode. Eventually, the lizard moved away from the water, withdraw phase, to complete and end the drinking bout.

Tongue action: When drinking from a dish, the tongue protruded, dipped down into the water, and returned to the mouth (Fig. 6). Specifically, onset of protraction stage began when the jaws parted and the tongue emerged. The tongue moved first forward as it emerged but then arched downward so that first tip then fore tongue entered the water. During this protrusion, the tongue became dorsoventrally flattened and laterally spread, but it did not curl or bend back upon itself. Onset of the retraction stage was usually marked by formation of a depression dorsally at about the boundary between fore and hind tongue. The smooth retraction of the tongue returned it to the mouth and the jaws closed.

Lacerta viridis used the same two behavioural stages when drinking small volumes in drops or water films (Fig. 7). However, differences occurred in the tongue action. When drinking from a water drop, the tip of the protruding tongue made contact with the substratum and the fore tongue rolled over the tongue tip, flattening and expanding laterally, so that the dorsal surface was pressed into the water drop or 'mopped' upon the film of water covering the substratum. As the retraction stage began, a dorsal depression again formed on the tongue. Tongue protrusion began 3–4 ms after the initiation of gape opening, and retraction began 2–5 ms before gape closing when the water was in a dish. Corresponding times for drinking water drops are 2–4 ms and 2–6 ms, respectively, protrusion and retraction.

Kinematics

Gape, tongue, and throat movements

A representative pattern of jaw and tongue movements during drop drinking is shown in Fig. 8.

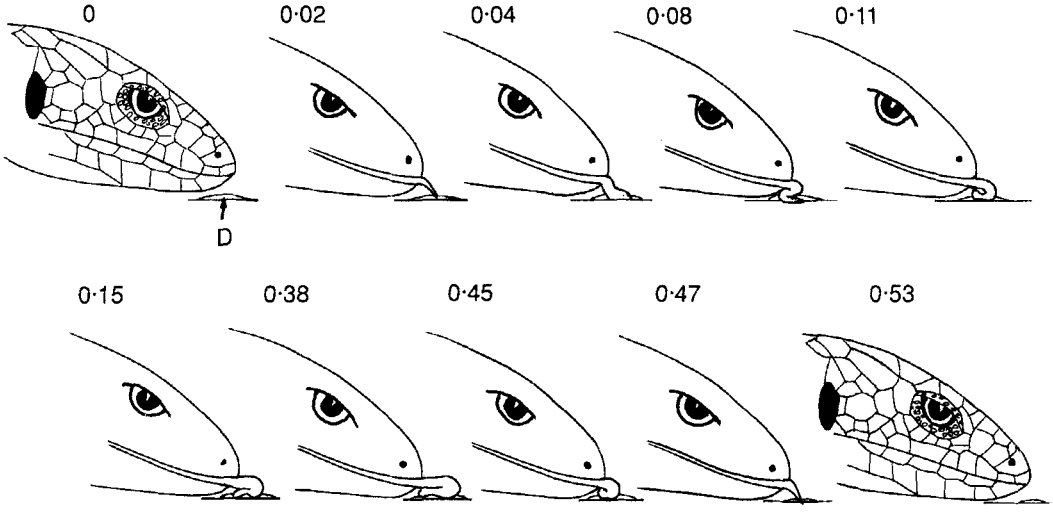

FIG. 7. Immersion Phase: Successive movements of the tongue in *Lacerta viridis* drinking from a water drop.

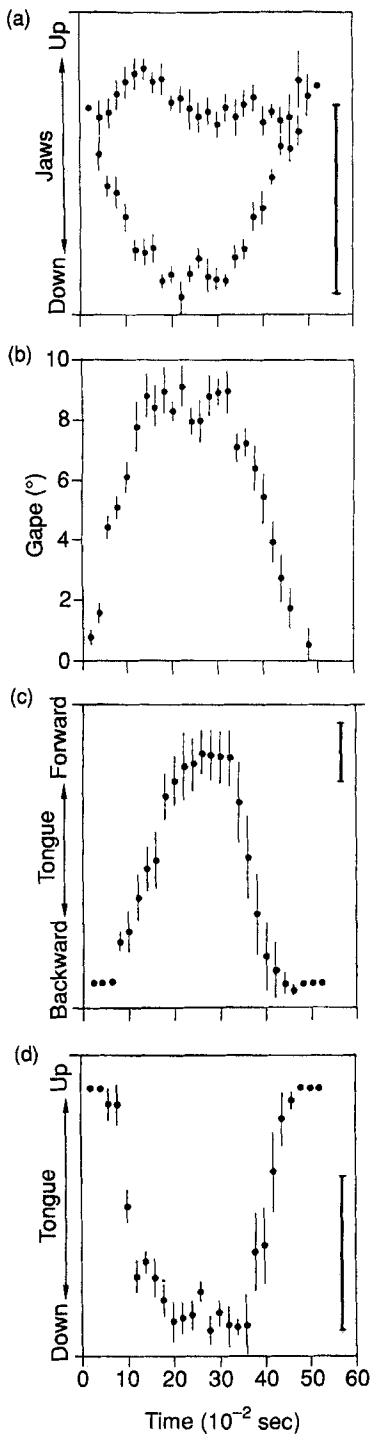

FIG. 8. Immersion Phase: Quantitative profiles for five variables describing the kinematics of drinking from a drop in *Lacerta viridis*. Each point on the curves indicates mean (●) and standard deviation (intersecting vertical line through each circle). The vertical bar at the right of each graph represents 1 mm. The plotted points for the upper and lower jaws are, respectively, UJ and LJ and for the tongue, the point TO in Fig. 1.

