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# DRINKING OF THE PIGEON (COLUMBA LIVIA L.)

by

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(With 10 Figures)  
(Acc. 10-V-1982)

## 1. Introduction

Birds drink in many different ways. Most of them drink like fowl or waterfowl; they walk to or through the water, move their beak down, open and close their beak several times, take some water, tip up their head and let the water run down by gravity (cf. *Gallus*, WHITE, 1970, in McLELLAND, 1980). However, many variations occur, for example galahs can hover over one spot above the water long enough to take a few sips, and swallows fly back and forth over the water scooping up water with the lower mandible (CAMERON, 1938). SCHÖNHOLZER (1959) suggests that the parrots (Psittacae) use an intermediate method between birds having the "tipping up" mechanism, and the birds which suck water in a way which is well-known from pigeons. The extensive study of HOMBERGER (1980) confirms this. From detailed film analyses she shows that within the Psittacae four different drinking methods can be distinguished (p. 187): 1, Cacatuinae scoop water with the lower bill; 2, Loriinae lap water with the brush-tipped tongue; 3, Psittacinae ladle water with the tip of the tongue; 4, Psittrichadinae (p. 107) and Loriculinae (p. 117) press the tongue against the palate and drink with a suction-pump action using only the upper beak and tongue. Although HOMBERGER (1980) did not formulate a detailed mechanical description

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for the suction action, the latter description is of interest since pigeons also drink by a suction mechanism.

LORENZ (1939, p. 71) states that the pigeons pump the drinking water by peristalsis of the oesophagus, but he did not test this, and the suggestion went unchallenged until McLELLAND (1980, p. 90) stated that pigeons have a sucking mechanism which, however, is still little understood.

Not only Columbidae show a suction action during drinking. According to STRESEMANN (1927-1934, p. 762) the sandgrouse (Pterocletidae) show a similar drinking behaviour, and this was the main reason to unite this family with the Columbidae in the order Columbiformes. LORENZ (1939) puts a strong emphasis on this by stating that sandgrouse were the only other bird family showing this "doubtlessly very old characteristic", so that a behavioural character derived a taxonomic value (cf. for discussion WICKLER, 1961); structural characters were used by BERLIOZ in GRASSÉ (1950) and by GRZIMEK (1969) to put the families together.

However, the value of the type of drinking as a taxonomic character is dubious. First, not all pigeons and not all sandgrouse show this particular mechanism (CADE, WILLOUGHBY & MACLEAN, 1966); and SCHÖNHOLZER (1959, p. 388) indicates that their way of drinking is only partially similar. From an analysis of motion pictures she states that after a few suction movements sandgrouse tip their beak up out of the water before swallowing, whereas pigeons do not tip up their bills. Furthermore, suction drinking is not restricted to the Columbiformes. POULSEN (1953) and IMMELMANN (1962) state that some Australian Estrildidae of the genus *Poephila* drink like the doves and WICKLER (1961) confirms this from motion pictures for *Geopelia cuniata* and *Poephila acuticauda*. CADE, WILLOUGHBY & MACLEAN (1966) add to this that also the mousebirds (Coliiformes) drink by sucking and SAUER (1956) describes a similar drinking behaviour for a warbler, *Sylvia borin* (Passeriformes).

IMMELMANN & IMMELMANN (1967) describe the estrildid's way of drinking as follows (p. 642): "sie pumpen also das Wasser bei eingetauchtem Schnabel durch Peristaltik des Vorderen Ösophagus ein und brauchen die Wasseraufnahme auch während des Schluckens nicht zu unterbrechen". CADE & GREENWALD (1966) describe the mousebird's way of drinking for *Colius colius* and *C. indicus* as follows: "the bird drank by immersing its beak to the base and sucking in water seemingly by a pumping action of the hyoid apparatus. At no time did a bird remove its beak from the water before it was finished drinking and tip up in the manner of a typical passerine." SKEAD (1975) describes a combination of sucking

and "tipping up" in *Dicrurus adsimilis* (Passeriformes), similar to that found in sandgrouse. He states (p. 141): "The whole bill is immersed in the water accompanied by a vigorous pumping action of the throat before it tips up to swallow the water."

The mechanisms suggested by IMMELMANN & IMMELMANN (1967) and CADE & GREENWALD (1966), and the combined mechanisms described by SCHÖNHOLZER (1959) and SKEAD (1975) were not analysed on a functional anatomical level<sup>1</sup>). The aim of this paper is to formulate a mechanical model for the drinking of pigeons and to integrate this in the discussion on the evolution of the drinking system in Columbidae.

It will also be shown that the mechanical analysis of drinking leads to a prediction about the necessary properties of glands in the mouth and pharynx, as required for the proper operation of the suggested suction mechanism. If these properties are found to exist one may consider such a finding as a support for the mechanical mechanism as analysed in this paper (see the discussion about structural explanation, ZWEERS, 1979, 1982c).

The present paper focusses on drinking mechanics. Drinking can be distinguished from pecking in each of the different subacts of which it is composed. This enables the comparison of the stereotypy of drinking with that of pecking, and indicates to what extent the pecking and drinking system are mechanically integrated (see ZWEERS, 1982d).

## 2. Methods and materials

### 2.1. Cinematography, radiography, marking and terminology.

Twenty specimen of *Columba livia* L. of the breeds white carneau, pouter pigeon, turbit and homer were studied by cinematography and radiography. The experimental arrangement is similar to that used by ZWEERS (1974) for cinematography (the speed of the film is 120 and 64 f.p.s.); and the arrangement of ZWEERS, GERRITSEN & KRANENBURG-VOOGD (1977) was used for radiography (the speed of the film is 48 f.p.s.). Lead markers were surgically implanted according to the technique used by ANKER, SIMONS & DULLEMEIJER (1967). The markers were placed as follows (cf. Fig. 1): 1, in the frontal bone; 2, in the temporal bone; 3, in the occipital bone; 4, at the tip of the upper beak; 5, at the tip of the lower beak; 6, in the rictus on the lower beak; 7, in the lingual bulges or the lingual tip; 8,

<sup>1</sup>) Drinking behaviour of pigeons has also been studied from quite different points of view. McFARLAND (1964, 1965a, b, 1970) and McFARLAND & L'ANGELLIER (1966) studied the homeostatic mechanism guiding the appetitive behaviour; BRELAND & BRELAND (1961), JENKINS & MOORE (1973) and WOLIN (1968) studied the response to food and water as reinforcers in terms of the change of the gape size; ZEIGLER & KARTEN (1973), ZEIGLER, MILLER & LEVINE (1975), ÅKERMAN, ANDERSSON & SVENSSON (1960), and ÅKERMAN, FABRICIUS & STEEN (1962) studied parts of the neurocybernetic chains involved in eliciting appetitive behaviour, but unfortunately not those occurring during the mechanical process of the water transport.

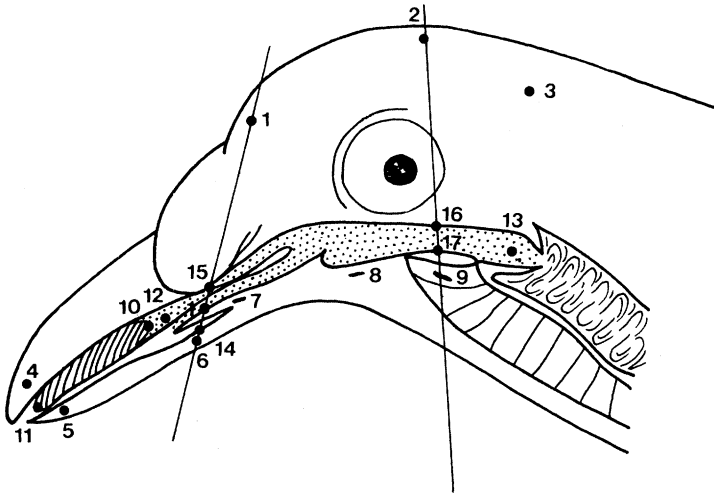


Fig. 1. Markers, dose of ingested water, air and cavity parameters in the pigeon's head for radiographic analysis. Number 1 to 9 indicate lead markers. The dose of water is between the numbers 10 and 11, and the stippled area filled with air runs between the numbers 12 and 13. The distance between the numbers 14 and 15 is the height of the buccal cavity, and between the numbers 16 and 17 the height of the pharynx.

in the lingual base; 9, in the wall of the glottis (= opening of the larynx). The water was mixed with a barium-sulphate suspension for a good contrast on the X-ray pictures; the water-box was  $10 \times 10 \times 5$  mm.

Morphological terminology follows that of ZWEERS (1982a, b) and ZWEERS, PELT & BECKERS (1981). The main terms used for the epidermal structures in this paper are given in Fig. 2. The tongue fold marks the border between the lingual base and the lingual alae. The plane on the tongue fold perpendicular to the palate is defined as the border between the mouth and the pharynx. The plane running between the dorsal and the ventral pharyngeal valves is defined as the border between the pharynx and the oesophagus.

The terminology for the movement analysis is as follows. The consummatory act of drinking is called a scene; it runs from the final visual fixation of the water until the head has been re-elevated and the last of an uninterrupted series of doses of water has entered the oesophagus. The pigeon generally takes a whole series of doses before re-elevating its head, this series is called a bout of drinking cycles. Such a cycle occurs when the moving epidermal structures return to their starting position; for example a pro- and retraction of the lingual base. Cycles may show repetition in one scene.

## 2.2. Measured parameters.

The following parameters were measured from the cinefilms: the distance between the beak tips (1), the level of the meniscus of the water in the water box (2), the level of the water around the beak (3), and the appearance of water drops thrown out along the beak.

The following parameters were measured from the X-ray motion pictures (Fig. 5): 1, the distance between the beak tips (4 and 5, numbers in brackets refer to numbered points in Fig. 1); 2, the distance between the frontal marker and the caudal lower beak marker (1 and 6); 3, the distance between the frontal marker and the lingual base marker (1 and 8); 4, the distance between the temporal marker and the lingual base marker (2 and 8); 5, the

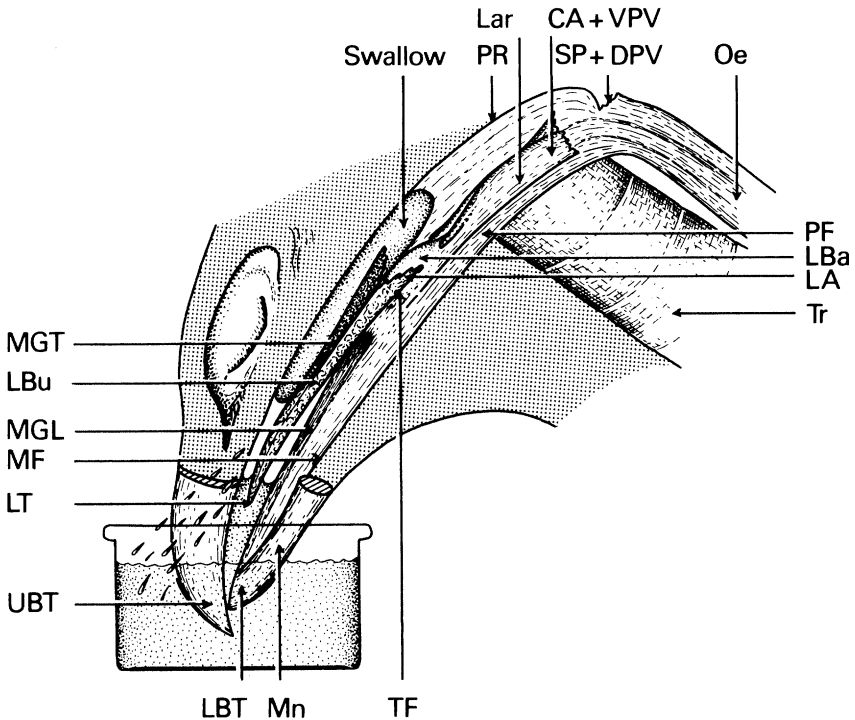


Fig. 2. Inner view of the feeding system of the pigeon showing the main epidermal structures directly involved with the transport of seeds. The system is in the pharyngeal suction phase. The ventral pharyngeal valves previously erect are now depressed while they run rostrad. The dose of water has a momentum caudad resulting from the lower air pressure area developed in the pharynx, and the dose is running to the oesophagus. The lingual bulges and tip seal off the rostral end of the dose, whilst throwing out a few drops at the rictus. See the text for explanation. Abbreviations: CA, gl. cricoarytenoidea; DPV, dorsal pharyngeal valve; LA, lingual alae; Lar, larynx; LBa, lingual base; LBT, tip of the lower beak; LBU, lingual bulges; LT, lingual tip; MF, floor of the mouth; MGL, medial groove of the lower beak; MGT, medial groove of the tongue; Mn, mandible; Oe, oesophagus; PF, floor of the pharynx; PR, roof of the pharynx; SP, gl. sphenopterygoidea; TF, tongue fold; Tr, trachea; UBT, tip of the upper beak; VPV, ventral pharyngeal valve.

distance between the caudal lower beak marker and the lingual base marker (6 and 8); 6, the distance between the frontal marker and the glottis marker (1 and 9); 7, the distance between the temporal marker and the glottis marker (2 and 9); 8, the distance between the caudal lower beak marker and the glottis marker (6 and 9); 9, the length of the open space in mouth and pharynx (12 and 13); 10, the height of the oral cavity along the line connecting the frontal and the caudal lower beak markers (14 and 15); 11, the height of the pharynx space along the line connecting the temporal and the glottis markers (16 and 17); 12, the distance between the rostral end of the open space in mouth or pharynx and the upper beak tip (4 and 12); 13, the distance between the caudal and rostral ends of the dose of water (10 and 11); 14, the distance between the upper beak tip and the caudal end of the dose (4 and 10); 15, the distance between the upper beak marker and the rostral end of the

dose of water (4 and 11); 16, the distance between the lingual base marker and the caudal end of the dose (8 and 10).