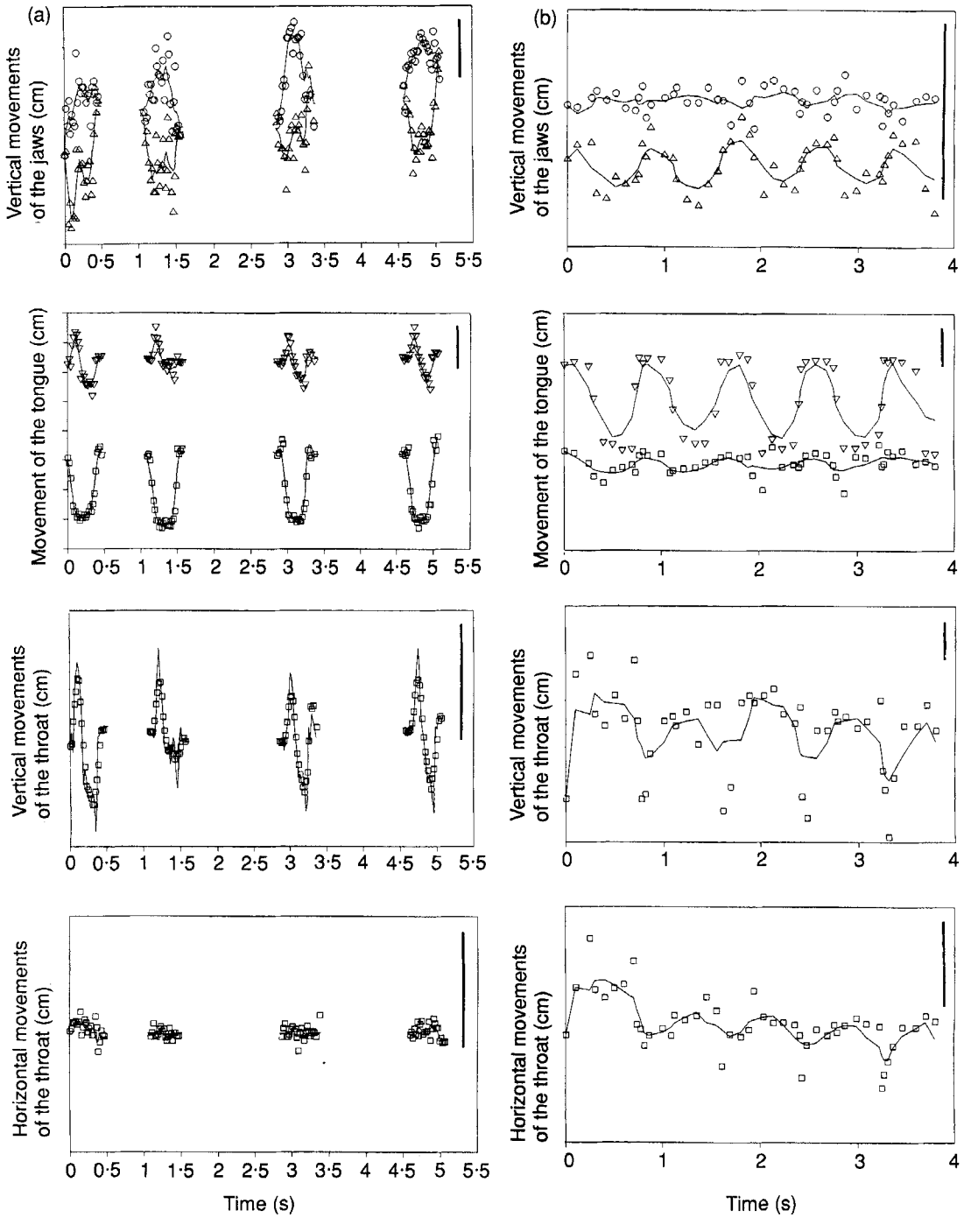

FIG. 9. Representative kinematic profile of the jaws, tongue and throat movements during successive cycles of the immersion (a) and emersion (b) phases in *Lacerta viridis* drinking from a drop. The points correspond to digitized data and the curves to the smoothed data. The arrows indicate, respectively, the up-down and anterior-posterior direction. The vertical bars in each graph represent 1 cm. (○) Upper jaw (UJ in Fig. 1); (△) lower jaw (LJ in Fig. 1). For the tongue the vertical (▽) and horizontal (□) displacement of the point TO in Fig. 1 is plotted. For the throat the vertical and horizontal displacement of the point TH in Fig. 1 is plotted.

Jaw movements such as jaw displacements (Fig. 8a) and gape angle (Fig. 8b) did not exhibit a four-stage pattern (slow opening, fast opening, slow closing, fast closing) as occurs during food transport (Goosse & Bels, 1992). Instead, the gape angle increased and decreased regularly (Fig. 8b). Opening and closing stages were separated by a 'plateau' during which the tongue was in continuous contact with the water. Slight vertical excursions of the upper jaw occurred, but most gape changes were due to movements of the lower jaw. The tongue tip travelled horizontally as it left the mouth, but it then turned down so that most of its displacement was in a vertical plane as it entered or returned from the water (Fig. 8c, d).

The hyoid skeleton supported the walls of the throat. Its impression in the skin could be seen externally and its positional changes during drinking phases followed. Plotted points of the hyoid indicated both a slight vertical and horizontal shift in hyoid position during tongue movements during the immersion phase (Fig. 9). Throat (hyoid) elevation correlated with tongue protrusion ($r = 0{\cdot}78$); throat depression correlated with tongue retraction ($r = 0{\cdot}80$).

Fluid movement

General overview: During the immersion phase, the protruded tongue became loaded with water and was returned to the mouth. Once in the mouth, the jaws closed pressing the tongue into the vomeronasal fenestra in the palate, specifically compartment 1. As the tongue started out again at the beginning of the next cycle, most of the water delivered from the previous cycle remained in compartment 1. The protruded tongue entered and loaded again with water. However, during its next return to the mouth, the hind tongue picked up the previous drop, until then held in compartment 1, and simultaneously carried it posteriorly into compartment 2. The dorsal and ventral sides of compartment 2 moved forward at this moment to receive this pulse of water. The new water delivered by the returning tongue refilled the first compartment as the jaws once again closed (Fig. 10).

Thus, tongue retraction functioned both to transport new water into the mouth (anterior tongue) and simultaneously transport preceding water into the next compartment (posterior tongue). Most water remained in compartment 1 for only one tongue cycle before being transported into compartment 2. Opening of the jaws not only allowed protrusion of the tongue, but also created a receiving area for returning water carried in on the retracting tongue. Further, the depression or dimple formed in the dorsal surface of the returning tongue appeared to offer a holding area for the water riding inward on the returning tongue. Water received from compartment 1 collected initially in compartment 2. As compartment 2 filled during successive cycles, some water also began to enter compartment 3, but the quantity was modest early in the drinking sequence.

Water displacement from compartment C2 to compartment C3 was complex. During early drinking cycles, water was not present in C3 and most liquid transfer was from C1 to C2. After a various number of cycles (5–10), a small amount of water began to enter C3 via two routes. One route was through a single, mid-dorsal channel; the other route was through a bilaterally paired, ventrolateral channel. Both channels were part of C2, but both served as routes by which some water found its way into C3. However, most transfer of water into compartment 3 did not occur until the emersion phase when the head was elevated (Fig. 5). During the emersion phase, the head lifted bringing the snout first level with, then tilted it above, the throat. Water that had gathered in the second compartment and any remaining water in the first compartment drained now into the third compartment. Cycles of tongue protraction/retraction continued but became less frequent