The actual positions (in a lateral view and relative to the skull) of the glottis marker and lingual base marker were found by enlarged graphical reconstruction of the distances 3 and 4 on the line between the frontal and the temporal marker, as well as that of the distances 6 and 7 on the same line. The following parameters were measured from these reconstructions: 17, the position of the lingual base marker relative to the mouth and pharynx roof; 18, the position of the glottis marker relative to the pharynx roof; 19, the distance between the glottis marker and the lingual base marker; 20, the length of displacement of the lingual base marker between succeeding frames; 21, the size of displacement of the glottis marker between succeeding frames.

The actual intake of water consists of many similar cycles, showing only differences in duration. The X-ray films were analysed as follows: Ten series of frames of complete drinking scenes of different pigeons were selected on the base of the accuracy of the lateral view, their sharpness and contrast, and the visibility of lead markers with reference to the contrast medium. From these series six cycles were selected as being representative *i.e.* closest to the average values. Prints were made of all of these frames. The parameters taken from these photographs were averaged to give a generalized picture of the movements during a drinking cycle.

### 3. Results. Drinking: a double-suction transport of water

Drinking behaviour differs from other types of behaviour and as such is easily recognizable. A bout of drinking cycles consists of from a few, to up to as many as 20 cycles. The drinking cycle with much water available is somewhat different from the cycles shown when there is less than 8 mm available. The data measured from a high speed film of a representative drinking scene of eleven movement cycles are shown in Fig. 3. The data from an X-ray film of 17 movement parameters from three representative movement cycles of a drinking scene are shown in Fig. 5. An enlarged reconstruction of the movements of the lingual base and the glottis is shown in Fig. 6. Radiograms from different animals showing representative stages of a drinking cycle have been put together in Fig. 8.

#### 3.1. Change of parameters.

The changes of the gape, of the meniscus in the water box, of the meniscus of the water along the beak, and the presence of ejected water drops are shown in Fig. 3. There are 11 cycles shown in Fig. 3. In 5 cycles prior to these 11 cycles the beak was submerged as far as halfway the nostril (that is 12-15 mm from the beak tips). These 5 cycles were similar to the first cycle of the series of 11 cycles shown here. The meniscus in the small water box is almost straight, but that along the beak is convex and hence some mm higher.

The general picture found when drinking while water was available in excess is as follows. The beak is open four times longer than it is closed.

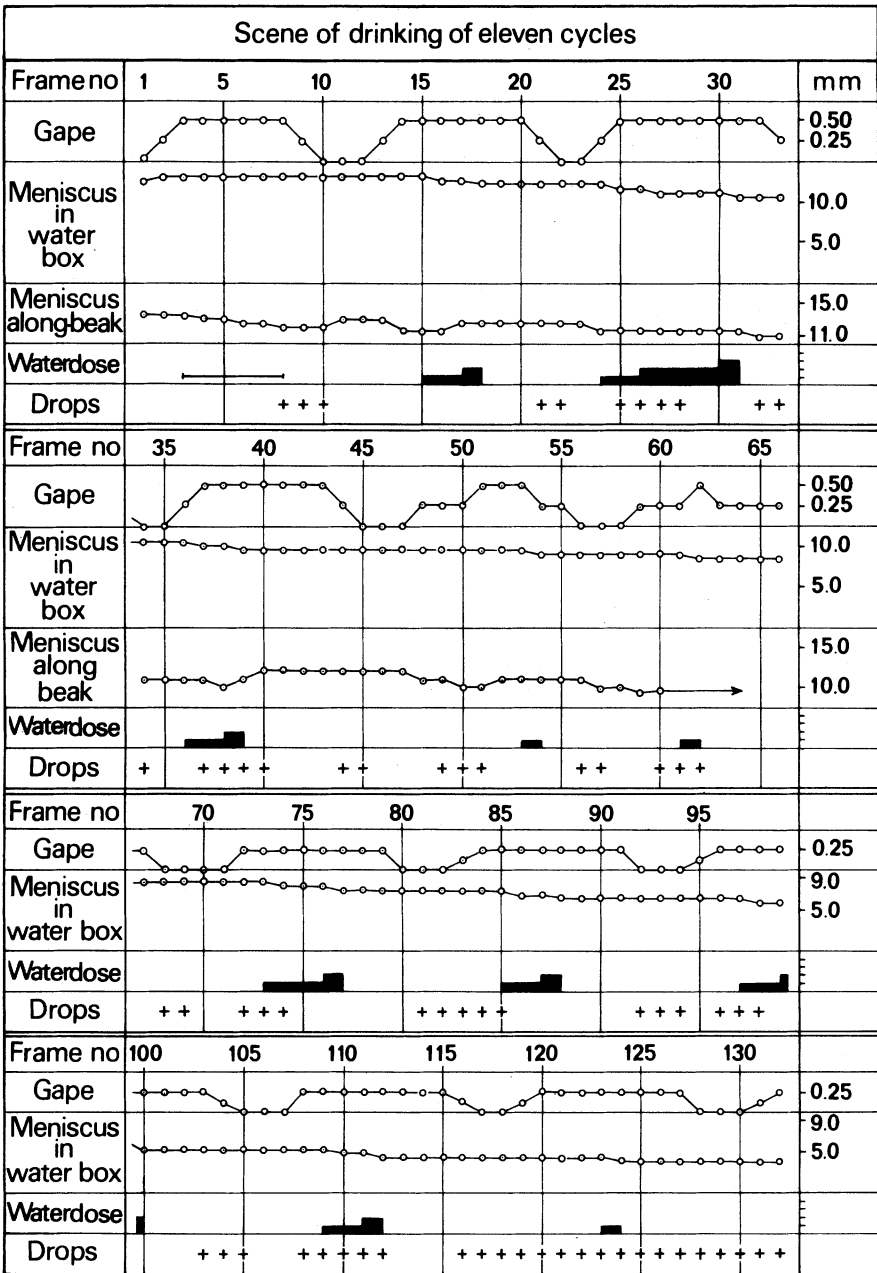


Fig. 3. Reconstruction of 5 movement parameters of a scene of drinking which comprises 11 movement cycles. During this scene water was only available in excess during the first movement cycle because the box was continuously filled with water until that cycle. In all other cycles the meniscus dropped with each swallowing cycle. The relative size of the dose ingested and the moment of its increase are indicated with a block diagram. The moment that drops were visible at the side of the beak has been indicated with crosses. During the scene the gape decreases and the period during which drops are thrown aside increases. The actual amount of water that is swallowed varies between 0.2 and 0.6 ml and tends to decrease during the scene.



Increase and decrease of the gape take as much time as the closed period and increase is generally equally fast as the decrease of the gape. The maximal size of the gape is never found to exceed 1.2 mm and is generally about 0.5 mm. The external beak meniscus drops just prior to the lowering of the box meniscus. When the gape reaches its maximum the beak meniscus rises to the original level. The moment of water uptake coincides with that when the meniscus in the box lowers. The uptake of water starts at the end of the increase of the gape and continues almost until the start of the closing movement. The actual amount of water swallowed is about 0.6 ml per cycle.

The picture changes somewhat when the water level is about 8 mm or when this level decreases during drinking (see the last two rows of Fig. 3). (This occurs when the level of the water is about 8 mm in the water box). The beak is pushed against the bottom of the box (Fig. 4). The meniscus along the beak drops when the gape is about halfway its course to maximal opening or reaches this position and rises again to its former level shortly thereafter. The meniscus in the water box shows measurable decreases shortly after the moment of decrease of the meniscus along the beak. The start of the uptake of the water is taken as the beginning of the decrease of the meniscus in the water box, so water uptake starts when the gape size has reached its maximum or shortly after this moment. The

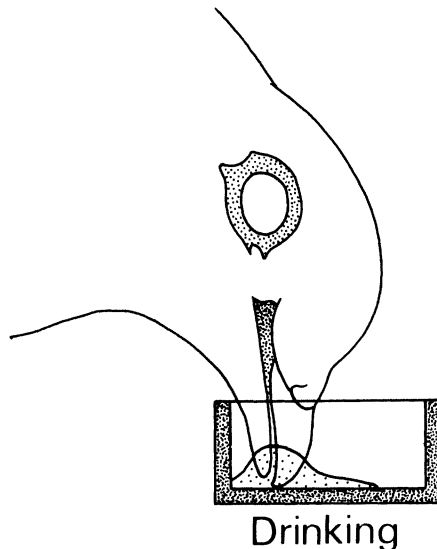


Fig. 4. Pigeon, swallowing the last few drops from a flat perspex plate. The convex meniscus along the beak is shown. The gape is maximal and water is sucked in.

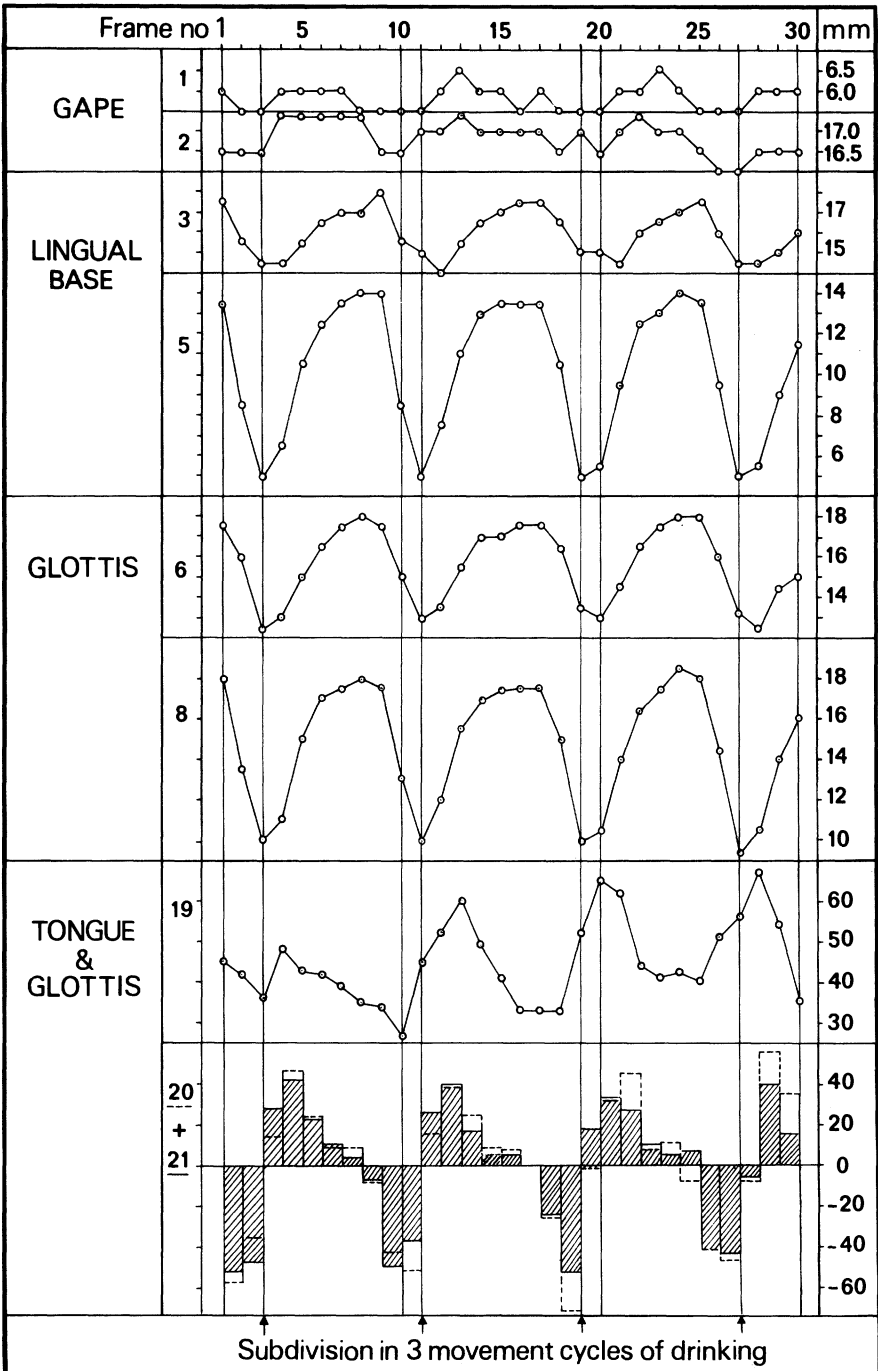
speed of opening and closing of the beak during a bout of drinking cycles decreases. The time during which the beak is kept closed, however, stays fairly constant. The volume of the swallowed water per cycle decreases somewhat. Waterdrops thrown aside of the beak were seen during the beginning of the intake and during the closing phase of the beak. When a very small amount of water is available these drops were seen almost continuously and the amount of water swallowed decreases to about 0.2 ml per cycle.