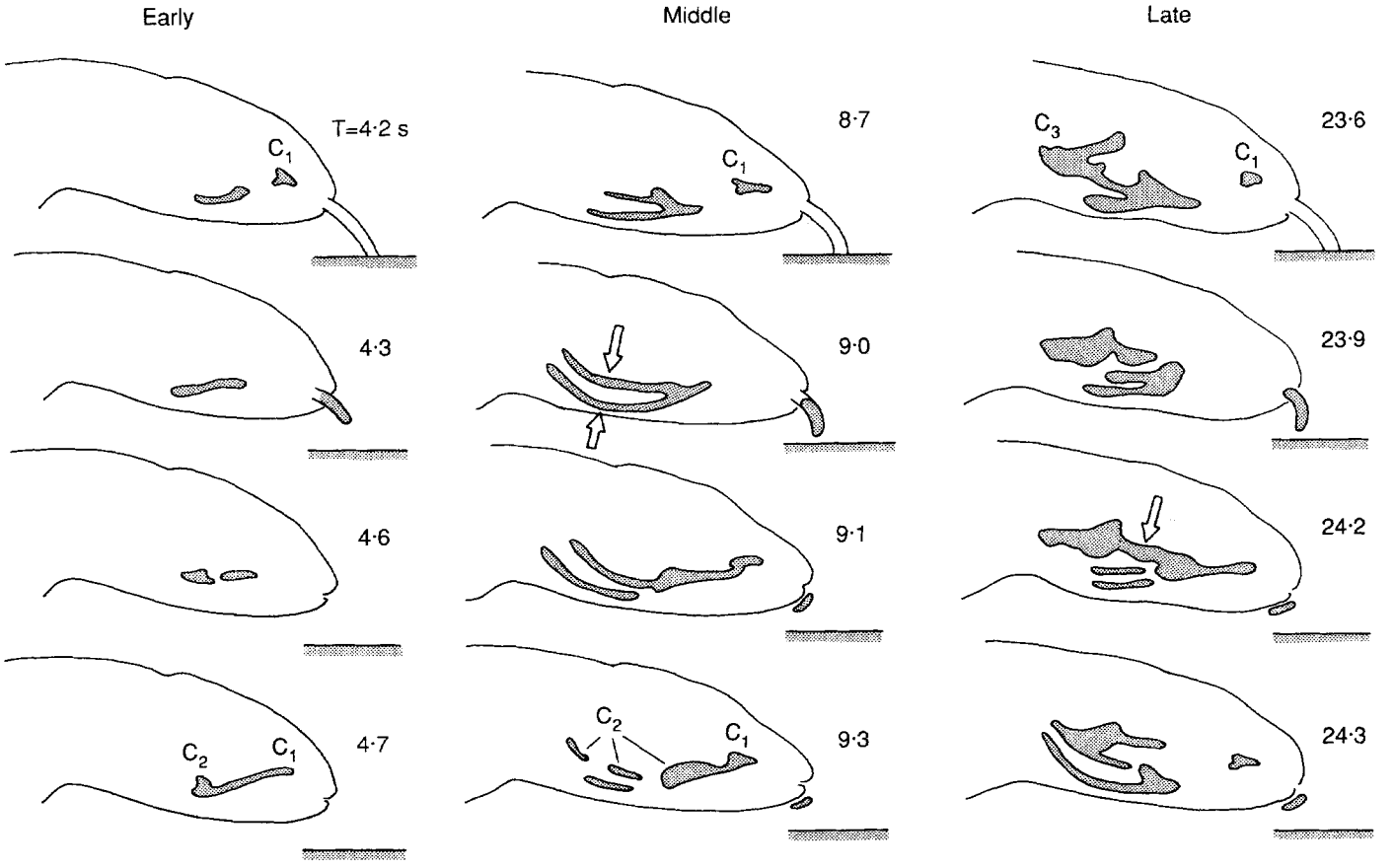

FIG. 10. Outlines of barium water from cineradiographic sequences of drinking. A cycle from early, from middle, and from late in an immersion phase is shown. During early, note that water collects in only C1 and part of C2; both compartments are separate (top) and merging of water in both occurs following tongue retraction (bottom). During the middle of the phase, note that more of C2 becomes filled and the ventral-lateral channels are evident (arrows); some water remains on the chin. During late in the phase, note that C3 has now begun to fill via the dorsal channel (arrow) and along the ventral-lateral channel. Elapsed time(s) are indicated next to each outline of the head.

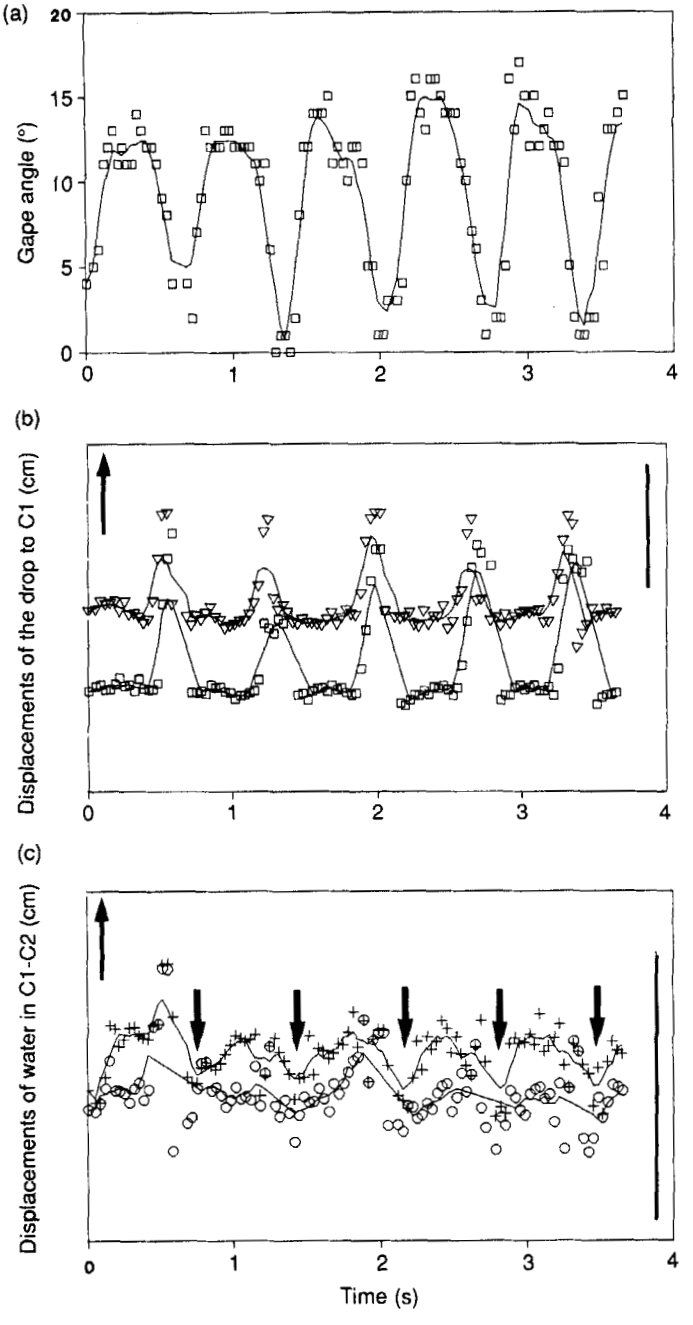

FIG. 11. Immersion Phase: Representative kinematic profile of the water displacements through the buccal cavity during immersion phase. The points correspond to the raw digitized data and the curves to the smoothed data. The vertical bars represent 10 mm. (a) Gape angle; (b) displacements of a new drop (□) to the compartment C1 by the tongue. This new drop (ND in Fig. 1) merges with the anterior edge of water in C1 (▽). The arrow indicates the up–down direction; (c) simultaneously to each merging new water drop in C1 (b), the posterior edge of water volume of C1 (○, point 2 in Fig. 1) merges with water filling C2 (+, point 3 in Fig. 1). The arrow indicates the anterior–posterior direction, and large arrows the merging movements.

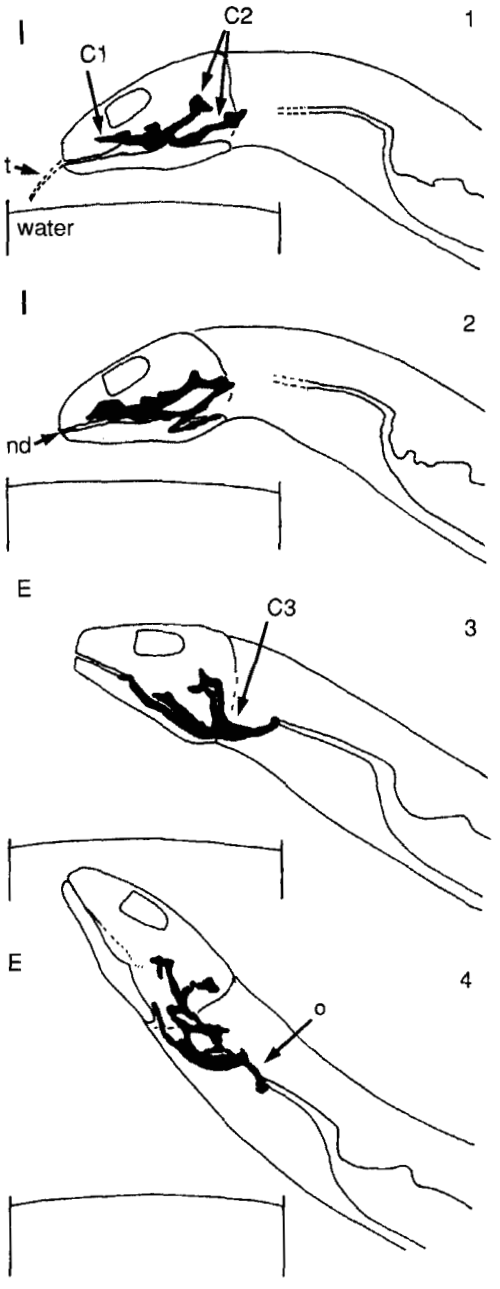

FIG. 12. Immersion/Emersion Transition: Displacement of the water through the buccal compartments at the transition from immersion (I) and emersion (E) phases in a drinking bout of *Lacerta viridis*. Lizard ends immersion phase (top) and progresses through emersion phase subsequently. Outlines were made directly from a cinematographic film with the lizard drinking barium fluid. Note that fluid (dark outline) fills and moves successively through buccal compartments reaching the opening to the oesophagus as the head is elevated. C1, C2 and C3 are defined in Fig. 3. o, oesophagus; nd, new drop; t, tongue. Numbers 1 to 4 correspond to these numbers in Fig. 5.

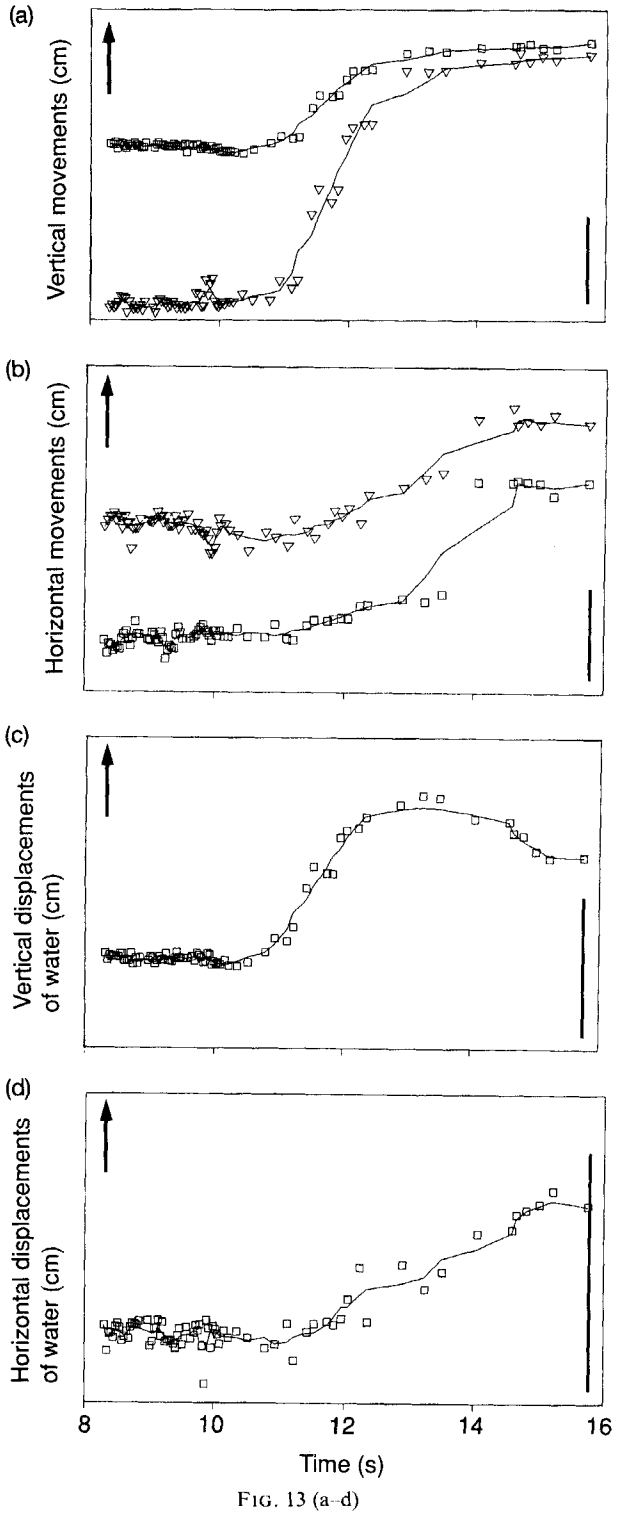
(a)
Vertical movements (cm)
(b)
Horizontal movements (cm)
(c)
Vertical displacements of water (cm)
(d)
Horizontal displacements of water (cm)
8
10
12
14
16
Time (s)

FIG. 13 (a–d)

and more irregular. Occasional expansions of the throat occurred as well, but the amplitude of these throat oscillations was smaller than during immersion phase (Fig. 9). The anterior entry into the oesophagus opened suddenly, usually after most of the water had collected in the adjoining third compartment. Then, gradually the rest of the oesophagus opened sequentially allowing water to flow through it and reach the stomach.