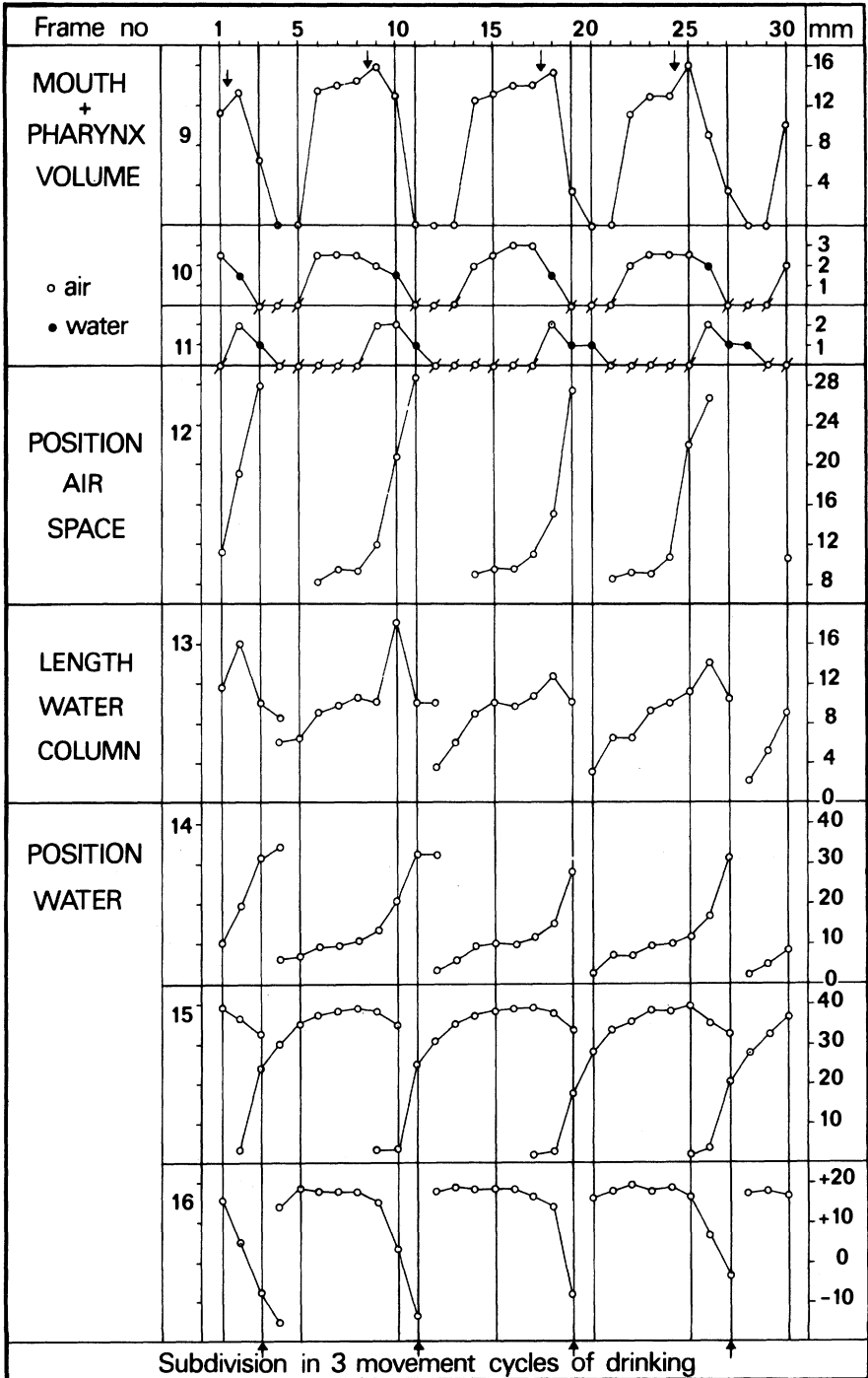
The movements during 3 successive and typical drinking cycles taken from X-ray motion pictures are illustrated in Fig. 5. The parameters indicated in the Figures were numbered according the list of parameters in section 2.2. The gape is represented by two parameters: 1, the distance between the beak tips and 2, the distance between the frontal marker and the caudal lower beak marker. Two different parameters were taken for the change of the gape size since this change is rather small relative to the size of the measuring error (being 0.5 mm), so that differences between both curves can be related to this measuring error. Both parameters show a similar result. The beak is opened rapidly to about 1 mm and is held in that position for a relatively long period. Then the beak is closed and stays closed for a period lasting two to four times shorter than the period in which the mouth is kept in a fixed open position.

The movement of the lingual base marker is described by three parameters: 3, the distance between the frontal marker and the lingual base marker; 4, the distance between the temporal marker and the lingual base marker; and 5, the distance between the caudal beak marker and the lingual base marker. The actual change in position for these parameters exceeds the measuring error about 4 times or more. The parameters 3 and 4 increase and decrease simultaneously and their amplitude is about 4 mm (Fig. 5). The lingual base marker moves dorsocaudad, slows down, is kept in a dorsocaudal position for a moment (though not exactly in the same point, see Fig. 6 and after the next paragraph), then a sharp reversal takes place and the marker returns very quickly ventrorostrad to its starting position. Parameter 5 gives the most

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Fig. 5a and b. Reconstruction of 17 movement parameters from a highly representative drinking scene. Three movement cycles are shown. Their subdivision is indicated with small arrows at the ordinate. In parameters 10 and 11 open circles indicate that the cavities are filled with air, black dots indicate that water is in the cavities, and cross-lined circles indicate that the cavity is empty and the walls are pushed together. The full line in the block diagram of the parameters 20 and 21 indicates the glottis and the dashed line indicates the lingual base. A block above the base-line indicates a rostrad movement, and below the baseline a caudad movement. See text for explanation.





direct information, because the change in position of the lingual base marker from rostroventral to caudodorsal is in line with the line connecting the caudal beak marker and the lingual base marker so that the maximal amplitude (about 9 mm) is measured. However, information about a movement perpendicular to parameter 5 can not be deduced from this parameter. This is important, since parameter 5 details about the movement of the lingual base marker parallel to the palate but not about a movement perpendicular to it (see after the next paragraph for description of such movements).

The movement of the glottis marker is described by the following parameters; 6, the distance between the frontal marker and the glottis marker; 7, the distance between the temporal marker and the glottis marker; and 8, the distance between the caudal beak marker and the glottis marker. The parameters 6 and 7 increase and decrease simultaneously and their amplitude is about 5 mm (Fig. 5). The glottis marker moves simultaneously with the lingual base marker. Parameter 8 gives (similar to parameter 5 for the movement of the lingual base marker) the most direct information about the movement of the glottis parallel to the palate. The amplitude of this movement is about 9 mm. No information about an eventual movement perpendicular to the movement parallel to the palate can be deduced directly from these three parameters.

To analyse whether the line of movement dorsocaudad was the same as that ventrorostrad for the lingual base marker and the glottis marker, a reconstruction of three linguoglottal cycles is shown in Fig. 6. For this reconstruction the distance between the temporal marker and the frontal marker has been taken as the base of the triangle which is formed by the temporal, the frontal and either the lingual base or the glottis marker.

These reconstructions show the following. Both markers move synchronously (see also parameters 5 and 8 in Fig. 5) initially fast dorsocaudad, then rapidly slow down and change to ventrocaudad relatively slowly over about 1.5 mm, to regain speed when turning to move ventrorostrad. Rostrally the speed of the movements decreases again making a relatively slow curve dorsorostrad over about 1.5 mm to start the next cycle. As can be seen in Fig. 6, the sequence of the positions of the two markers does not result in exactly similar curves. The differences between both are described by studying the course of the parameters 19-21 (Fig. 5), indicating respectively: 19, the distance between the glottis marker and the lingual base marker; 20, the size of the displacement of the lingual base marker between successive frames; and 21, the same for

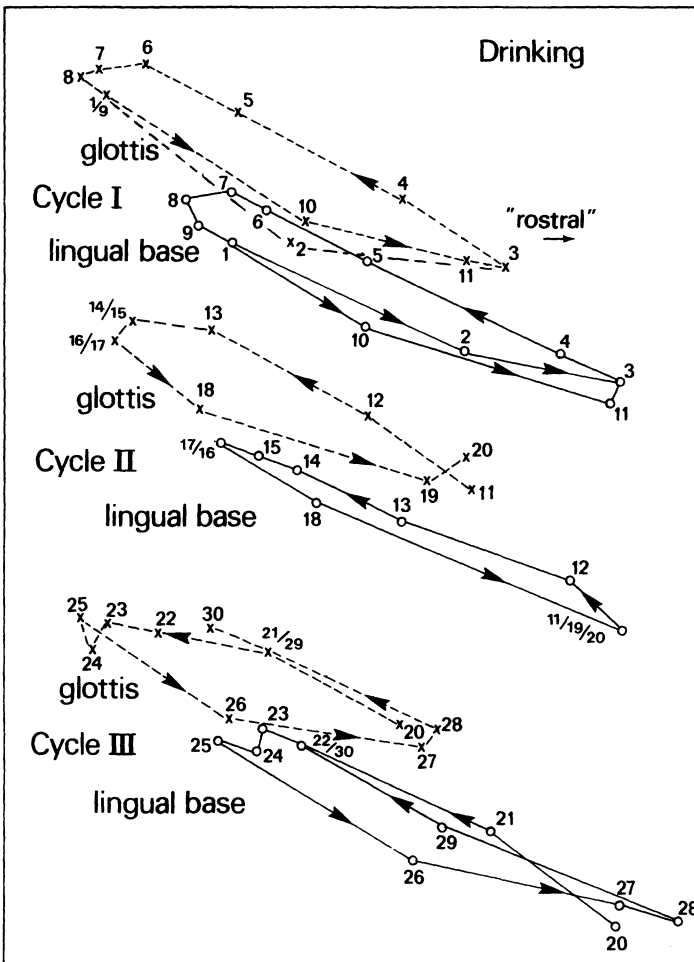


Fig. 6. Graphical reconstruction in a lateral projection of the movements of the lingual base and the glottis in three movement cycles of a drinking scene. The beak tips are at the right. It is clear that the glottis and lingual base run caudad "through" dorsal along the roof of the cavities, and that they run rostrad "through" ventral being incorporated as a part of the floor of the cavities. See text for explanation.

the glottis marker. Fig. 5 shows for parameter 19 an increase, followed by a sharp reversal and an equally rapid decrease which slows down, is kept constant for a while and increases again. From Fig. 6 it can be seen that it is the glottis that increases its speed first relative to that of the lingual base when they run dorsocaudal, if they run ventro-rostrad it seems to be the other way around. However, more data are needed for a general picture.

In the particular reconstruction of Fig. 5 the distance between the markers, after being stabilized as the net result of the differentially changing speeds of the two elements, increases over the cycles. The parameters 20 and 21 describe the changes in size of the displacement of the markers when they move caudad (positive values) and rostrad (negative values). The relation between the values of both markers per time unit are as would be expected from the course of parameter 19. The small changes of the displacement perpendicular to the rostrocaudad movement are ignored here.

The volumes of the buccal and pharyngeal cavities are described with the aid of three parameters: 9, the length of the open space in the mouth plus the pharynx; 10, the height of the buccal space in the mouth along the line connecting the frontal marker and the caudal lower beak marker; and 11, the height of the pharyngeal space along the line connecting the temporal marker and the glottal marker. Initially the length of the open space in the mouth (9 in Fig. 5) is zero, it then enlarges rapidly (beginning rostrally), stays constant for about 0.02 sec and increases again in the caudal direction but to a lesser degree. Initial increase is caused by a sudden ventrad movement followed by a caudad movement of the tongue while the beak is already being opened. The second increase (this increase is indicated with small arrows at the top of Fig. 5b) is caused by a sudden ventrad movement of the floor of the pharynx. After a maximum has been reached the length of the open space rapidly decreases. This reduction occurs after the linguoglottal apparatus has moved rostrad again and is the result of a dorsorostrad movement (= an elevation) of the floor of the mouth and pharynx against the palate. For parameters 10 and 11 open circles and black dots are used to indicate the respective heights of the buccal and pharyngeal cavities. Black dots indicate that water is in the cavity and the open circles indicate that air is in the cavity, other circles ( $\emptyset$ ) indicate that these cavities are closed and empty. The height of the buccal cavity (10, in Fig. 5) increases suddenly, stays constant for a short time, decreases suddenly, stays then constant for a short time again. The only moment that there is water in the caudal part of the mouth (syn. the buccal cavity) is at the sudden rapid decrease of the length of the cavity of the mouth. The height of the pharynx (11, in Fig. 5) shows the following picture.

A long period at a minimal volume, probably zero, then a sudden increase which is followed by a rather rapid reversal and a somewhat slower decrease. The only moment that water is found in the pharynx is during the middle part of the decrease in the height of the pharynx.

The position of the open air-filled space (12, in Fig. 5) in the cavities is described by the distance between the rostral end of this space and the marker on the tip of the upper beak. The graphs show a steady position of the rostral end of the space, then this space (an "air body") starts running caudad, attains a very high speed at the level of the caudal part of the mouth (11 to 16 mm from the upper beak point) and in the pharynx (16 to 24 mm from the tip of the upper beak) and disappears into the oesophagus (about 26 to 30 mm from the tip of the upper beak).

The amount of swallowed water is represented by parameter 13, being the length of the water column in the mouth and/or pharynx, measured as the distance between the caudal and the rostral end of the water mass. A gradual increase in its length is followed by a short period of constancy or slowing down of the increase of the water column in the beak. A sudden sharp rise in length occurs (while the water runs into the caudal part of the mouth and pharynx) which is followed by a sharp reversal and a fast decrease in length (while the water runs into the oesophagus).

The position of the water mass is described by 3 parameters (Fig. 5): 14, the distance between the marker on the tip of the upper beak and the caudal end of the water mass; 15, the distance between the tip of the upper beak and the rostral end of the water mass (parameters 14 and 15 indicate changes in length of the water mass); and 16, the distance between the lingual base marker and the caudal end of the water mass. Parameter 14 indicates that first the water level rises slowly, stays about constant at 10 mm for a short time and then a sudden increase occurs until the caudal end of the swallowed water disappears in previously swallowed water in the oesophagus. The total distance over which the water is transported is 30 to 40 mm. Parameter 15 describes the change in position of the rostral end of the water mass.