Immersion phase: The anterior–posterior displacement of the water through the buccal compartments is presented in Fig. 11. Cyclical changes in gape angle (Fig. 11a) correspond with tongue protraction (peaks) and retraction (valleys), and are correlated with water movement (Fig. 11b, c). The new drop (ND) merges with water into C1 during tongue retraction (Fig. 11b). At the same time, the drop in C1 merges with the water into C2 (Fig. 11c). Merging of the new drop with water in C1 is especially evident in the last two cycles of Fig. 11b.

Tongue movements were accompanied by small vertical and horizontal displacements of the throat (Fig. 9). When the tongue protruded, the throat moved slightly upward and forward, whereas retraction of the tongue reversed these throat displacements. The throat movements were related to tongue displacements as shown by the high correlation between x- and y-peak displacements of the tongue and throat displacements (x direction: $r = 0{\cdot}82$, $P \leqslant 0{\cdot}05$; y direction: $r = 0{\cdot}85$). However, these throat oscillations were not directly correlated with water displacement ($r < 0{\cdot}3$ between x and y throat movements and x and y displacements of water transport from C1 to C2, or anterior to posteriorly within C2).

Emersion phase: During the emersion phase, the liquid moved from C2 to C3, then from C3 into the oesophagus (Fig. 12). Plots of selected points (Fig. 13) illustrate the substantial changes in vertical position during emersion as the head was raised. In general, displacement of the water from C2 to C3 began during the last several (2–5) cycles of the immersion phase. During the emersion phase, which was always accompanied by head tilting, the lizard also continued tongue protraction/retraction cycles accompanied by shallow throat displacements. However, displacement of the liquid from C2 to C3 and within C3 was not correlated with throat movements. Similarly, water entry into the oesophagus was not related to throat displacements ($P < 0{\cdot}20$ between x and y throat movements and water displacements). As mentioned above, liquid moved from C2 to C3 by two routes, via a single dorsal channel and via a paired ventro-lateral channel within the pharyngeal cavity. The oesophagus opened suddenly and water from C3 entered (Fig. 13c, d). Once entering, water flow through the rest of the oesophagus to the stomach was gradual and may have been aided by peristaltic action within the oesophagus itself, but such flow was independent of any tongue or throat movements. Area outlines of the barium fluid were traced at successive points in a drinking bout. These showed the transfer of fluid through the buccal cavity and its eventual entry into the oesophagus (Fig. 14).

FIG. 13. Emersion Phase: Representative kinematic profiles of the water displacements through the buccal cavity during emersion phase. The points correspond to the digitized data and the curves to the smoothed data. The vertical bars in each graph represent 10 mm. (a) Vertical movement of the head (□, point HE in Fig. 1) and the upper jaw (▽, point UJ in Fig. 1); (b) horizontal movement of the head (□) and the upper jaw (▽); (c) vertical displacement of water from C3 to the oesophagus; (d) horizontal displacement of the water from C3 to the oesophagus. Displacements of water correspond to vertical and horizontal displacements of point 6 in Fig. 1. The arrows indicate, respectively, the up–down and anterior–posterior directions. Water fills the oesophagus (c and d) simultaneously with vertical (a) and horizontal backward (b) displacements of the head.

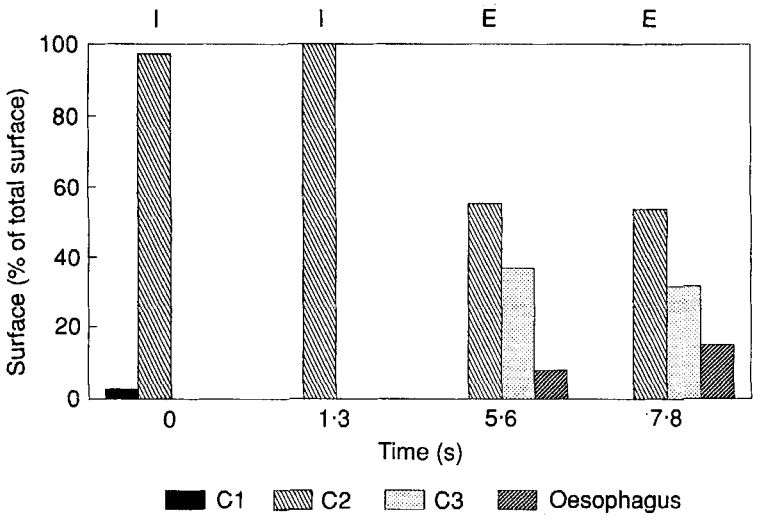

FIG. 14. Water surface area in the successive buccal compartments through time. The water moves from C1 to C2 during the immersion phase and from C2 to C3 and the oesophagus during the emersion phase. Surface areas were calculated directly from barium shadows on cinefluoroscopic films and the area in each compartment shown as a percentage of the total. Results from four successive frames are shown, two during immersion phase (I), and two during emersion phase (E) of a drinking bout.