Initially there is no rostral end because there is no air space between the water in the mouth and that in the water box and a short period occurs with a slightly elevated meniscus between the beak tips. Then a sudden large increase in the distance between the rostral end of the water mass and the beak tips occurs. This is followed by a gradual slowing down, which coincides with the period during which the beak is closed between two gape cycles. At the end of a water transport period, the distance between the rostral part of the water mass and the upper beak tip decreases. This is the inevitable result of the shape of the oesophagus. The water follows the ventral wall of the rostral oesophagus, which bends ventrorostral just caudally from the ventral pharyngeal valves (see Fig. 2, and ZWEERS, 1982a). Parameter 16 indicates that first, for a relatively



long time (the period of the linguoglottal retraction) the distance between the lingual base and caudal end of the swallowed water is about constant, and then during the lingual protraction decreases extremely rapidly to zero and thereafter increases equally quickly on the other side of the marker, indicating that the dose of water has passed the lingual base.

### 3.2. The double-suction or vacuum-pump mechanism.

From the previous description of the change of parameters, the mechanical process of drinking can be viewed as a double-suction process comparable to the operation of a vacuum pump. The actual intake of water is subdivided into 5 phases: 1, the capillary action phase; 2, the lingual suction phase; 3, the pharyngeal preparation phase; 4, the pharyngeal suction phase; and 5, the oesophageal collection phase. The phase 1 to 4 may be repeated as a unit many times. This unit constitutes one movement cycle of drinking. The transport of the water will be described as a result of the movements of epidermal structures. The best parameter to follow this process is the change in position of the caudal end of the water mass (see no. 3, in Fig. 7). The division into five phases does not mean that the physical processes resulting in the caudal transportation of the caudal end of the water mass are completely different in each phase. The subdivision coincides with a changing contribution of the physical processes to the caudad displacement of the water mass (dose of water).

#### 3.2.1. *Capillary action phase (Fig. 7, phase 1).*

The intake of water starts by putting the tips of the slightly opened beak in the water. The water level inside the beak is higher than that in the water box. This is due to the convex meniscus which develops around beak tips if they are put into the water when they are in the closed position. This is, however, also due to capillary action and suction, the latter probably occurs somewhat later in phase 1 (see Figs. 7 and 8.1). The flexible rami of the lower beak and the flexible rictus allow a straw-like capillary action of the beak, even when the tips are open about 1 mm. Since the distance over which the beak tips can be pushed into the water diminishes with a lowered water level (under experimental conditions, section 2.1.) and since the caudal end of the water mass inside the beak is at about the same distance from the beak tips under conditions of high and low water levels, the capillary action must have been increased. This is ascribed to the generally decreasing gape size corresponding with a lowering of the water level (cf. Fig. 3).

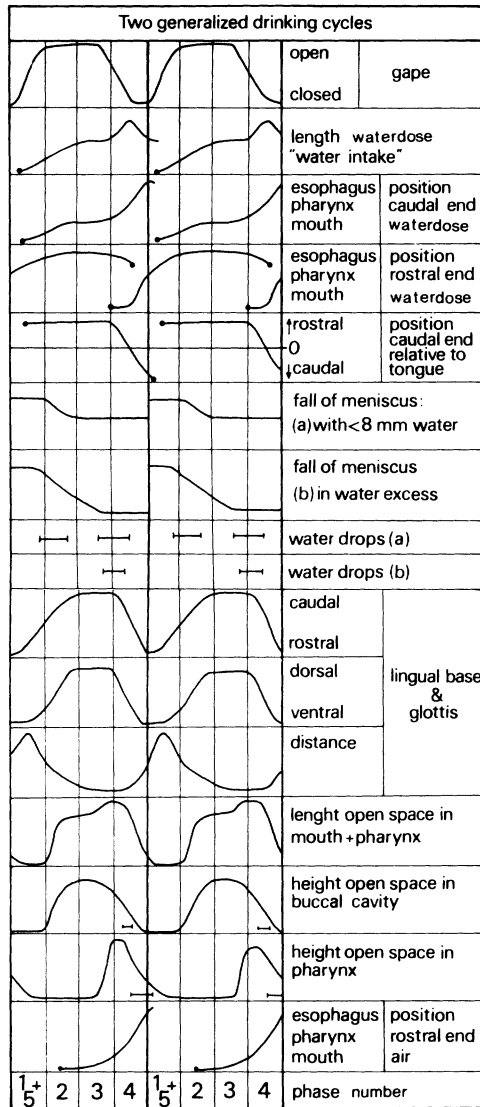


Fig. 7. Generalized picture of 18 parameters of two drinking cycles. Each cycle is subdivided into 5 phases, of which phase 5 of the first movement cycle coincides with phase 1 of the next drinking cycle. Prior to phase 1 the final fixation and the final approach occur. Horizontal bars drawn in the graphs of the height of the buccal and pharyngeal cavities indicate the moment during which water is in these cavities. See text for explanation.

The position of the caudal end of the water mass is constant relative to the position of the lingual base (cf. Fig. 7, phase 1 and nr. 5 from top), though the latter is already moving caudad. This must mean that a process is taking place which adds to the capillary action. This process is suction caused by the development of lower air pressure in the mouth (see the rostral hatched area in Fig. 8.4.). This comes into existence because the caudad running lingual base and lingual alae act as a piston in the straw-like beak in the following way. They start to run caudad through dorsal along the roof of the mouth, simultaneously the lingual tip and the lingual bulges are kept against the floor of the mouth while they start to run caudad<sup>1</sup>). Since, they close and enlarge the mouth cavity at the dorsal end these actions cause the development of a lower air pressure in the mouth. However, in this phase this process probably adds relatively little to the intake of water. In the next phase, however, the suction process is responsible for the intake and transport of water. The exact importance of each of the three ways of taking in water over the very small distance occurring in phase 1 is unknown.

### 3.2.2. *Lingual suction phase (Fig. 7, phase 2).*

The length and the height of the open space in the mouth increase at the beginning of this phase. During the first half of this phase they increase rapidly and they are roughly constant during the second half. These actions cause by their relatively large increase of the open space in the mouth an additional decrease in air pressure. This results in the suction of water. The suction resulting from the piston-like action of the tongue by a caudad enlargement of the mouth cavity (see the capillary action phase) is completed in the lingual suction phase by a ventrad enlargement of the mouth cavity. The latter occurs also as a result of the caudad movement of the lingual tip and bulges along the ventral wall and of the lingual alae and base along the dorsal wall of the mouth cavity. Since the shape of the cavity is somewhat conical and points rostrad, the effect of these movements is not only caudad extension but also a ventral extension of the air space. The mouth is kept open with a small and constant gape during these actions, so that as a result of its straw-like action water-intake can occur.

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<sup>1</sup>) It follows from the shape of the articulation facets between the basihyal and the paraglossal that the lingual tip and bulges must be depressed when the lingual alae are elevated (cf. ZWEERS, 1982a).

During the second part of phase 2 the position of the caudal end of the water mass is constant, also the size of the open space in the mouth (= buccal cavity) remains the same, while the caudad movement of the lingual "piston" slows down and finally stops. These data indicate that the further intake of water must stop since no further enlargement of the buccal cavity occurs neither by ventral nor by caudal extension of the cavity. It is suggested that the suction is strong enough to increase the water intake despite the small gape size.

### 3.2.3. *Pharyngeal preparation phase (Fig. 7, phase 3).*

As the next step in the transportation of the dose of water, which is kept in the same place for the duration of this phase, a series of preparatory actions occurs to build up a new area of low air pressure situated more caudally in the pharynx. This series of actions begins with a downward movement of the glottis, which is immediately followed by a similar movement of the lingual base and alae (see Fig. 6). This causes a large caudad extension of the air space into the pharynx. At the same time the air (and hence the area of low air pressure) moves caudad because the height of the buccal cavity is reduced (see Fig. 7), and this is combined with an increase of the height of the free space in the pharynx. The decreased height of the buccal cavity can easily be caused by the wide sheet of intermandibular muscles (see ZWEERS, 1982a) elevating the floor of the mouth cavity. Since during these preparatory actions no movement of the caudal end of the water mass is seen, there must be a time delay between the formation of this second lower air pressure region and the start of the water movement. At the end of this phase the mouth is closed. This closure combined with the elevation of the floor of the mouth and (in the next phase) the rostrad running tongue, causes the expulsion of water drops, which is continued in the next phase. The drops expelled under "low" water conditions (Fig. 7, nrs. a) could result from leakage during the first suction action since no outside water closes the slight gape of the tips under these conditions.

### 3.2.4. *Pharyngeal suction phase (Fig. 7, phase 4).*

In this phase the water, now as a separate dose because of the closure of the beak, is forced over the lingual alae, the lingual base, the glottis and the ventral pharyngeal valves and into the oesophagus. This passage results from the momentum which the water is given by the lower air pressure area developed in the pharynx in the previous phase. Together with the water, air in the lower air pressure area is swallowed because it

runs before the water. This air is found as an air bubble in the oesophagus and it joins previously swallowed air bubbles (Fig. 8.4.).

The length of the dose of water increases suddenly to a maximum because of the caudad replacement of the air space, and decreases again at the expense of the rostral end. The latter occurs because of the momentum the water received and the "through ventral" running rostral moving lingual tip and bulges empty the mouth (= buccal) cavity. The air found in the next drinking cycle can enter the system along the beak rims during this ejection and of course through the glottal opening.

In this phase some variability was found with reference to the time delay between the lingual movement and the movement of the dose of water. Fig. 8.3., for example, shows that the dose moved relatively late, since the tongue was already far on its way rostral.

In summary, the main actions processing the transportation of a water mass by suction are as follows: 1. a piston-like action in the mouth caused by the caudad moving lingual alae and base; and 2, a suctioning action in the pharynx by the decrease of the air pressure by a ventrad enlargement of the pharyngeal cavity. These processes are typical of a vacuum pump.

### 3.2.5. *Oesophageal collecting phase (Fig. 7, phase 5).*

The final phase generally coincides with the first phase of the next drinking cycle. The collection of water in the oesophagus is illustrated by the radiograms of Fig. 8. Figs. 8.1, 8.2 and 8.3 are from pouter pigeons which have a very wide rostral oesophagus. These radiograms show that the trachea (drawn with dashed lines) runs ventrad in the rostral part of

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Fig. 8. Radiograms from different stages of a drinking cycle. The small black strips or discs are the lead markers. In each figure, the doses of ingested water are numbered. The water is dotted and the air is hatched. The radiograms and their outline drawings show the following: 1. Capillary action phase of dose 1; the collecting phase of dose 2 in which the water runs down in the oesophagus beyond the ventral pharyngeal valves. 2. Lingual suction phase of dose 1; the collecting phase of dose 2. There are few air bubbles underneath the trachea, these are necessarily swallowed prior to each dose. The water is collected in the oesophagus, not in the crop. 3. Pharyngeal preparation phase of dose 1. The generalized picture of this phase is that preparation takes place for a sudden caudal enlargement and caudad displacement of the lower air pressure area, while almost no water transport is found. Since the water has yet to be transported (the water did not yet run over the glottis) and the tongue has already moved somewhat rostral, this radiogram illustrates that the actual swallowing act shows some variability. 4. Pharyngeal suction phase of swallow 1. The general picture of this phase is shown here. The dose of water moves over the glottis and the ventral pharyngeal valves into the rostral oesophagus while the lingual base and the glottis move very fast rostral being continuously with the mouth floor (this high speed causes the blurring of both lead markers in the lingual base and the wall of the glottis). Water and air of the previous 2-14 swallows is found in the oesophagus. A next dose (15) is at the very start of the capillary action phase.

p. t. o.

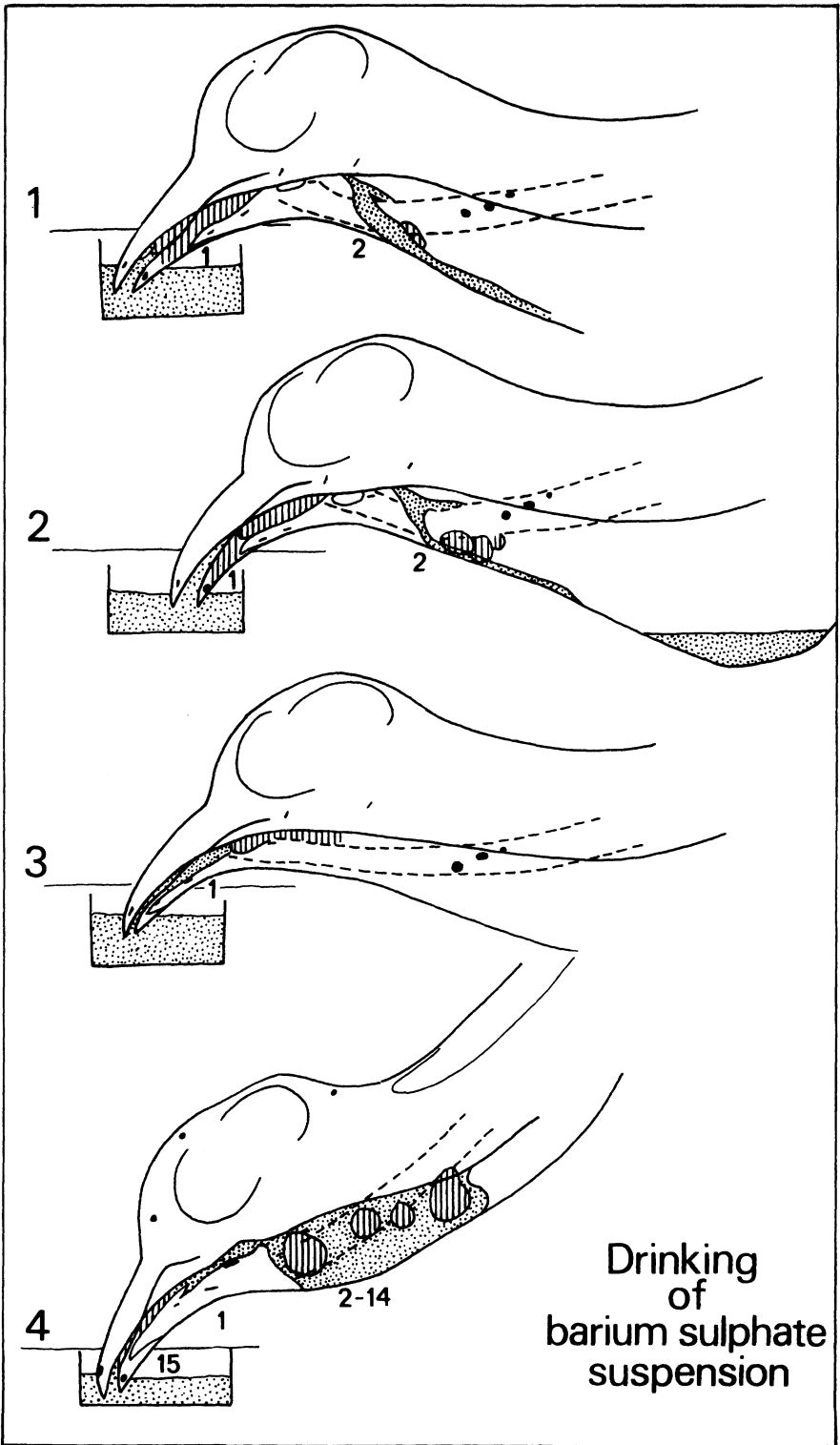
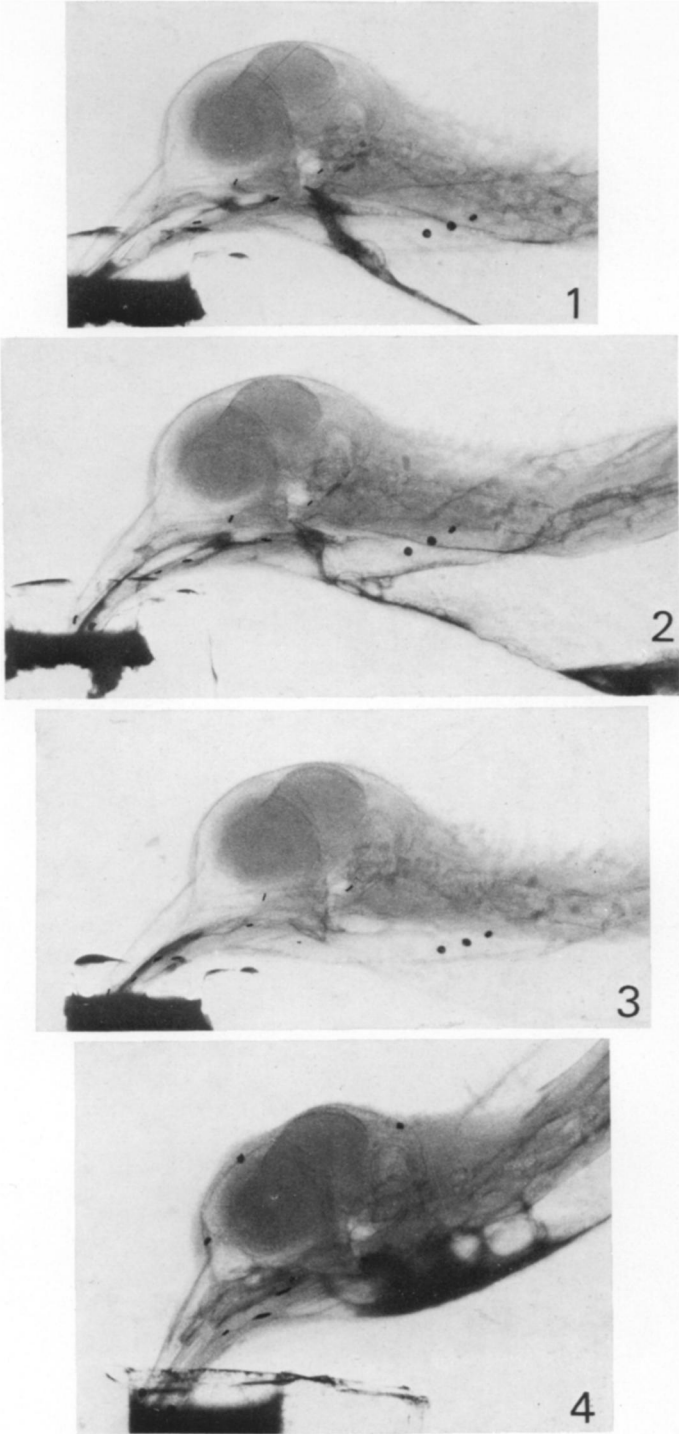


Fig. 8.



the oesophagus as a tube within a wider tube. More caudalwards the trachea runs separate from the oesophagus and finally it runs dorsally from the oesophagus. The swallowed water runs down left and right from the trachea and is collected at the lowest part of the oesophagus (Fig. 8.2.). This transport is not by means of a peristaltic process as could be concluded from the three black lead discs surgically glued to the dorsolateral wall of the oesophagus. Hence, it is concluded that the water transport in the oesophagus occurs by gravity. (Radiograms of peristalsis in the oesophagus illustrating the transport of grass seed bolusses can be used for comparison; ZWEERS *et al.*, 1977, p. 84).

It could be asked whether there is an additional suction system in the oesophagus, *i.e.* by an enlargement of the oesophagus causing a third area of low air pressure. This possibility was investigated by providing the oesophagus with a plastic tube (inner diameter 4 mm) and thus equalling the outside and the oesophageal air pressures. The tube was positioned in a turbit caudal to the musc. cutaneus colli and dorsolateral to the musc. claviculohyoideus and musc. claviculoglandularis, so that the fistel did not interfere with any muscle (cf. ZWEERS, 1982a). The swallowed water ran out through the tube. It was found that the drinking of the pigeons was as usual in all its aspects, so it must be concluded that no low air pressure exists in the oesophagus during drinking.

The wave-like movement along the throat (cf. SCHÖNHOLZER, 1959) could well be caused by the fast pro- and retraction of the linguo-laryngeal elements combined with an action of the musc. claviculohyoideus (see ZWEERS, 1982a).

The movements of water and air bubbles in the oesophagus during drinking can be explained as being a passive effect of the vigorously pro- and retracting linguo-laryngeal apparatus and gravity (cf. Fig. 8.4, which is made from a turbit, which has a narrow oesophagus).

## 4. Discussion

### 4.1. Earlier mechanical models.

The drinking mechanisms proposed by STRESEMANN (1927-1934) and LORENZ (1939) for the pigeon by way of an oesophageal suction as a result of peristaltic movements could not be confirmed. No peristalsis of the rostral oesophagus takes place during drinking, only the collection of water, and its passive transport by gravity occurs. Cases in which a suction mechanism is said to be caused by action of the oesophagus cannot be compared with the pigeon (cf. POULSEN, 1953, and IMMELMANN &



IMMELMANN, 1956, for some Estrildidae; LORENZ, 1939, for *Pterocletes*). Similarly, proposed suction mechanisms which do not describe how each epidermal element contributes to the mechanisms are of no use for comparison with the double suction mechanism of pigeons (cf. PERZINA, 1892, for Apodidae; SAUER, 1956, for *Sylvia borin*). HOMBERGER, 1980, describes the water uptake in the mouth for Psittichadinae and Loriculinae (p. 107) as a result of “von vorne nach hinten ablaufende, wellenartige Andrücken der Zunge an den Gaumen, unter gleichzeitigem, leichtem Zurückziehen der Zunge”; but she does not explain the transport by indicating how each single element contributes to water transport, and no attention is paid to the actual swallowing s.s. (*i.e.* the transport through the pharynx). CADE & GREENWALD (1966) write about “a pumping action of the hyoid apparatus” for *Colius*’ drinking, but they do not explain how the apparatus works.

Cases of bird species whose drinking is described as a suction followed by “tipping up” of the beak are of particular interest, since this first part may be analogous to the first step in the pigeon’s drinking, followed by passive water transport through the pharynx into the oesophagus. SKEAD (1975) describes for a drongo (*Dicrurus adsimilis*) a vigorous pumping of the throat prior to tipping up its head for actual swallowing of the water. SCHÖNHOLZER (1959) describes for *Pterocletes* a similar series of events. Also WICKLER (1961, p. 337) recognizes the two-step behaviour for *Pterocletes*. He talks about: “Einsaugen” and “Schlucken”, he, however, does not draw the conclusion that the first step, “Einsaugen”, might be similar in pigeons and sandgrouse, and that only the second step, “Schlucken”, might be different.

HOMBERGER (1980, p. 116-118) describes two types of movements occurring in one drinking sequence of *Loriculus*: 1, a simple “Vor-Rück-Bewegung der Zunge” being some way of swallowing; and 2, a more complicated “saugend-pumpende Zungen-bewegung”. She describes these types as alternatives rather than as complementing each other, since they occur in separated movement cycles. It could be suggested that the functional part of the first type always occurs as a non-functional part of the second type in each cycle.

#### 4.2. Extension of the model by incorporation of glands.

Our analysis showed that in pigeons the water transport during drinking is very probably caused by a double-suction mechanism. However, for a proper operation of the two-step mechanism, two conditions must be fulfilled. These are: 1, the linguolaryngeal epidermal structures should

slide along the floor of the mouth or along the palate almost without friction; and 2, the wide openings of the internal secondary choanae, the glottis, the entrance of the pharynx and the entrance of the oesophagus should be kept hermetically closed for at least short periods of time. The first condition could be met by the production of friction decreasing substances at particular places. The second condition could be met by particular mechanical action and the production of fenestra-closing substances. The proposed double suction mechanism may lead, therefore, to deductions about the properties of mucous-producing glands, being the only source of mucous production. If these deductions appear to fit the actual positions and characteristics of glands, these glands and their actions can be incorporated in a more complete description of the mechanism of drinking. A description of the pigeon's mouth and pharynx glands is available (ZWEERS, 1982a and b) and the way in which such deductions serve in the explanation of structure in morphology has been clarified by ZWEERS (1982c).

During the first suction the mouth is kept closed, except for its most rostral part. The rims of the upper and lower beak fit closely as a result of the flexible rami of the lower beak. Neither friction-reduction, nor fenestra-closing mucous is required along these rims; and no glands are found in this area. Some mucous at the flexible rictus could make the beak more strawlike. The *gl. anguli oris* might produce such mucous.

Friction decreasing substances seem to be required between the lingual alae and the floor of the pharynx as well as between the lingual bulges and tip and the floor of the mouth, since these elements slide very quickly along each other.

In order to serve the first suction-step the lingual bulges run caudad along the floor, and the lingual alae and lingual base run caudad along the palate. Meanwhile the mouth floor is kept slightly elevated so that the lingual elements stay fitted in the conical mouth cavity as a piston in a cylinder. The pro- and retraction of the lingual apparatus would be made easier, and damage of the epidermal structures would be prevented, when friction between lingual and mouth elements, as well as between larynx and pharyngeal elements is reduced. Mucous should be available over the length of the lingual pro- and retraction. The simplest way to meet these requirements is to have a series of small glands in the epidermal elements themselves where they slide along each other. These glands should have short ductuli efferentes and they should produce mucous upon sliding contact so that mucous is directly available. These requirements are met as follows: the *gl. lingualis superior anterior* has a

series of small glands on the ventral side of the lingual bulges, the *gl. lingualis superior posterior* lies on the ventral side of the lingual alae, and the *gl. mandibularis* forms a series of similar small glands in the floor of the rostral pharynx facing the lingual alae. The large glands of the *gl. mandibularis anterior* may, of course, add to friction decrease in the mouth, since they have their orifices in the median ventral to the lingual tip.

For a proper operation of the second suction action, by which water runs through the pharynx into the oesophagus, all four openings of the pharynx must be kept closed. This is required as long as there is time needed for the generation of low air pressure in the pharynx to give the water enough momentum for a "jump" over the larynx. These openings are: the entrance of the pharynx, the *mons laryngealis*, the internal secondary choana and the entrance of the oesophagus. The larynx must also be kept closed because of possible over- or underpressure in the trachea and for keeping water out of the trachea.

The entrance of the oesophagus must also be kept closed for other reasons. If it was not closed the water already swallowed would either run back rostrad by gravity or it could be sucked back rostrad. Further, if there were an opening between pharynx and oesophagus then the enlargement of the pharyngeal air space could easily be compensated for by some small indentation of the wall of the oesophagus, since the size of the pharyngeal enlargement is very small relative to the size of the oesophagus and since the walls of the oesophagus act easily as that of a deflated balloon.

The *mons laryngealis* can be closed completely by the complex drill-chuck actions of the arytenoids, the cricoid and the procricoid of the larynx. Such a closure probably occurs during drinking for two reasons. When in slightly anaesthetized birds small drops are pipetted onto the lingual base, a forceful closure of the glottis occurs (ZWEERS, PELT & BECKERS, 1981). Further, GOODWIN (1965) indicated that pigeons do not breathe during drinking and probably have a closed glottis since he described pigeons drinking with their heads completely submerged. Further GOODWIN (1970, p. 22) adds to this: "Immediately after the bird lifts its head and slightly expands its gape, presumably taking a deep breath just as we do after drinking deeply". It is, therefore, very likely that the larynx is actively closed during drinking by a reflex triggered by the contact of water with the floor of the mouth and the lingual base. No mucous is needed here, and no glands are found.