Discussion

Tongue use in drinking

Drinking behaviour in *Lacerta viridis* involves a complex mechanism of tongue loading and unloading with water synchronized with jaw movements. During drinking in *L. viridis*, the tongue both brings water to the buccal cavity and transports it through the buccal cavity (Figs 4 and 5). There are several possible mechanisms acting singly or together to load the protruded tongue with water. (1) Surface tension between water and tongue may cause some water to adhere to the tongue during transport to the mouth. (2) Spaces between epidermal scales may load with water (Plate I). The imbrication of the small scales runs transversely across the hind and fore tongue. When the tongue arches forward during protraction, the posterior, free-edges of these scales may lift slightly, opening tiny recesses between them (Plate Id). Such recesses fill with water and/or increase surface area for adhesion (surface tension) between water and tongue.

Although our analysis could not confirm such water-loading mechanisms, the observed changes in tongue shape are compatible with such hypotheses. For instance, dorso-ventral flattening and lateral spreading of the tongue (Fig. 6) may increase surface area during water loading. Furthermore, dermal sinuses (lymphatic ?) and intrinsic tongue musculature underlying the epidermal scales suggest a basis for configurational changes in tongue size and shape that may be important in facilitating both loading and unloading of water.

Once retracted to the mouth, there are two possible mechanisms by which the water is unloaded from the tongue. (1) The elevation of the lower jaw presses the water drop held on the tongue into contact with the palate structure (Figs 8 and 9). Surface tension between water and palate may now draw the water from the tongue. The fenestrae vomeronasalis, part of C1 (Fig. 3), offers a recess to

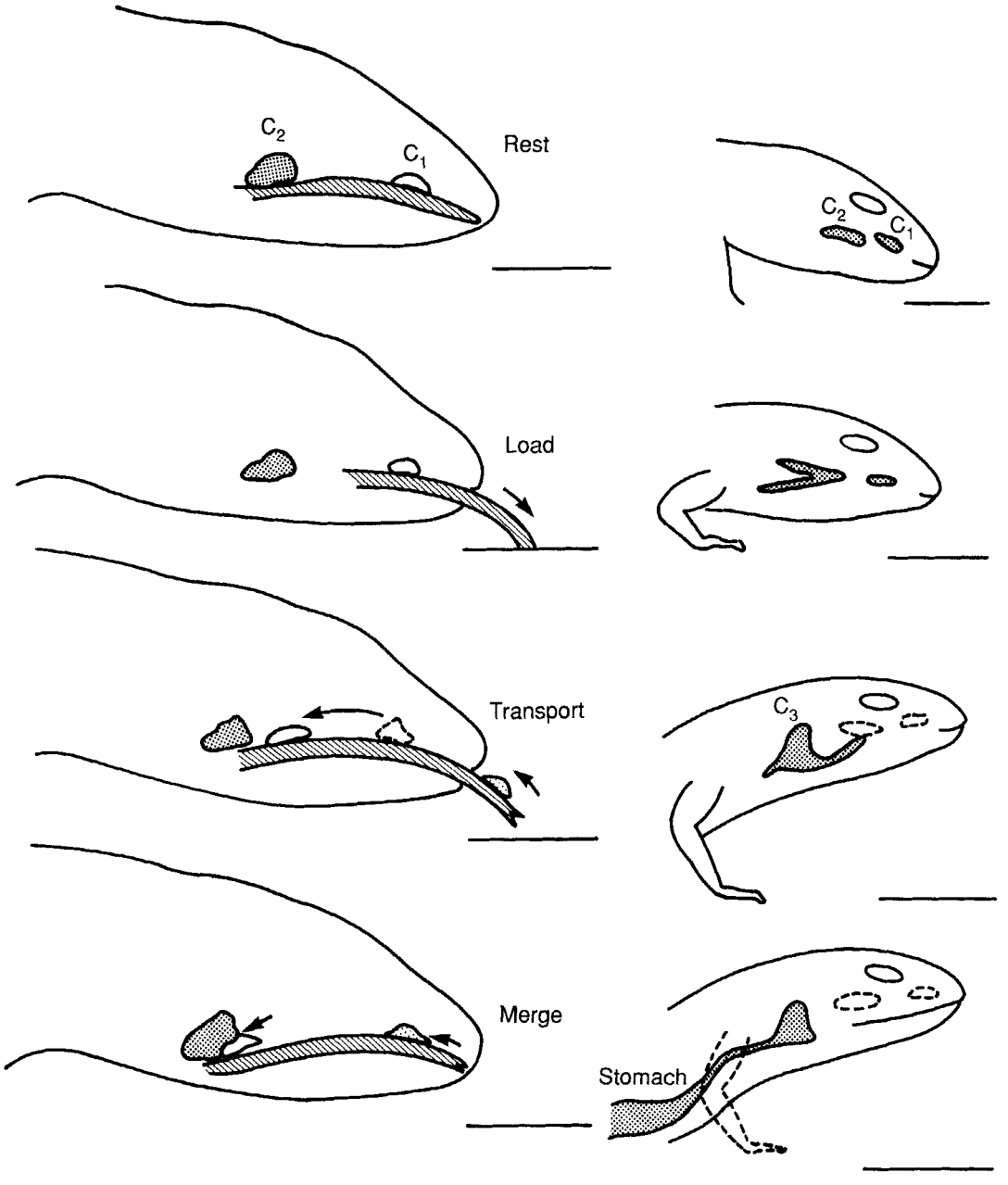

FIG. 15. Drinking model in *Lacerta viridis*. On the left, the role of the tongue during the immersion phase is presented. The tongue performs two functions. First, the protracted tongue loads with water and upon retraction delivers this water to the mouth where it takes up temporary residence in C1. Secondly, during retraction the hind tongue functions in intra-oral transport moving water from C1 to C2. On the right, the mechanism for filling of C3 and entry of water into the oesophagus are shown. Filling of C3 takes place primarily through effects of gravity. As the head tilts, water fills C3 from more anterior compartments. The oesophagus opens and water flows next to the stomach.