During the linguolaryngeal retraction the lingual elements are simultaneously pressed against the palate and the internal choana; however, as soon as the floor of the pharynx is depressed and the linguolaryngeal apparatus protracted, the opening of the internal choana is exposed, but it has to be kept closed so that an area of low air pressure in the pharynx can be developed. Since no structures are available which could close the choana actively, the production of large quantities of mucous seems to be indispensable. The best places to produce mucous, to be immediately available upon slight pressure of moving elements over the glands, seem to be the dorsal part of the lingual base and the ventral pharyngeal valves moving along the palate, or the parts of the palate immediately laterally from the choana. Preferably many small glands with short ductuli efferentes and supported by bony elements so that slight press suffices to make them emit mucous, should be present. The possibilities for positioning exactly this type of glands are found. The first is represented by the *gl. lingualis inferior* supported by the *basihyoid* as well as the *gl. cricoarytaenoidea* in the ventral pharyngeal valve, which is supported by the cartilaginous rings of the trachea. The second possibility is represented by the *gl. palatina posterior externa* in the hard caudal palate, supported by the *os palatinum*. Slight rubbing of the caudal palate of lightly anaesthetized birds indeed leads to the production of much mucous which appears to close the choana immediately upon release.

The entrance of the oesophagus is, of course, closed during the generation of the first lower-air pressure area in the buccal cavity, since the lingual and laryngeal elements run along the palate. A particular construction is required when the floor of the pharynx is depressed and simultaneously the entrance of the oesophagus is closed, which together lead to the second lower-air pressure area. The data from the X-ray analysis show a small but constant-sized depression of the floor of the pharynx at the end of the laryngeal retraction along the palate. Apart from the question of how this slight depression of the pharynx floor is realized (see for this point section 4.4.), the oesophagus should be kept closed for the time needed to give the column of water in the mouth enough momentum to pass through the pharynx. The mucous needed for this closure must be collected at the tips of the spines of the valves closing the oesophagus. It may be collected by scraping it off the hard caudal palate during retraction of the linguolaryngeal apparatus and/or the valves themselves may possess glands that come into action as soon as the surface of the structures is rubbed. The *gl. palatina posterior externa* in

the caudal palate and the gl. sphenopterygoidea in the dorsal pharyngeal valves and the gl. cricoarytaenoidea in the ventral pharyngeal valves are such glands.

#### 4.3. Stereotypy of drinking (Fig. 9).

The relationships between the concepts stereotypy and the fixed action or fixed motor pattern are reviewed by SCHLEIDT (1974) and LORENZ (1981) (see also LORENZ, 1932, 1939; MARLER & HAMILTON, 1966; THORPE, 1956; TINBERGEN, 1951). SCHLEIDT recommends for the descriptive analysis of stereotypy, being the only criterion for the recognition of a fixed action pattern, the use of three of its aspects: completeness, coupling and variability. SCHLEIDT concludes according to LORENZ (1981, p. 111, 148) that: What remain constant (from the slight intention movement to the full performance of an innate motor pattern) are the relationships of phase of the elementary movements and the proportions between the amplitudes of these elementary movements. This section focusses on the qualitative description of the full performance of the consummatory act of drinking with special attention to the coupling of those elementary movements which must be coupled for constructional reasons. No attention is paid here to phase and amplitude relations which are subject of ongoing research on the electromyographical level. The description is carried out with the aid of the descriptive framework of a comparator model used for the description of pecking of pigeons (see ZWEERS, 1982a) and it is summarized in Fig. 9. The proprioception is left out of this account.

Drinking behaviour is released in any thirsty pigeon. During the downstroke of the head, prior to actual water intake, the head is fixed for a moment at a certain level above the water. This is called the final fixation. Other short periods of head fixation sometimes also occur at higher levels above the water. This final fixation is similar to that found during pecking (ZWEERS, 1982a). Visual stimuli from the water supply, such as water-like appearance, and/or the dimensions and position of the drinking-water, recruit the final approach. The final approach is composed of a head depression, some slight lingual movement cycles (which probably moisten the mouth to reduce friction) and a small beak opening, and usually eye closure. The first three parts of this final approach are clearly coupled for constructional reasons since they all rely upon the same visual information taken during the final fixation.<sup>1)</sup> They all are

<sup>1)</sup> This information probably cannot be taken at a lower level above the water, since then the point of interest is out of focuss and possibly out of the pigeon's visual field.

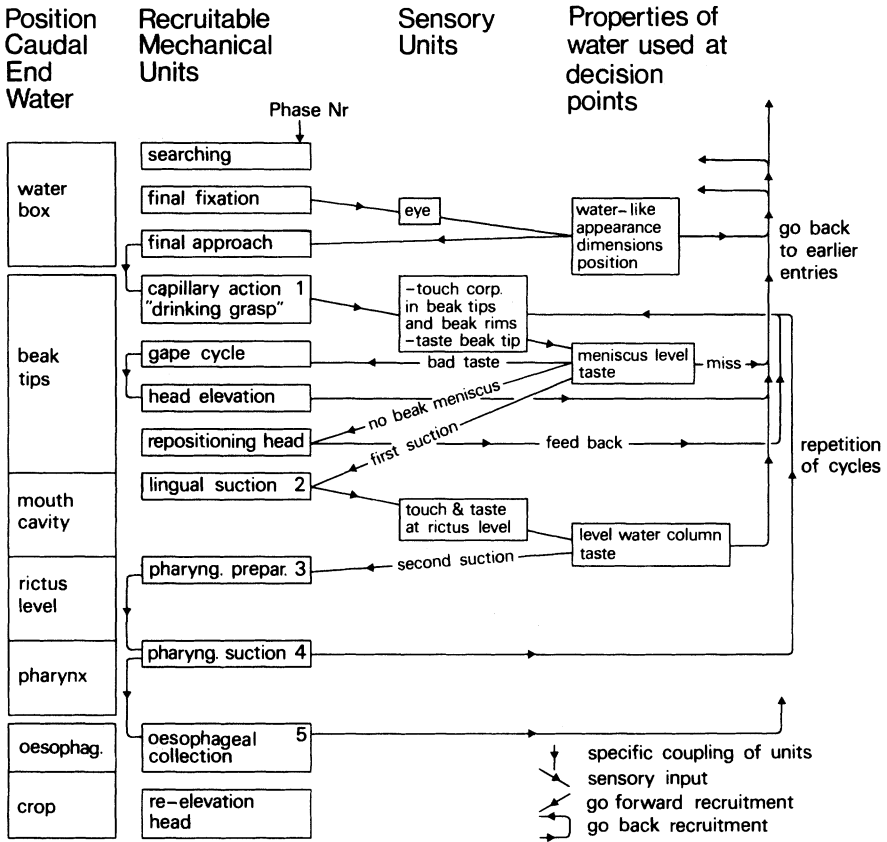


Fig. 9. Diagram of the different temporal sequences of mechanical units suggested for the drinking act according to a comparator model. See text for explanation.

preparatory to actual water intake because they must be carried out before water intake is possible. As soon as the beak tips reach the water level the head depression is stopped, which under normal conditions is related to the height of the meniscus of the water along the beak (see section 3). The following capillary phase is therefore directly coupled to the final approach, since the bird does not have an earlier reference point for the proper continuation of its behaviour. The bird has a bill tip organ of many corpuscles of Herbst and further corpuscles of Merckel are present and also taste organs are found in the beak tips. Thus the pigeon has the possibility of a check on the taste and the meniscus of the water during the capillary phase before active water uptake.

There is an indication that the bird must adjust the system to a certain norm for the level of the meniscus along the beak tips during the capillary action which is required for an adequate lingual suction. It is assumed that this adjustment occurs by a comparator mechanism comparable to the mechanism that adjusts the position of a seed when it is not directly correctly grasped for an adequate transport through the mouth (ZWEERS, 1982d) when only a small drop of water is available for a thirsty pigeon, the bird will reposition its head again and again in such a way that the water meniscus runs as high as possible along the very tips of the beak before it is able to swallow a part of this drop. Hence the bird tries (via a feed back mechanism) to arrive at a certain norm (a minimum height of the water level along the beak) which automatically is reached during drinking under normal conditions, but which now requires an extra taxis component, being the repositioning of the head.

An indication that pigeons use their beak tip taste organs not to overstep a certain norm before they take in the water comes from the work of BERKHOUDT (p.c.). Alert pigeons which were water deprived were given acid and bitter tasting drinking water. These birds did not react and they continued the drinking normally. Strong acid solutions, however, were rejected immediately during the capillary phase and they re-elevated their head. Whether here a comparator mechanism operates also or not, it is clear that in both cases the pigeon arrives at a decision point about the continuation of its behaviour which is masked during normal drinking.

Normal drinking continues with the lingual suction phase. Once released, this phase is never found to be interrupted although its amplitude can vary (see section 3). At the end of this phase the water intake comes to a stop for a short moment at the rictus level. Both touch and taste organs are present at that level and since the transport stops temporarily the drinking system has another chance to decide about continuation or returning to other behaviour. This decision point is always masked during normal drinking since it is found that lingual suction is always directly followed by pharyngeal preparation and then by pharyngeal suction which automatically results in oesophageal collection since the water obtains a certain momentum and runs down by gravity. However, when non-alert pigeons, being well-trained in drinking from a particular drinking box were given an acid solution instead, they showed a capillary as well as a lingual suction phase and the head was re-elevated and the water ran down along the beak rims and was shaken off (BERKHOUDT, p.c.).

The pharyngeal preparation phase is followed by the water transport in the pharyngeal suction phase and automatically the oesophageal collection phase as a result of the momentum from the second lower air pressure area. Hence, once the water has received its momentum the system is unable to stop it before it reaches the rostral part of the oesophagus. For this reason the latter three phases must operate as one mechanically coupled unit.

It is clear that the pumping mechanism itself cannot discern whether the pigeon has drunk enough. An indication may come from a boundary condition, such as the oesophagus having a certain tension as a result of the total swallowed water mass.

The following conclusions can be drawn. The consummatory act of drinking (if defined as running from the final fixation until the re-elevation of the head back to the same level as that of the final fixation) is a pattern which under normal conditions (such as moderate drive and plenty of water) shows up as a stereotyp pattern of movements of epidermal structures and of water. Only variations in the length of the bout of drinking cycles occur. However, when conditions change (such as a large increase in drive, only a drop of water available, or acid drinking water) it transpires that this consummatory act can be broken up into smaller parts, but for mechanocybernetical reasons no further subdivision is possible. That means that once they are released they will be carried out completely since there is no mechanocybernetical way to interrupt them. These smallest mechanocybernetically fixed units are: 1, the final approach phase (being a head depression, lingual movements, beak opening) plus the capillary phase; 2, the lingual suction phase; 3, the pharyngeal preparation phase, the pharyngeal suction phase plus the oesophageal collection phase; and 4, the re-elevation of the head plus the passive transport of water into the crop. However, it is clear, that in order to be able to call the observed pattern a drinking pattern at least one drinking cycle must be carried out successfully together with the final approach and the head re-elevation. This means that to call a pattern properly drinking, the pattern must be defined with reference to its role fulfilment, and with this addition the recognition of the "being fixed or stereotyped" becomes a matter of the hierarchical level of organization that is studied.

The recognition of smaller fixed pattern units on a lower level than the consummatory act of drinking also means that there are decision points between these units which could be masked when a bird is drinking under normal conditions. In the present case there are probably two such



masked decision points: 1, when water transport is relatively fixed for a moment at the beak tips in the capillary phase (see the refusal of acid water of an alert pigeon in its capillary phase); and 2, when the water is fixed for a moment at the rictus level (see the rejection of acid water of a non-alert pigeon after its lingual suction phase).

I suggest that the previous remarks about subunits in the consummatory act of drinking add something to the decision-structure concept which DAWKINS & DAWKINS (1973) have applied to the statistical analysis of the temporal patterning of acts during drinking in chicks in order to trace the moments when a decision is made. They subdivided the behaviour in phases by the introduction of "landmarks points", being frames of their video tape which show a clearly measurable and abrupt change in the position of the eye during the chicken's drinking (1, start downstroke; 2, bill strikes water; 3, bill comes out of water; 4, end upstroke). They found that aborted downstrokes sometimes occur and they concluded that "there might be certain favoured points in the downstroke where decisions are taken whether to continue with the drink, or break it off" (p. 92). This statistical approach informs about the moment when a decision could be made, it gives neither the cause nor the place. Both latter aspects could be clarified by a function-anatomical analysis, which moreover would inform about possibly masked decision points which cannot be traced with a purely statistical analysis of normal behaviour. For example, *Gallus* also has taste organs at the beak tip as well as at the rictus level, and moreover the tipping-up way of the chicken's drinking is also a two-step behaviour with the water being twice relatively at rest, so that in the analysis of DAWKINS & DAWKINS (1973), two decision points could have been masked. With reference to the downstroke of the head it is remarked that the chicken can have several periods of fixation followed by an approach to a lower level. Only the final approach starts from a certain level and cannot be interrupted for the same reasons as for the pigeon. However, sometimes non-alert well-trained birds skip the final fixation so that the start of the final approach cannot be traced.

#### 4.4. Valves and scrapers.

Of course, swallowing occurs during drinking as well as during pecking. The aim of this section is to show that the single pumping cycle during the swallowing of water is basically similar to the three types of movement cycles which can occur during the swallowing of a pea. Therefore,

swallowing is defined as the transport of water or a seed from the rictus level through the pharynx into the most rostral part of the oesophagus.

The actions of the linguolaryngoalvular elements occur during drinking and they all function during one movement cycle: their retraction causes the piston effect in phase 2, their depression causes the development of a second area of lower air pressure in phase 3, the water transport occurs during their protraction in phase 4 (see section 3). However, ZWEERS (1982d) distinguished three different types of movement cycles for the swallowing of peas. The lingual alae and base, the larynx and the ventral pharyngeal valves movements in each cycle are basically similar, however, they function successively in subsequent movement cycles since seed-transportation is step-wise. These types of cycles were called the lingual alae transport, the larynx transport and the ventral pharyngeal valve transport. During the transport of a large seed the movements of the linguolaryngoalvular elements are largely the same as during the swallowing of a water mass. They are found to be basically similar since they all consist of a retraction "through dorsal" which is followed by a protraction "through ventral".

This similarity is also found in the detailed movements of the epidermal structures involved. In the lingual alae transport in earing these alae are erected at the start of the retraction through dorsal. As a result the lingual bulges and tip are depressed and therefore they run along the floor of the mouth. During drinking the same coordination is found. However, functionally speaking, the effects are different. In eating the erected lingual alae prevent a pea glued to the lingual base from rolling rostrad when it touches the palate during the caudad movement of the lingual base. In drinking the erected alae play a role in causing suction of a water mass (cf. the piston-mechanism).

Similar remarks can be made for the larynx. During swallowing in eating peas the larynx runs relatively through dorsal caudad, functioning as a caudad moving constriction in the pharynx which pushes the pea caudad through it (cf. "properistaltic" mechanism in ZWEERS, 1982d). During the swallowing of water the larynx also runs caudad through dorsal, although it now slides along the palate, functioning as an element that rubs the palatine glands so that they produce mucous which closes the secondary choana for a proper closure of the pharyngeal lower air pressure area.

The same applies for the ventral pharyngeal valves with reference to their rostrocaudad movement and their relative dorsoventral position (they also move caudad through dorsal and rostrad through ventral).

However, they act differently with reference to their erection. During eating the valves run caudad in an erected position, functioning as scrapers which pick up the seeds that were glued to the caudal palate. On their way rostrad the valves are depressed and they move relatively through ventral so that they do not push the seeds rostrad along the palate. During drinking the valves also run caudad along the palate but in a depressed position and rubbing along the palatine and its own glands so that mucous is produced for the closure of the entrance of the oesophagus. At the end of their retraction they are erected so that they cause the enlargement of the pharynx cavity during the pharyngeal preparation phase, thus functioning as valves between the pharynx and the oesophagus.

It is concluded that the coordination of the various movements of the lingual, the laryngeal and valvular elements during swallowing is basically similar in eating and drinking. There is, however, a striking difference in the time patterning of the erection of the ventral pharyngeal valves. If the peculiar suction mechanism for drinking in pigeons is supposed to have been developed from the way food particles are swallowed, either during evolution or ontogeny or both, the main novel feature is the time of erection of the ventral pharyngeal valves.

For a proper understanding of the functioning of the peculiar muscular apparatus operative in the highly specialized swallowing peas and water by the pigeon the following remarks are made. A complete description of the lingual and laryngeal apparatus can be found in ZWEERS (1982a) and in ZWEERS, PELT & BECKERS (1981) respectively.

The pro- and retraction of the linguolaryngoalvular elements is brought about by the large pro- and retractor lingual muscles, the *musc. geniohyoideus* and the *musc. stylohyoideus*. The elevation of the floor of the mouth and of the pharynx can be accomplished by the wide sheet-like intermandibular muscles connecting the left and right mandibular rami over their full length. Hence, these muscles are very well able to allow the larynx to serve as a caudad moving constriction of the pharynx which pushes a seed caudad. The depression of the mouth and pharynx floor are caused by the long *musc. claviculoglandularis* and the *musc. claviculo-hyoideus* (see Fig. 10) as well as by the *musc. tracheolateralis* running along the trachea.

For an efficient scraping mechanism four conditions must be fulfilled: 1, the scrapers (= the ventral pharyngeal valves) must be erected during the retraction; 2, the scrapers must be depressed during the protraction; 3, the distance between the lingual alae and the scrapers must be as short

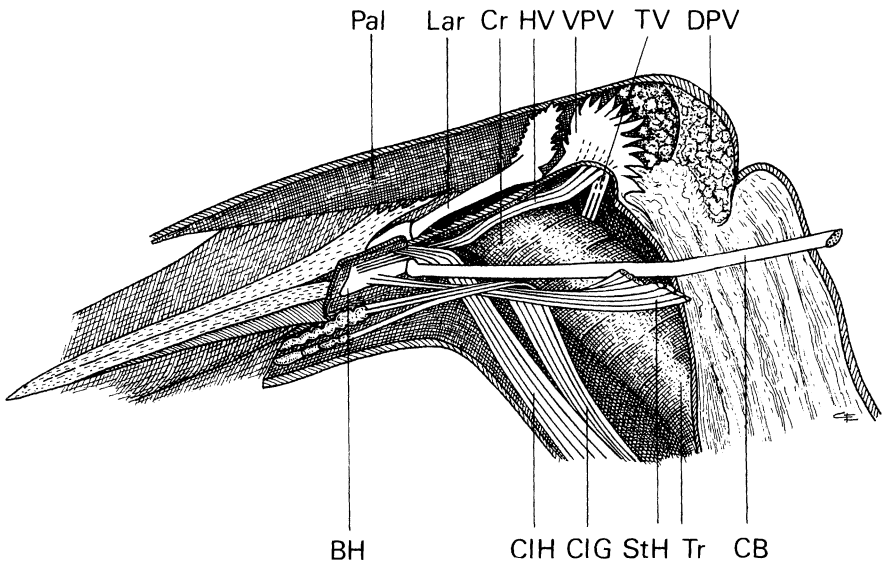


Fig. 10. Oblique view of the muscle-bone apparatus underlying the ventral pharyngeal valve. The linguolaryngoalvular apparatus starts protracting. The caudal part of the floor of the pharynx is depressed by the contraction of the *musc. hyovalvularis*. This muscle erects the ventral pharyngeal valves, which are pressed against the caudal palate, so that they push down the floor. The larynx is depressed since this muscle runs dorsally from the larynx; the muscle also protracts the pharyngeal valves relative to the basihyal. The rostral part of the floor can be pulled down by the *musc. claviculohyoideus* and the *musc. claviculoglandularis*. Abbreviations: BH, basihyal; CB, ceratobranchial; ClG, *musc. claviculoglandularis*; CIH, *musc. claviculohyoideus*; Cr, cricoid; DPV, dorsal pharyngeal valve; HV, *musc. hyovalvularis*; Lar, larynx (glottis); Pal, caudal palate; StH, *musc. stylohyoideus*; Tr, trachea; TV, *musc. tracheovalvularis*; VPV, ventral pharyngeal valve (see ZWEERS, 1981a, for a more extensive description).

as possible at the end of the protraction (so that they come as far rostrad as possible, and in front of the seed that was glued to the palate); and 4, the depressed scrapers and the larynx must run far ventrally during their protraction (so that they let the seed pass along the palate freely during their protraction). The erection and depression of the scrapers could be carried out by an antagonistic pair of muscles operating the scraper by connecting it to the larynx for erection and to the first tracheal ring for depression. Such an arrangement is found in *Corvus*, as has been described by БОСК (1978). He described a muscle that connects the cricoid with the rostral side of the scraper's tip, and another muscle that connects the cricotracheal area with the caudal side of the scraper's tip. In *Columba*, however, a different construction is found as only the latter muscle is present. This small *musc. tracheovalvularis* (see Fig. 10 and ZWEERS, PELT &

BECKERS, 1981) is apparently the depressor of the scraper. The muscle, however, serving to erect the scraper in the pigeon runs quite differently from the functionally similar muscle in the crow. This muscle runs from the rostral side of the scraper's tip rostrad dorsally from the larynx and inserts far rostrally on the basihyal (see Fig. 10 and ZWEERS, 1982a). Such a muscle has not been found in any earlier description of the lingual system of birds and might, therefore, serve a specific function not being present in most other birds. As a result of the peculiar course and connections of the *musc. hyovalvularis*, this muscle can fulfil the conditions 1, 3 and 4, while it does not oppose condition 2 if the *musc. tracheovalvularis* is active during the protraction. Therefore, it is concluded that the *musc. hyovalvularis* in combination with the specifically shaped erectable scraper is a specific apparatus for a fast transport of seeds through the pharynx.

For an efficient mechanism for the development of the pharyngeal lower air pressure area at least two conditions must be fulfilled: 1, in combination with mucous the valves must close the entrance of the oesophagus at the end of the retraction since no other epidermal structure is present to serve this goal; and 2, the valves must produce the pharyngeal area of lower air pressure by causing the ventrad enlargement of the pharynx. The only other elements which could serve this function are the *musc. claviculoglandularis* and the *musc. claviculohyoideus* and these muscles, however as a result of their unfortunate connections and very long course they are unable to perform the depression of the pharynx floor with the high accuracy which has been found in the analysis (see Fig. 10 and section 3). The *musc. hyovalvularis* connects the valve and the basihyal and runs dorsally from the larynx, so that this muscle has a working line which can fulfil both conditions. If this muscle contracts the valves are erected, so that their horny spines push against the caudal palate, as a result the valves' base is pushed ventrad against the caudal end of the larynx. Further, the contraction of this muscle pushes the larynx ventrad since its working line runs dorsally from the larynx. As a result of the two actions, caused by the contraction of the hyovalvular muscle, an open space in the pharynx develops which has a highly constant volume in each movement cycle. After these actions the protraction starts, while the water mass in the mouth is given a momentum caudad by the low air pressure in the pharynx. It is concluded that the *musc. hyovalvularis* in combination with the specifically shaped erectable scraper is a specific apparatus for a fast transport of a water mass through the pharynx. This conclusion and the conclusion in the

previous paragraph show that swallowing of seeds and swallowing of a water mass are carried out by similar structural elements and with similar actions, however, they are applied with different amplitudes and in slightly different combinations to fulfil each role properly.

#### 4.5. Evolution of the double-suction mechanism of drinking in pigeons.

A description of the evolutionary scenario of a specific mechanism requires according to the usual “monistic adaptationist programme”<sup>1)</sup> the deduction of the most plausible selection pressure for the development of such a mechanism. This deduction for the seed’s transport and the double-suction mechanism in pigeons could be as follows.

A strong selection pressure on fast transport of food particles in the pigeon could have occurred and once the proper mechanism to perform this had been evolved, a simple change in the time coordination of one aspect, — the moment of erection of the ventral pharyngeal valves —, could have led to the double-suction mechanism of drinking.

The granivorous pigeons must, like ruminants, digest a large amount of food in order to get enough protein. A fast transport of the food particles through the mouth and pharynx seems of selective advantage. In ZWEERS (1982d) it has been argued that a “slide-and-glue” mechanism for transport of seeds through mouth and pharynx is much more economical than a “catch-and-throw” mechanism. Both mechanisms are used by pigeons, however, the phylogenetically older “catch-and-throw” method by which the food is thrown up and caught again in the beak occurs only with larger food particles which are too heavy to be glued on the tongue. With smaller seeds the use of the slide-and-glue mechanism is preferred. This method seems to require less expenditure of energy, because neck and head movements necessary in the catch-and-throw mechanism do not occur in the slide-and-glue mechanism. Further, it

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<sup>1)</sup> See for a discussion of the “adaptationist programme” LEWONTIN (1978) and GOULD & LEWONTIN (1979). This programme carries the implicit assumption that selection pressure nullifies the anatomical relationships of the parts and maximizes the role fulfilment of these parts separately. After breaking up the organism in parts these parts are interpreted as built maximized for their role fulfilment and any submaximal role fulfilment is due to an optimal compromise among competing selection pressures, neglecting any architectural and ontogenetic restriction.

The term “monistic” is used here according to POPPER (1972, p. 274). A “monistic” interpretation of an organ is that possession and use of an organ are “merely two different abstractions from what is biologically and genetically one and the same reality”. A “dualistic” interpretation separates between possession and use of an organ, and between a behaviour controlling and an executive part of an organ.

seems to be more reliable since the transport is automatically carried out by the movements of the tongue, and it is not dependent upon a correct coordination between head, neck, gape and tongue movements. Lastly, transport by glueing a food particle to the tongue occurs faster than transport by catch-and-throw (see ZWEERS, 1982d). Also the slide-and-glue mechanism occurring in the pharynx (being the scraping mechanism of the ventral pharyngeal valves, which during their retraction scrape the seed which was glued to the palate caudad) is much more economical than the catch-and-throw mechanism in the pharynx (being the pro-peristaltic mechanism by the elevated larynx causing a constriction in the pharynx during its retraction, which pushes a seed caudad). In any case the slide-and-glue mechanism is faster in the pharynx than the catch-and-throw mechanism used for large particles. The relative slowness of the latter mechanism leads to a jam of large particles in the pharynx. This forces the pigeon to stop pecking in order to empty its pharynx. Of course, measurements have to be made for a proper comparison of both mechanisms in terms of intake of food amount per time-unit, combined with calorific calculations to obtain an estimate of the net-energy intake per type of transportation. Also observations about the preference and the sequential order of pecking over a long stretch of time from ad-lib available small- and large-sized seeds, have to be made to get more insight into the advantages of each of the methods of transportation. It is not unlikely that the slide-and-glue method leads to a greater intake of food per time-unit.