collect and temporarily hold this water, preventing its escape when the tongue protracts at the onset of the next cycle. (2) Straightening of the retracted tongue upon its return to the mouth presses the lingual scales together, collapses the recesses between them, and may force water out into C1. This would complement the tendency of water to move into available recesses in the palate. (3) The relatively small gape during drinking (Fig. 8) ensures that, as the tongue protracts, its surfaces maintain sliding contact with the palate. This may help further to wipe the tongue of any water it might still hold, and thus retain this water in the mouth.

Water displacement through the buccal cavity

At the beginning of a drinking bout, the water accumulates only in C1 and first portion of C2 (Fig. 10). The tongue has two effects on the water displacements through the buccal compartments C1 and C2. During tongue retraction, the water drop in C1 is carried posteriorly into contact with, and merges with, the water in C2 (Fig. 11c). The next drop, brought by the tongue into the buccal cavity, enters C1 to refill this compartment (Fig. 11b). This may allow frequent chemosensory testing by Jacobson's organ upon arrival of each pulse of new water delivered into the buccal cavity. Displacement of the water from C2 to C3 occurs primarily during the emersion phase which is always accompanied by upward tilting of the head (Fig. 14). Small tongue protrusion/retraction cycles and movements in the throat also persist during head tilting. It was not possible to quantify separately the three effects (tongue protraction/retraction cycles, throat movements, head tilt) on water movements from C3 into the oesophagus. However, we hypothesize that of the three, head tilting is the sole or at least most important factor encouraging entry of water into the oesophagus. There are two reasons for this. First, water, in fact, enters the oesophagus during head elevation and not sooner (Figs 12 and 13). Secondly, in none of the digitized sequences did we observe any throat or tongue movements coinciding with the entrance of the water into the oesophagus. Throat movements may help expand the pleated oral epithelium thus releasing water held in its folds by surface tension. This allows the released rivulets of water to join the larger pool of water collecting in C3. But, such throat movements do not directly seem to cause the opening of the oesophagus.

*Drinking model for **Lacerta viridis**: lingual drinking mechanism*

On the basis of these empirical observations and their implications we propose a drinking model (*sensu* Zweers, 1991) that we term the lingual drinking mechanism. In this model, displacement of water into and through the buccal cavity is based primarily upon active tongue movements and gravity flow. Capillarity or surface tension may be important in timely adhesion of water to tongue or buccal cavity. But, unlike some avian species (Koolos & Zweers, 1989; Heidweiller & Zweers, 1990), capillarity is not a central contributor to water movements in these lizards. Instead, the tongue of these lizards performs a dual role. First, it participates in water collection (protrusion) and then water delivery (retraction) into the mouth, compartment 1. Secondly, during retraction, the hind tongue participates in intra-oral water transport from this compartment (C1) posteriorly to compartment 2. Thus, the fore tongue functions to collect and transport water into the buccal cavity; the hind tongue functions for intra-oral transport of water (Fig. 15).

As successive tongue cycles bring water into the buccal cavity, receiving areas within it fill. Swallowing of this water into the stomach is based upon gravity flow and the opening of the oesophagus (Fig. 15). Lifting of the head brings the pool of collected buccal water above the level of the largest, and most posterior of the buccal spaces (compartment 3). Water flows to this third

compartment primarily under the action of gravity. Occasionally, movements of the throat are evident during this emersion phase, but these are not synchronized with intra-oral fluid movements. They are part of the breathing mechanism and if they contribute to swallowing, they do so by flattening pleats within the oral epithelial lining that may have captured small rivulets of water held by surface tension within these folded pleats.

Comparison of drinking and lapping within lizards

During lapping in *Ctenosaura similis* and *Tupinambis nigropunctatus* (Smith, 1984), the gape profile is similar to that of drinking in *Lacerta* (Fig. 8). The hyoid apparatus in iguanids and teiids moves very slightly during tongue cyclics of the emersion and immersion phases (Smith, 1984). In lacertids, such hyoid movement is related to hind tongue movement (Figs 8 and 11). The throat movements (Fig. 9) may be produced by forward and backward movements of the hind tongue itself or by slight movements of the entire hyoid apparatus produced by hyoid protractor muscles (Throckmorton *et al.*, 1985; Bels & Goosse, 1989; Bels, 1990). Flattening and lateral expansion of the tongue seems to be absent in the iguanian *Ctenosaura*, but present in the scleroglossans *Tupinambis* and *Lacerta*.

Drinking in varanids (scleroglossans) is completely different. Varanids drink by submerging the snout in water. Smith (1986) reports that 'the tongue is usually but not always protruded and withdrawn slightly'. She also observed that throat movements were associated with tongue displacements. As a mechanism of loading water, Smith (1986) hypothesized that the tongue, transversely narrower than in *Lacerta*, may pick up some water and bring it to the buccal cavity. However, the head tilting we noted in *L. viridis* does not occur in varanids which use continuous 'sucking' movements to fill the digestive tract with water.

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