If the slide-and-glue mechanism in the pharynx is of selective advantage with respect to food-intake, this seems to be of interest with reference to drinking. In drinking, transport until in the oesophagus is performed during one movement cycle of the linguolaryngoalvular elements. In pecking, the movement cycles of these elements must be repeated since the food transport occurs in steps. In the previous section (4.4.) it has been shown that all these types of movement cycles are basically one movement pattern (although they show different amplitudes) with one difference. In the pecking cycles the ventral pharyngeal valves are erected at the beginning of, and remain erected during, the retraction of the pharyngeal elements, in the drinking cycles this valve is erected only briefly at the beginning of their protraction. By a relatively simple change in time coordination of the muscles used in pro- and retraction and those involved in valve erection, the valves act either as a scraper or as a block closing the oesophagus and simultaneously creating a low air pressure in the pharynx. It is suggested that this drinking modification occurred later

in evolution and was based upon the already properly working slide-and-glue mechanism. HOMBERGER (1980) comes to a similar conclusion about the suction drinking of *Psittichas*; she defines (p. 153) particular pharynx structures primarily as an adaptation to feeding and secondarily to drinking.

The neodarwinian "adaptationist programme" requires now the deduction and selection of the most plausible selection pressure on fast drinking of the double-suction type. MURTON (1965) has deduced this for fast drinking of pigeons. That deduction can be illustrated by a similar deduction for the evolution of suction drinking in several species of the Estrildidae by IMMELMANN & IMMELMANN (1967).

Drinking by the double-suction mechanism is faster than drinking by the tipping-up mechanism, since no head and body movements have to occur during the former type. IMMELMANN & IMMELMANN (1967) showed this in Estrildids by comparing species displaying either the first or the second mechanism. It is from this that the suction mechanism used by pigeons also has to be considered as a fast water transport. However, whether this could have evolved because of environmental influences cannot be answered so easily. IMMELMANN & IMMELMANN (1967) could give a neodarwinian and monistic explanation according to the adaptationists' program of the evolution of the specialized pumping way of drinking, since these finches live in arid areas where no shelter from predators is found around water holes. It is conceivable that strong selection pressure existed to develop a method of fast water uptake. MURTON (1965) gave a similar explanation for the drinking method of sandgrouse, which he considered to be an early offshoot of the stock which gave rise to the pigeons. He suggested that the method of drinking of sandgrouse which looks like a combination of pumping and tipping-up has been further specialized in pigeons.

In my opinion there is another plausible line of monistic reasoning according to the "adaptationist programme". Since most pigeons lived in humid conditions there is no reason to suggest that in the feeding niches of pigeons water has been scarce and/or cover absent. Therefore it is supposed that no selective pressures by predators or by competition with respect to the water available have been acting. However, heavy predator selection pressure could have set a premium on fast eating when pigeons, like other granivorous animals have to feed over long periods of time in the open fields. It is suggested that the pharyngeal valve system when used for drinking can easily be explained as evolved from the pharyngeal valve system once this was evolved under strong selection pressure, as a



system used for fast seeds' transport through the pharynx. This is plausible for two reasons: 1, the use of the ventral pharyngeal valves as valves in drinking does not require any reconstruction of the pharyngeal area once it is evolved as a system for a fast scraping transport of seeds (see section 4.4., where it has been concluded that one and the same apparatus is equally well workable for a scraper action as for a valve action); 2, the recoupling of the moment of erection of the pharyngeal valves to the lingual pro- and retraction, which is required for suction drinking is in itself a relatively simple recombination. However, whether this recombination is easy to establish depends upon the rigidity of the central mechanism for the swallowing during eating.

Finally, I would indicate that the monistic neodarwinian description of the evolutionary scenarios presented above according to the "adaptationist programme" are not entirely satisfactory for two reasons. The first reason is that we are left with two alternative and untestable hypotheses without a procedure to decide which hypothesis is the better one. The second reason is that the basic assumption of the "adaptationist programme" (one independent mechanism and one dominant selection pressure) probably does not exist for the drinking system. Although the described evolutionary scenario of the pharyngeal system for pecking could have brought its peripheral construction and actions very close to the construction and actions required for suction drinking (section 4.4.) a dominant selection pressure which could cause the final steps of the central coordination to suction drinking must still be found.

It should be suggested from the "monistic adaptationist" point of view that such a pressure must have been rather high. The reason therefore is that the valves' erection in the slide-and-glue mechanism was part of an uninterrupted set of coupled actions which is different from that in the double-suction mechanism. This means that there are two different fixed central coordination patterns. Therefore, maximization of the drinking behaviour from a tipping-up to a double-suction mechanism requires either the change of the maximized central coordination of the fixed swallowing units of pecking, or the development of a new coordination pattern. Both changes might need high selection pressures. Whether these occur is not clear. Positive selection pressure may occur from a decrease of the energy spent for the intake of a dose of water. However, also negative selection pressure may occur as a result of the relative increase of helplessness during suction drinking. The latter feature is shown in GRZIMEK films where pigeons drinking from waterholes were once caught by a turtle and once by a heron.

I suggest that an equally complex situation without a dominant selection pressure must have occurred at the beginning of the evolutionary scenario of the pigeon's drinking. Therefore, a multifactorial analysis of mutual relationships with neighbouring systems and with influencing ecological systems is a first requirement now. It is attractive to use for a further analysis of the scenario a dualistic neodarwinian hypothesis (see note on p. 309) as has been suggested by POPPER (1972) rather than a monistic one. This gives the possibility for the assumption of an independent development of a central non-lethal propensity structure for suction drinking which does not need a selection pressure aprioristically. The pigeon could have followed his "propensity for suction drinking" (once the peripheral structures of the pecking system were brought by predator selection pressure close to the peripheral structures needed for suction drinking, and once the central coordination pattern was brought close to that of suction drinking by its "propensity") and apparently no selection pressure did fade it away.

## 5. Summary

1. The consummatory part of the drinking behaviour of pigeons is studied by a frame-by-frame analysis of high-speed films and X-ray motion pictures.

2. A double-suction or vacuum-pump model is formulated for the mechanics of drinking. Consummatory drinking is a series of similar movement cycles, each transporting one dose of water into the oesophagus. The swallowing movement cycle shows five phases: 1, capillary action of the beak tips; 2, lingual suction; 3, pharyngeal preparation; 4, pharyngeal suction; and 5, oesophageal collection. A double build up of an area of low air pressure occurs. As a result of the retraction of the tongue in the mouth (acting as a piston in a cylinder) low air pressure develops in the buccal cavity and water is sucked into the mouth. Secondly, a lower air pressure area develops in the pharynx as a result of a depression of its floor, so that the water in the mouth is given a momentum caudad, by which it is forced over the larynx into the oesophagus. Neither peristaltic action, nor an alternative lower air pressure area is recorded in the oesophagus. The collection of the swallowed water at the lowest place occurs by gravity.

3. Using the mechanical requirements of the double-suction model the presence and distribution of glands was predicted. As predicted the following glands were found: the gl. lingualis superior et inferior, the gl. mandibularis anterior et posterior, the gl. palatina posterior externa, the gl. cricoarytenoidea and the gl. sphenopterygoidea.

4. The application of a comparator model for the description of the stereotypy of the pecking behaviour for the drinking behaviour showed that the drinking swallowing cycle and the three types of eating swallowing cycles were basically similar. The difference, apart from those of amplitude, was the coupling of the erection of the ventral pharyngeal valves to the pro- and retraction of the linguolaryngeal apparatus. The erection occurs during drinking at the very start of the protraction, but during pecking at the start of the retraction. Further, the consummatory act of drinking is composed of some smaller fixed elementary movement units. These units are fixed for mechanocybernetical reasons. The decision points between these units though masked under normal conditions, were found at the start of the capillary phase and during the preparatory phase by experimental manipulation.

5. A possible evolutionary scenario for the double-suction mechanism is discussed. It is suggested that: 1, the feeding system is maximized for food transport by using the slide-and-glue mechanism rather than using the ancestral catch-and-throw mechanism; that 2, the feeding system was maximized for water transport by using the double-suction mechanism rather than the ancestral tipping-up mechanism; that 3, high selection pressure on fast transport of seeds has occurred and that lack of selection pressure on fast drinking was probable. From this may be concluded that the slide-and-glue mechanism is the primary mechanism and the double-suction secondary. This secondary development is in itself a simple change of coupling of one of the subunits already developed as a pecking submechanism, the erection of the ventral pharyngeal valves. Although this recoupling falls completely within the mechanical boundary conditions of the slide-and-glue mechanism so that no reconstruction of the mechanical part of the system is required, nevertheless some strong selection pressure might be necessary for the evolution of a double-suction mechanism since valve erection was found to be part of different centrally coordinated fixed elementary units in swallowing both during eating and drinking. Such an external selection pressure could not be found. Finally, it was shown that for the explanation of the evolutionary scenario of suction drinking the "monistic adaptationist programme" was not sufficient, and a dualistic neodarwinian approach and a multifactor analysis were advocated.

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## Zusammenfassung

1. Die erbkoordinierten Bewegungen beim Trinkverhalten der Tauben wurden mit Hilfe einer Bild-für-Bild Analyse der Hochgeschwindigkeitsfilmen und Röntgenfilmen untersucht.

2. Für den Mechanismus der Wasseraufnahme wurde das Modell einer Vakuumpumpe formuliert. Erbkoordiniertes Trinken ist eine Reihe von identischen Bewegungszyklen; in jedem Zyklus wird ein Schluck in den Oesophagus transportiert. Solch ein Zyklus zeigt fünf Phasen: 1, die kapillarische Aktion der Schnabelspitzen; 2, die saugende Aktion des rostralen Teiles der Zunge; 3, die preparierende Aktion der Pharynx; 4, die saugende Aktion der Pharynx; und 5, die sammelnde Aktion des rostralen Oesophagus. Kennzeichnend ist dass zweimal ein Raum mit niedrigem Luftdruck hervorgerufen wird, zuerst in der Mundhöhle, zufolge der Retraktion der Zunge im Schnabel, die wie ein Sauger in einem Zylinder wirkt, und zweitens durch Vergrößerung des Pharynxraumes zufolge der Depression des Pharynxbodens, die dem Schluck einen kaudalen Moment über die Larynx in den rostralen Oesophagus gibt. Peristaltische Aktion oder ein alternativer Raum

mit niedrigem Luftdruck ist nicht registriert worden; nur Sammlung des Wassers ist zufolge der Schwerkraft im niedrigsten Gebiet der Oesophagus gefunden worden.

3. Aus den weiteren mechanischen Forderungen des Vakuumpumpenmodells wurde die Anwesenheit von Drüsen deduziert. Die Position, die Form und die Ductuli efferentes der folgenden Drüsen sind abgeleitet worden und dann nach ihrer Vergleichung mit einer mikroskopischen und elektronen-mikroskopischen Analyse der Mund- und Pharynxstrukturen erklärt worden: die Gl. lingualis superior et inferior, die Gl. mandibularis anterior et posterior, die Gl. palatina posterior externa, die Gl. cricoarytenoidea und die Gl. sphenopterygoidea.

4. Die Verwertung eines Komparationsmodelles der Stereotypie des Pickverhaltens für das Trinkverhalten hat gezeigt, dass der Trinkzyklus fast identisch ist mit der Kombination von drei Phasen des Pickverhaltens (die Phasen der Alae linguales, der Larynx und der Valvulae pharyngeales aufeinanderfolgend). Der Unterschied zeigte sich in der Kupplung der Aufrichtung der Valvulae pharyngeales ventrales mit der Pro- und Retraction des linguolaryngealen Apparates. Die Aufrichtung dieser Klappen findet am Ende der Retraction während des Trinkens statt, doch am Anfang der Retraction während des Pickverhaltens. Die Analyse zeigt auch, dass das Trinkverhalten aus kleine Elementareinheiten zusammengesetzt ist. Diese Elementareinheiten funktionieren starr infolge mechano-kybernetischer Ursachen. Während des Schluckens in normalen Umständen sind diese Einheiten ohne Unterbrechung gekuppelt, sodass Entscheidungspunkte zwischen diesen Einheiten möglicherweise maskiert sind. Im Anfang der Kapillar-Phase und während der Preparation-Phase konnten sie jedoch gezeigt werden.

5. Über eine mögliche Evolution des Doppelsaugermechanismus wurde diskutiert. Folgendes stellte sich heraus: 1, das Futteraufnahmesystem wurde für einen schnellen Samentransport zufolge des Gebrauches des Rutsch-und-Kleb-Mechanismus an Stelle des Gebrauches des phylogenetisch alten Wurf-und-Greif-Mechanismus maximalisiert; 2, das Futteraufnahmesystem wurde auch für einen schnellen Wassertransport zufolge des Gebrauches des Doppelsauger-Mechanismus statt des phylogenetisch alten Kopfaufhebe-Mechanismus maximalisiert; und 3, simultan mit der Maximalisierung fand ein hoher Selektionsdruck statt, in Bezug auf einen schnellen Samentransport, ansonsten war der Selektionsdruck in Bezug auf einen schnellen Wassertransport nicht vorhanden. Aus diesen Argumenten ist konkludiert worden, dass das Trinkverhalten der Tauben durch den Doppelsaugermechanismus ein sekundäres Phänomen sein kann, während der Rutsch-und-Kleb-Mechanismus für das Pickverhalten ein primäres Phänomen ist. Die sekundäre Entwicklung war an sich eine einfache Wiederkupplung der Aufrichtung der Valvulae pharyngeales ventrales mit der Pro- und Retraction des linguolaryngealen Apparates. Aber, obgleich diese Wiederkupplung innerhalb der mechanischen Grenzbedingungen des Rutsch-und-Kleb-Mechanismus besteht, sodass kein Umkonstruktion des mechanischen Systems notwendig wäre, soll als die Ursache für die Evolution des Doppelsauger-Mechanismus ein grosser externer Selektionsdruck notwendig sein, weil die Aufrichtung der Valvulae pharyngeales ventrales ein Teil verschiedener (zentralkoordinierte) Elementar-Einheiten des Schluckens während das Trink- und Pickverhaltens ist. Ein solcher Selektionsdruck ist nicht gefunden worden.